

Abstract—We modeled the probability of capturing Pacific mackerel (*Scomber japonicus*) larvae as a function of environmental variables for the Southern California Bight (SCB) most years from 1951 through 2008 and Mexican waters offshore of Baja California from 1951 through 1984. The model exhibited acceptable fit, as indicated by the area under a receiver-operating-characteristic curve of 0.80 but was inconsistent with the zero catches that occurred frequently in the 2000s. Two types of spawners overlapped spatially within the survey area: those that exhibited peak spawning during April in the SCB at about 15.5°C and a smaller group that exhibited peak spawning in August near Punta Eugenia, Mexico, at 20°C or greater. The SCB generally had greater zooplankton than Mexican waters but less appropriate (lower) geostrophic flows. Mexican waters generally exhibited greater predicted habitat quality than the SCB in cold years. Predicted quality of the habitat in the SCB was greater from the 1980s to 2008 than in the earlier years of the survey primarily because temperatures and geostrophic flows were more appropriate for larvae. However, stock size the previous year had a larger effect on predictions than any environmental variable, indicating that larval Pacific mackerel did not fully occupy the suitable habitat during most years.

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Effect of environmental conditions on the distribution of Pacific mackerel (*Scomber japonicus*) larvae in the California Current system

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The Pacific mackerel (*Scomber japonicus*) is a coastal pelagic species that ranges from southeastern Alaska to Banderas Bay, Mexico (Fig. 1) in the northeastern Pacific (MBC Applied Environmental Sciences¹). It is managed by the Pacific Fishery Management Council in U.S. waters and fished commercially in the U.S. and Mexico primarily by purse-seine vessels that also harvest anchovy (*Engraulis mordax*), jack mackerel (*Trachurus symmetricus*), market squid (*Loligo opalescens*), and sardine (*Sardinops sagax*). There is also a charter-boat sport fishery based primarily in southern California (Crone et al., 2009).

Like most coastal pelagic species, the Pacific mackerel fluctuates greatly in abundance through time (Soutar and Isaacs, 1974). These fluctuations are partly correlated with environmental conditions, such as temperature and upwelling rates (e.g., Parrish and MacCall, 1978). When Pacific mackerel populations are large, they form an important trophic link between small prey items (zooplankton and smaller fish) and larger avian, mammalian, and piscine predators (Castro Hernández and Santana Ortega, 2000). There-

fore, understanding environmental variables that affect Pacific mackerel distribution and abundance may help managers to better evaluate both the fishery and ecosystem conditions in the California Current system.

Three distinct stocks are believed to exist in the northeast Pacific Ocean: one in the Gulf of California, one near Cabo San Lucas at the tip of Baja California (22.9°N; Fig. 1), and one that ranges from Alaska to Cabo San Lucas. The northernmost stock is most common from Monterey Bay, California (36.9°N), to Punta Abreojos, Baja California (26.7°N; Roedel, 1952). These stocks were delineated on the basis of differences in vertebral meristics and physical features however, great heterogeneity in migratory behavior and physical features also exists within purported stocks (Roedel, 1952). Pacific mackerel are very mobile. Marked Pacific mackerel that were initially captured in the southern California Bight (SCB) have been recaptured as far north as Tillamook Head, Oregon (45.9°N), and as far south as Magdalena Bay, Baja California (24.6°N; Fry and Roedel, 1949). They generally migrate from south to north in summer and reverse the migration in winter. Pacific mackerel tend to move from inshore during the spawning season, March to May, to offshore as far as 400 km during the remainder of the year (MBC Applied Environmental Sciences¹).

¹ MBC Applied Environmental Sciences. 1987. Ecology of important fisheries species offshore California. OCS Report MMS 86-0093, 290 p. U.S. Dept. Int. Min. Manage. Serv., Pacific Region, Los Angeles, CA.

Larval samples collected during net tows as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program provide the only available fishery-independent data on Pacific mackerel abundance in the California Current system (Crone et al., 2009). These data have been used to estimate a time series of daily larval production at hatching (Lo et al., 2009; Lo et al., 2010) by a method somewhat similar to the daily egg production method (Lasker, 1985). Production is calculated on the basis of development and mortality rates of larvae, which are estimated from water temperature, larval abundance, and size. The time series of larval production may be incorporated into the stock assessment as an index of the stock size that produced the larvae (Dorval et al., 2007). However, the analysis was not included in the most recent stock assessment for Pacific mackerel (Crone et al., 2009), partly because of the concern that measurements within the current CalCOFI sampling pattern may not be representative of conditions for the entire range of the stock. Sampling was conducted over all, or nearly all, of the expected range of the stock during the early years of the CalCOFI survey (1951–80) but now occurs only in an area from Avila Beach (35.1°N) to San Diego (32.7°N). We refer to this area hereafter as the “core area” (Fig. 1).

We used CalCOFI data to model the likelihood of capturing Pacific mackerel larvae as a function of water temperature, zooplankton displacement volume, geostrophic flow (i.e., flow resulting from the pressure gradient force and Coriolis force), longitude, day of year, and the commercial-passenger-fishing-vessel (CPFV) index (a proxy for stock size). The model was a spatially continuous function (i.e., data were “smoothed” rather than presented as raw catch data) intended to provide predictions of the areas where Pacific mackerel were likely to occur near the time of spawning each year. The objectives of the study were 1) to explain why distributions of Pacific mackerel may have changed through time; 2) to compare trends in habitat quality in the core CalCOFI area and Mexican waters, where possible; 3) to determine how habitat conditions may affect larval production or other survey estimates that are potentially used in stock assessments; and 4) to allow for improved allocation of sampling effort in future surveys.

Materials and methods

Survey data

Pacific mackerel larvae and oceanographic data were collected during CalCOFI cruises from 1951 to 2008. Samples were collected in an approximate grid pattern centered on the southern California Bight and rotated -30° off the meridian so that the grid was oriented with (parallel to) the shoreline. The spatial and temporal extent of CalCOFI sampling varied during this period. The sampling pattern initially extended from the California–Oregon border to the tip of Baja California.

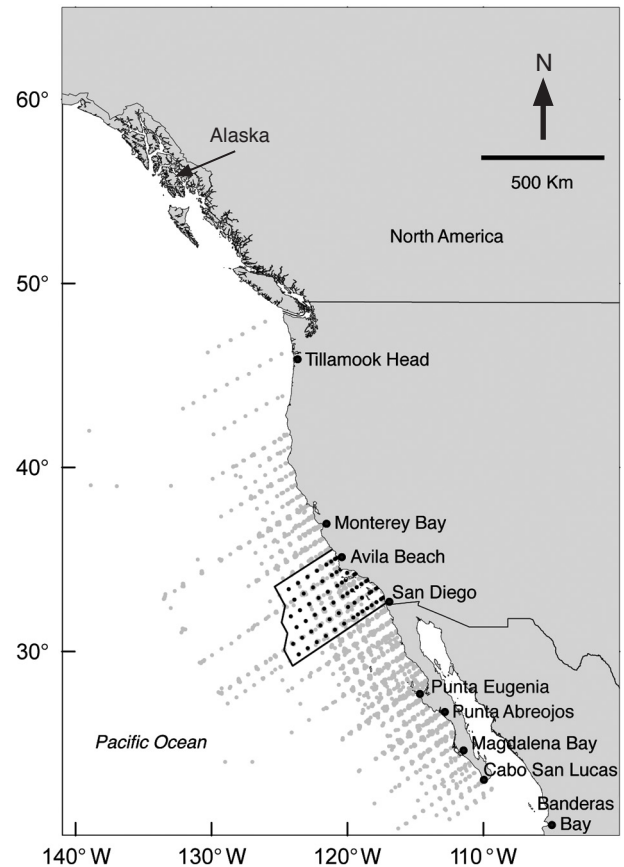


Figure 1

Approximate range of Pacific mackerel (*Scomber japonicus*) in the northeast Pacific. Light gray dots indicate locations where samples were collected as part the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program and that were used in the study. The area enclosed by the black line indicates the core CalCOFI area, which was sampled in all years of the survey. Black dots indicate the current 66-station sampling pattern that is conducted each quarter.

Data were collected in U.S. and Mexican waters during most sampling years from 1951 to 1984. Thereafter, sampling was restricted to U.S. waters. The core area from Avila Beach to San Diego in the California Bight was sampled consistently through the entire time series. Sampling was conducted approximately monthly from 1950 to 1960 and in 1966, 1969, 1972, 1975, and 1984; it was conducted quarterly from 1961 to 1965, 1978 to 1980, and 1985 to 2008 with target dates of January, April, July, and October. Sampling was conducted only triennially from 1966 to 1984, except that cruises were conducted in January, April, and June 1968. Only cruises conducted from April through September were included in our study. This period corresponds with the spawning period of Pacific mackerel, as indicated by the occurrence of their eggs in net samples. It has recently become possible to identify Pacific mackerel eggs (specifically to distinguish them from Pacific hake

[*Merluccius productus*] eggs; Watson²). Samples of eggs from CalCOFI tows collected during 1988–2009 were resorted to identify those of Pacific mackerel. Of the latter about 98% were captured from April through September.

Larvae were collected with 1.0-m-diameter bridled ring nets until 1977 and 0.71-m-diameter bridleless bongo nets thereafter. Nets consisting of 0.55-mm-mesh silk were towed obliquely at an angle of approximately 45° from 140 m depth to the surface for all samples until 1969. In 1969 the net was changed to 0.505-mm-mesh nylon and the beginning tow depth was increased to 210 m, as described by Smith and Richardson (1977) and Ohman and Smith (1995). Oceanographic data used to develop predictor variables for the model were dynamic height (referenced to 0/500 decibars) and water temperature. These data were measured or calculated from bottle casts and conductivity-temperature-depth sensor (CTD) casts at each station. Variables were interpolated to the nearest 10 m for depths of 0–100 m and at 125, 150, 200, 250, 300, 400, 500 m. Detailed sampling protocols for the CalCOFI bottle and CTD samples are described by Lynn et al. (1982).

Catch data collected from the commercial boats in the recreational fishery by the California Department of Fish and Game (CDFG) were used to estimate relative annual abundance of Pacific mackerel. Captains of commercial passenger fishing vessels have been required to provide logs of fishing effort and catch to the CDFG since 1936 (*cf.*, Hill and Schneider³). These data have been used to develop an index of abundance, known as the commercial-passenger-fishing-vessel or CPFV index, which represents data standardized by using a Δ -generalized-linear model approach (Stefansson, 1996) to account for potential changes in catchability associated with the CPFV fleet over time (Crone et al., 2009). Index values were provided by P. Crone.⁴

Larval densities

We estimated larval Pacific mackerel densities from net tows on the basis of volume of water sieved by the tow (Smith and Richardson, 1977). Estimates were then corrected for extrusion of very small larvae through the net mesh, and for avoidance of the net by larger larvae, by using the method described by Lo et al. (2009). Estimates for larvae less than or equal to 3 mm in length in each tow were divided by 0.28 to correct for extrusion. To correct for net avoidance, estimates were multiplied by a capture coefficient ($R_{L,h}$), which varied as a function of diel period (h ; i.e., hour) and fish length (L):

$$R_{L,h} = \left(\frac{1+D_L}{2} \right) + \left(\frac{1-D_L}{2} \right) * \cos \left(\frac{2\pi * h}{24} \right), \quad (1)$$

where D_L = the noon/night catch ratio for length L calculated as

$$D_L = 2.7 \exp(-0.39L). \quad (2)$$

Most captured larvae were in the range of 3–20 mm long, or were aged to be about 0–20 d (Lo et al., 2009). Because most larvae captured were estimated to be only a few days old and had poor swimming ability, we assumed their distribution was directly related to the distribution of spawning adults.

Model development

We used six initial predictor variables to model the presence of Pacific mackerel larvae. They were mean water temperature (°C), mixed-layer depth (m), an index of geostrophic flow, the log of volume displaced by zooplankton captured in nets (mL/1000 m³ filtered), the CPFV index of Pacific mackerel stock size for the previous year, and day of the year. Temperature was entered as a predictor of the physiological suitability of the habitat. Zooplankton displacement volume of the habitat and indicator of the water mass in which fish were located, was entered as an index of the standing crop of available food. Large jellyfish and tunicates whose individual volume was greater than 5 mL were excluded from zooplankton samples (Kramer et al., 1972). However, zooplankton samples were not specifically sorted into prey items and predators. Mixed-layer depth was used as an indicator of stratification of the water column, and geostrophic flow as a measure of horizontal current strength, both of which also potentially affected production and food availability (Mantyla et al., 2008).

The index of geostrophic flow was calculated on the basis of a fitted surface in dynamic height for each year, which was estimated by a method similar to that used to fit digital elevation maps to terrestrial slope data. First a surface was fitted by using the “loess” function (Cleveland and Grosse, 1991) in the R programming environment, vers. 2.12.0 (R Development Core Team, 2011). Geostrophic flow occurs perpendicular to the slope in dynamic height because of the Coriolis effect. Therefore the index of geostrophic flow was calculated as the slope of a line on the loess-estimated surface that extended for 10 km on each side of a sampling location in the direction of maximum slope, with flow direction perpendicular to this line. For points located on the outer edge of the surface, only the 5-km line that was located within the bounds of the surface was used. Visual inspection of plots indicated that the index matched contours in dynamic height well and thus provided a reasonable proxy for geostrophic flow.

Two blocking variables that were not related to the physical quality of the habitat were included as potential predictors of larval abundance. Day of year was used to account for changes in larval abundance asso-

² Watson, W. 2011. Personal commun. NOAA Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92107.

³ Hill, K. T. and N. Schneider. 1999. Historical logbook databases from California's commercial passenger fishing vessel (partyboat) fishery, 1936–1997. Scripps Inst. Ocean. Ref. Series 99-19, 65 p. Univ. Calif. San Diego, CA.

⁴ Crone, P. 2011. Personal commun. NOAA Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92107.

ciated with the phase of the spawning season in which samples occurred. That is, small larvae were more likely to be available for capture when sampling was conducted near the peak-spawning season. The CPFV index from the previous year was included as a general measure of stock size. It was used to account for the fact that larvae may have been less likely to occur in otherwise suitable habitat in some years simply because the population was smaller. We note that abundance estimates from recent stock assessments (Crone et al., 2009) could not be used directly in the model because no estimates were made before 1962. The correlation between the CPFV index and abundance from the stock assessment during 1962–2008 was $r=0.81$. The value for the previous year, rather than the current one, was used so that the measure was relatively independent of Pacific mackerel movement during the spawning season.

The probability of capturing one or more larvae was modeled with a semiparametric logistic model with the “gam” function (i.e., generalized additive model) in the “mgcv” package (Wood, 2006) for R. The form of the model was

$$\log_e\left(\frac{\hat{y}}{1-\hat{y}}\right) = \beta_0 + \sum_k S_k(x_k), \quad (3)$$

where β_0 = the intercept,

$S_k(\cdot)$ = the smoothing function, and

x_k = the value of the k th covariate.

The response variable, \hat{y} , was presence or absence of larvae. The smoothing function was either a restricted cubic spline with shrinkage (the “cs” curve in mgcv; cf., Wood, 2006) or a parameter estimate if a term was entered as a simple linear predictor.

Several constraints were added to develop models that were parsimonious enough to prevent over-fitting yet flexible enough to be biologically realistic for a species’ expected response along an environmental gradient (e.g., monotonic, unimodal, or skewed unimodal patterns). First, we limited the number of knots in the cubic splines to three. Thus, only curves that were skewed and unimodal or simpler were considered. The second constraint was that we increased the penalty per degree of freedom fit to each term by setting the “gamma” option in the “gam” function to 1.4 to minimize potential over-fitting (Wood, 2006).

We performed model selection using the shrinkage features in the “gam” procedure rather than fitting a large set of potential candidate models (i.e., subsets of environmental variables fitted with different amounts of flexibility for each term). The “select” option was set to true for all models. This procedure allowed coefficients with little or no predictive ability to be shrunk to zero, effectively dropping them from the model. The stock-size variable was entered as a linear term rather than a spline in the logistic models, because a monotonically increasing response was the only biologically sensible response to increasing stock size. The plankton-volume variable was allowed to be monotonic or simpler,

rather than constrained to a linear term, because very high plankton volumes could indicate that invertebrate predators on eggs and larvae were present, which could negatively affect the suitability of the habitat.

A second model was fitted by using the same procedures listed above, except that temperature and day of year were entered as tensor product (Wood, 2006) interactions with latitude. This competing model was considered because some Pacific mackerel exhibited peak spawning in August near Punta Eugenia, Mexico, rather than in April as most Pacific mackerel did in the SCB (Lo et al., 2010). This procedure resulted in a small second mode for histograms of temperature and day of year where Pacific mackerel were captured. The rationale for the use of this model was that the broader survey area likely contained a mixture of Pacific mackerel that were likely to spawn near the SCB at cooler temperatures in the spring and Pacific mackerel likely to spawn at warmer temperatures in the summer near Punta Eugenia. The interaction terms were fitted by allowing five knots for temperature or day of year and latitude, thereby allowing for a more flexible prediction surface with two peaks (e.g., a peak in April at high latitudes in the SCB and a second peak in August at lower latitudes near Punta Eugenia). This model was compared to the original model using Akaike’s information criterion (AIC; Akaike, 1974). The model with the lowest AIC of the two was selected as the final model for interpretation.

We initially fitted a model to predict densities of larvae for samples where at least one larva was captured. The intention was to calculate expected densities as the product of the two models with a two-stage or Δ -generalized-linear model (Stefansson, 1996; Welsh et al., 1996). However, variability in the models was so great that the approach provided little or no additional information, and the approach was abandoned.

Results

Distributions of larval Pacific mackerel varied greatly among years, but large clusters of larvae frequently were captured near Punta Eugenia in Mexican waters and nearshore in the southern California Bight (Fig. 2). Corrected densities varied by several orders of magnitude within and among years. The greatest numbers of Pacific mackerel larvae were captured in the early 1980s and fewest from 1999 through 2008. During years when both U.S. and Mexican waters were sampled (1951–84), greater larval densities generally occurred in Mexican waters until 1975, but larger catches occurred in the SCB in 1978, 1981, and 1984. Within Mexican waters, densities were typically greater near Punta Eugenia in the southern portion of the sampled region than they were near the U.S.–Mexican border.

The logistic model that included interactions for temperature and day was selected in preference to the model with no interactions based on AIC values of 3876 versus 3348. The difference of 528 units of AIC in-

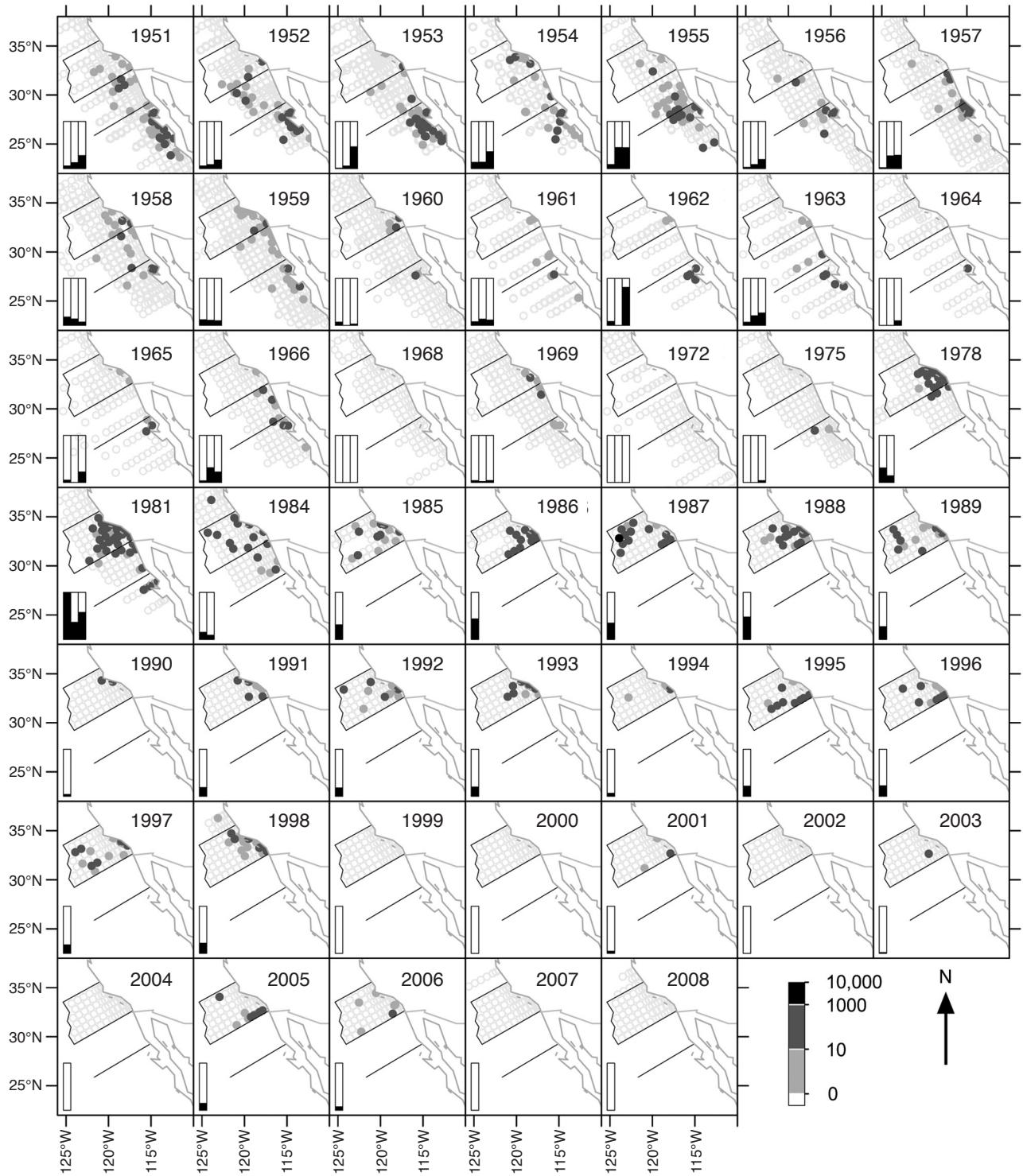


Figure 2

Corrected densities (number/1000 m³) of Pacific mackerel (*Scomber japonicus*) larvae captured in oblique tows from April through September, 1951–2008 as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program. Numbers were corrected for extrusion through the net mesh and net avoidance according to Lo et al. (2009). The area enclosed by a black line indicates the core area, which was sampled in all years of the survey. The lower black line indicates CalCOFI line 95 separating northern Mexican waters from southern Mexican waters near Punta Eugenia. Black “thermometer” bars in lower left corners indicate mean densities relative to the maximum density ever measured (1981) in the core area (left bar), northern Mexican waters (middle bar), and southern Mexican waters (right bar).

Table 1

Summary data determined with the logistic generalized additive model to predict presence of Pacific mackerel (*Scomber japonicus*) larvae. The model was based on 10,278 samples collected from 1951–2008 that had complete physical data for predictor variables. Smooth terms were natural splines with three knots, except for the *temperature*×*latitude* and *day-of-year*×*latitude* interactions, which were tensor product interactions of natural splines with five knots for temperature or day of year and latitude. Note that predictor variables were scaled from 0 to 1 before modeling (Wood, 2006).

Parametric coefficients	Estimate	Standard error	<i>z</i>	<i>P</i>
Intercept	−4.278	0.183	−23.34	<0.01
Commercial-passenger-fishing-vessel index	0.010	0.001	9.46	<0.01
Smoothing terms	Estimated degrees of freedom <i>c</i> ²	Reference degrees of freedom <i>P</i>	χ	<i>P</i>
Log zooplankton volume	1.883	1.987	19.55	<0.01
Index of geostrophic flow	1.919	1.994	172.96	<0.01
<i>Temperature</i> × <i>latitude</i>	15.585	17.355	172.96	<0.01
<i>Day of year</i> × <i>latitude</i>	12.116	13.456	67.90	<0.01

indicated that there was essentially no support for the model without interactions (Burnham and Anderson, 2001). The final logistic model indicated that presence of Pacific mackerel larvae could be predicted on the basis of zooplankton displacement volume, geostrophic flow, the CPFV index, the interaction between latitude and day of year, and the interaction between latitude and water temperature (Table 1). Mixed-layer depth was dropped from the model because the “select” procedure (i.e., “shrinkage”) indicated it was not a useful predictor. The model exhibited acceptable discrimination, as indicated by the area of a receiver-operating characteristic curve (i.e., where probability of concordance ranges from 0 to 1) of 0.80.

Partial effects of model predictors (i.e., the effect of a predictor at the median value of other variables in the model; Fig. 3) indicated that Pacific mackerel larvae were most likely to be captured when the stock size was large the previous year, as reflected by the CPFV index. Partial effects for the log of zooplankton displacement (peak $5.75 \log[\text{ml}/1000\text{m}^3]$) and geostrophic flow (peak 5.0×10^{-6}) were unimodal. The effect for geostrophic flow was skewed so that the greatest predicted probability of capture occurred at greater geostrophic flows. The interaction surface between temperature and latitude exhibited a peak at 15.5°C that was centered between 30° and 35°N latitude in the SCB, and a secondary peak at temperatures greater than about 22°C where only Pacific mackerel in Mexican waters were captured (Fig. 3D). The interaction surface between latitude and day exhibited the largest peaks in April in the SCB and in August for latitudes less than about 27°N (Fig. 3E) but was more uniform throughout the range of latitudes sampled than was temperature.

A larger proportion of the predicted high-quality habitat occurred in Mexican waters, particularly near Punta Eugenia, than in the core area during most years

when both areas were sampled (Fig. 4). The greatest predicted probabilities of capturing larvae occurred in the early 1980s, particularly in 1981, when large catches actually occurred. The most important predictor influencing these values was stock size, as indicated by the CPFV (Fig. 5), although the zooplankton and temperature predictors also indicated conditions were good for Pacific mackerel larvae in the SCB during the early 1980s. Model predictions followed the general trend in observed catches (Fig. 5, F and G) but did not coincide with the many zero catches that occurred in the 2000s (Fig. 2). The model indicated that mean likelihood of capturing larvae in the core area was only slightly less in the 2000s than in the 1990s.

The most consistent differences between the core area and Mexican waters were that the core area had more appropriate (greater) zooplankton displacement volumes but less appropriate (slower) geostrophic flows than Mexican waters (Fig. 5, B and C). The northern portion of Mexican waters sampled (north of CalCOFI line 95) generally had greater zooplankton displacement volumes but less appropriate geostrophic flows than the southern portion near Punta Eugenia.

All of the sampled areas exhibited greatest predicted probabilities of larval capture when their mean temperatures were near the 15.5°C temperature peak (Fig. 5, A, G, and H). For example, the area near Punta Eugenia exhibited greater probabilities of capture than the core area during the early 1950s. Mean temperatures were in the range of 15 – 16.5°C in southern Mexican waters at this time but cooler than 14°C in the core area. In contrast, the southern portion of the sampled area in Mexico was predicted to be relatively poor habitat for Pacific mackerel larvae in 1959 and 1965, despite the relatively high mean water temperatures ($>19^\circ\text{C}$) that approached the second, warmer predicted temperature peak in the model. This outcome was due to the effect of

temperature offset by reduced geostrophic flow and zooplankton abundance.

The two temporal blocking variables affected model predictions but were either unrelated to interannual differences in physical habitat (previous stock size), or only partly related (day of year). After the model controlled for stock size and time of sampling (Figs. 6 and 5H), model predictions indicated that the core area contained the best habitat available nearly as frequently as the southern portion of Mexican waters; the core area had the greatest mean predicted probability of capture in 9 of 21 years. The area of Mexican waters north of CalCOFI line 95 tended to be intermediate in terms of probability of capture. between the core area and the southern area near Punta Eugenia. The controlled probabilities of capture exhibited greater variability between the core area and Mexican waters among years, indicating the two areas may exhibit greater differences in habitat-suitability trends than were apparent from uncontrolled model predictions. Corrected predictions also indicated that habitat quality for larval Pacific mackerel in the core area generally was better from the 1980s to 2008 than in the early years of the CalCOFI survey, probably because of more appropriate temperatures and geostrophic flows (Fig. 5, A and C). The difference was somewhat masked in the uncorrected predictions because stock size was a dominant predictor, and sampling did not necessarily occur during the seasonal period when Pacific mackerel larvae were most likely to be captured (Fig. 5D).

Discussion

The model indicated that distributions of Pacific mackerel

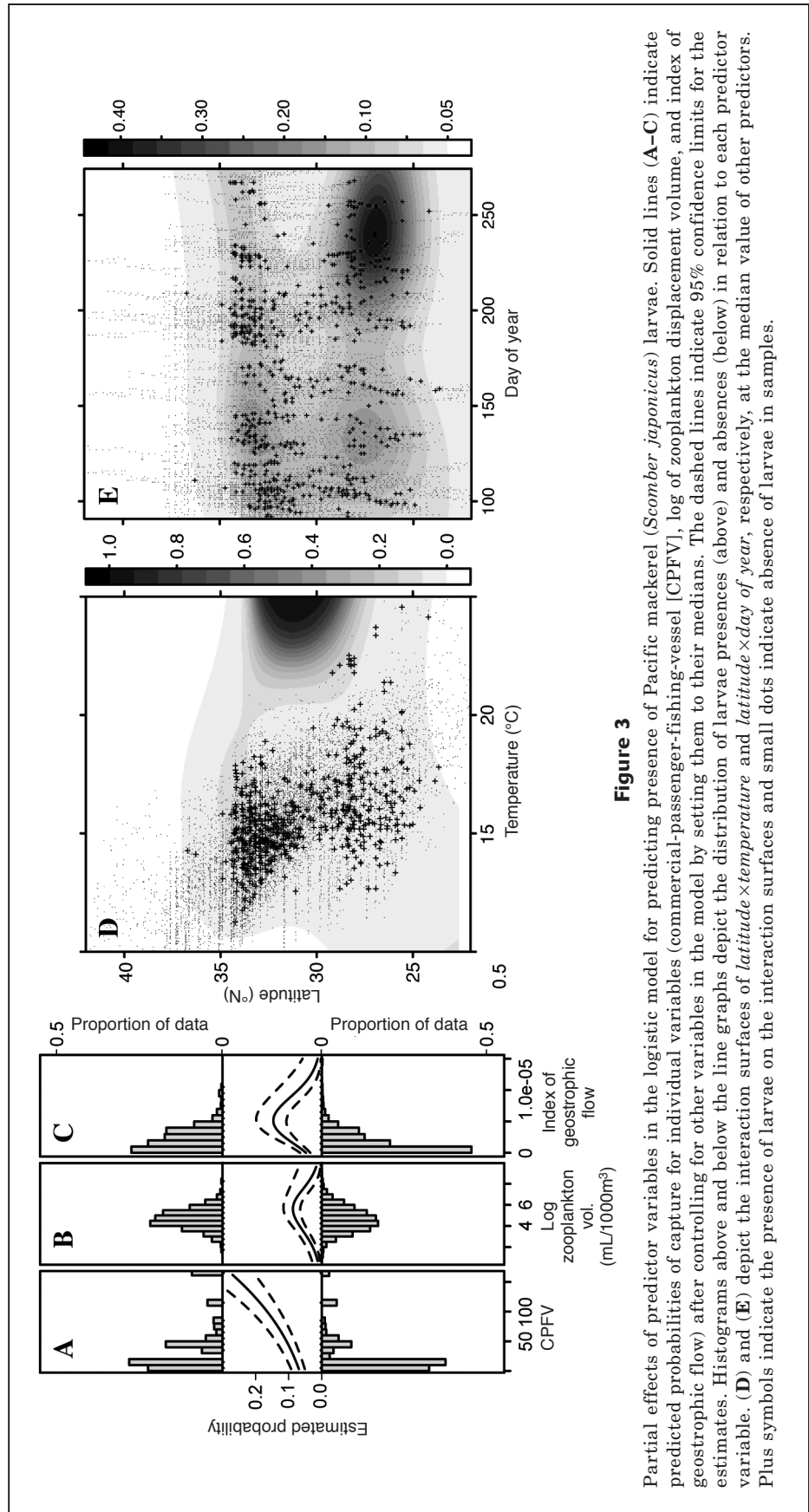


Figure 3

Partial effects of predictor variables in the logistic model for predicting presence of Pacific mackerel (*Scomber japonicus*) larvae. Solid lines (A–C) indicate predicted probabilities of capture for individual variables (commercial-passenger-fishing-vessel [CPFV], log of zooplankton displacement volume, and index of geostrophic flow) after controlling for other variables in the model by setting them to their medians. The dashed lines indicate 95% confidence limits for the estimates. Histograms above and below the line graphs depict the distribution of larvae presences (above) and absences (below) in relation to each predictor variable. (D) and (E) depict the interaction surfaces of *latitude × temperature* and *latitude × day of year*, respectively, at the median value of other predictors. Plus symbols indicate the presence of larvae on the interaction surfaces and small dots indicate absence of larvae in samples.

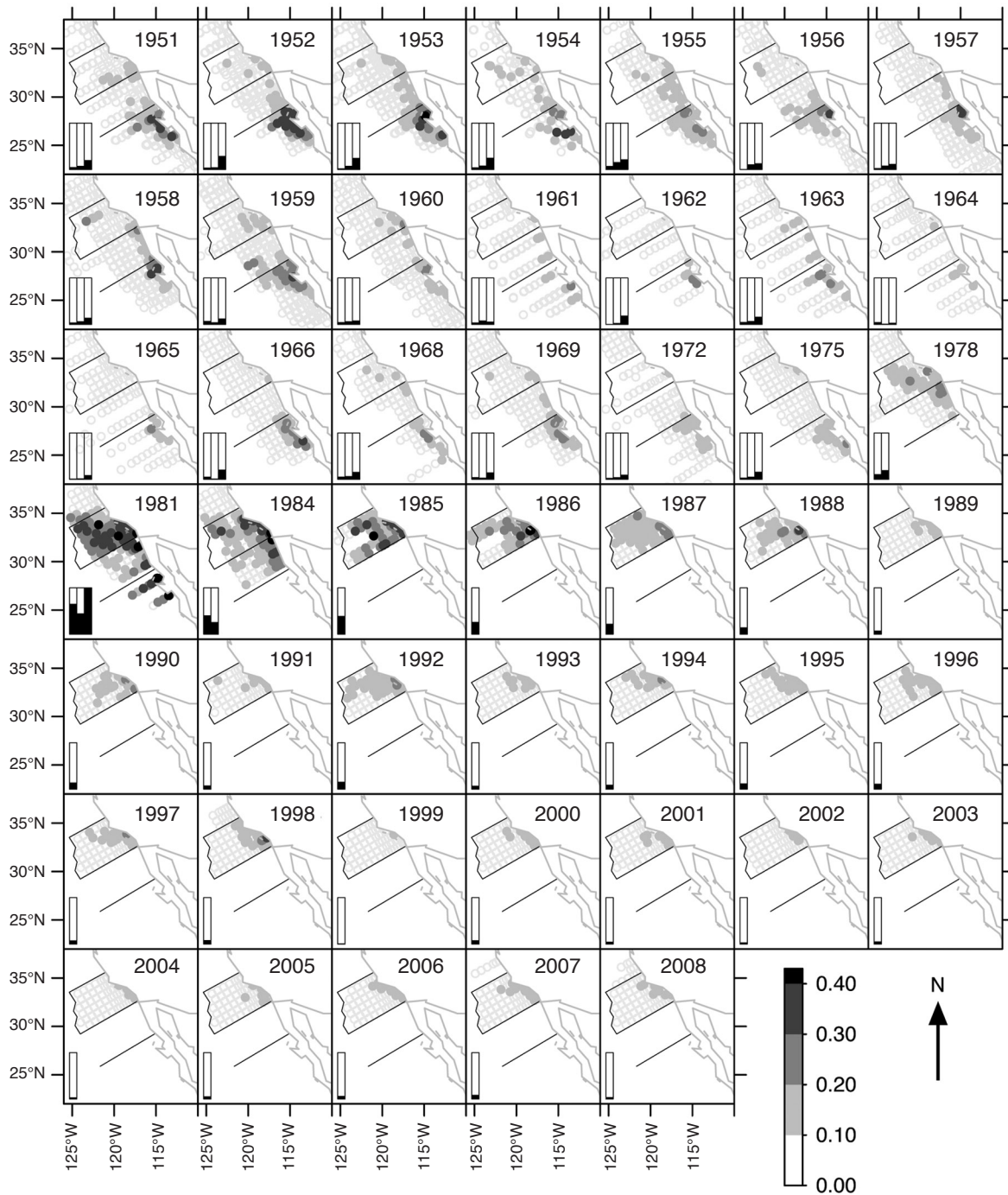
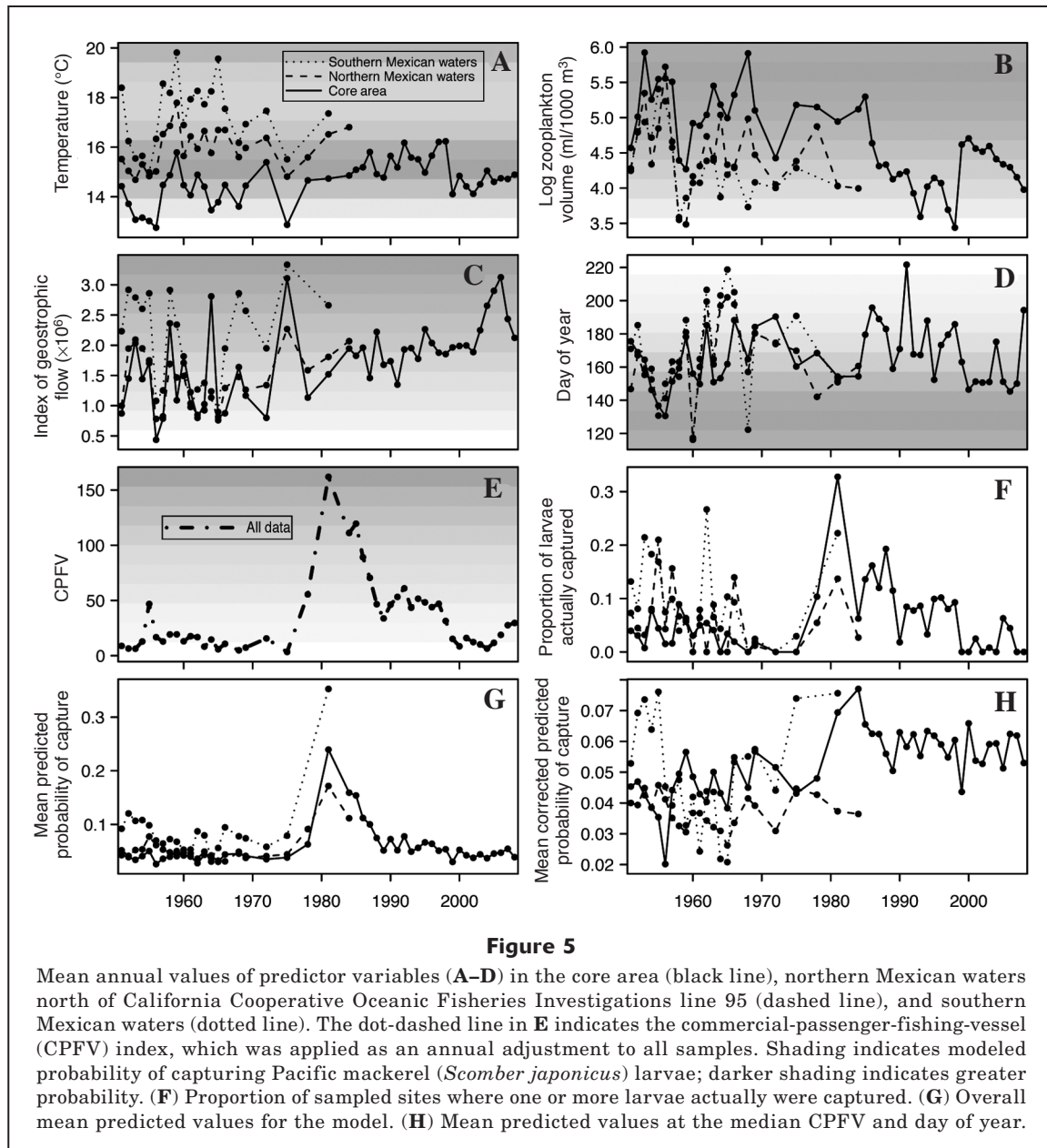


Figure 4

Predicted probability of capturing one or more Pacific mackerel (*Scomber japonicus*) larvae at sample locations based on the logistic generalized additive model for California Cooperative Oceanic Fisheries Investigations (CalCOFI) oblique-tow samples, 1951–2008. Only sites with a complete set of predictors are plotted. Area enclosed by the black line indicates the core area, which was sampled in all years of the survey. The black line indicates CalCOFI line 95 separating northern Mexican waters from southern Mexican waters near Punta Eugenia. Black “thermometer” bars indicate mean relative mean probability of capture in the core area (left bar), northern Mexican waters (middle bar), and southern Mexican waters (right bar). Where samples occurred so closely spaced that some overlap occurred, samples with the greatest predicted probability of capture are plotted on top.



larvae could be predicted by using zooplankton displacement volume, geostrophic flow, and temperature as predictors of physical habitat in the California Current system. However, modeling habitat preferences was complicated by the fact that two types of spawners occur: those that exhibit peak spawning during April in the SCB at about 15.5°C, and a smaller group that exhibits peak spawning in August near Punta Eugenia, Mexico, at 20°C or greater. Lo et al. (2010) also reported the existence of a secondary period of high larval abundance that occurs near Punta Eugenia in August determined from a combination CalCOFI data and data from the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) program. The IMECOCAL program began in 1997 and collects many

of the same types of data as CalCOFI between Ensenada and approximately Lázaro Cárdenas, Baja California (30.5°N). It is unknown whether the bimodal distributions in temperature and seasonal preferences reported here and by Lo et al. (2010) were caused by heterogeneity within the northernmost Pacific mackerel stock in the northeast Pacific or by captures of some Pacific mackerel from the more southern stock that occur near the tip of Baja California (Roedel, 1952). In either case, the relatively continuous distributions of temperatures and days in which Pacific mackerel were captured indicate that a gradient of behaviors existed.

We took an empirical approach to modeling multiple spawner types by fitting interactions between latitude and temperature, and latitude and day of year, to fit a

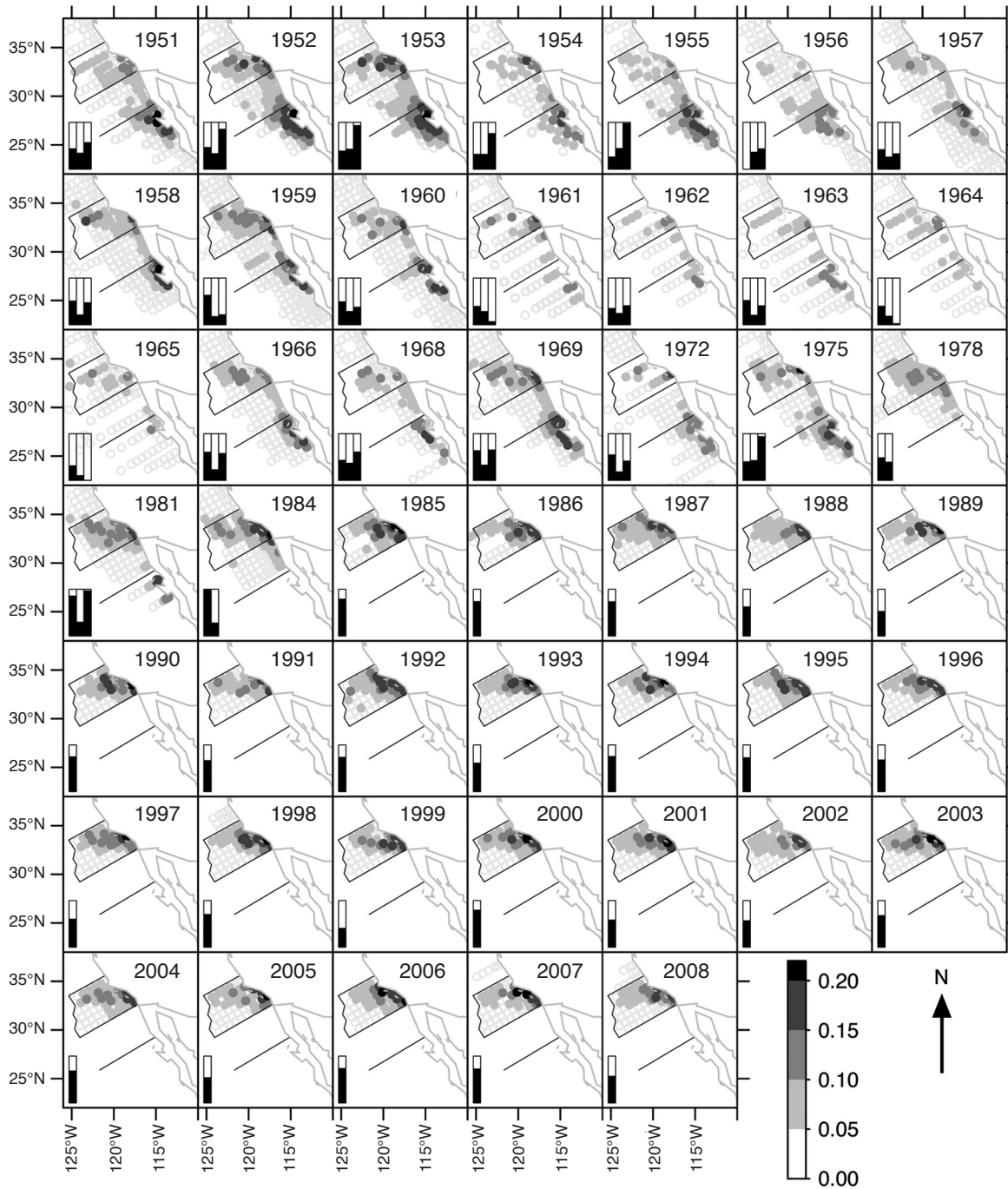


Figure 6

Predicted probability of capturing one or more Pacific mackerel (*Scomber japonicus*) larvae at sample locations based on the logistic generalized additive model at the median values of sampling day and commercial-passenger-fishing-vessel index (i.e., controlled for stock size and sample date). Area enclosed by the black line indicates the core area, which was sampled in all years of the survey. The black line indicates California Cooperative Oceanic Fisheries Investigations line 95 separating northern Mexican waters from southern Mexican waters near Punta Eugenia. Black “thermometers” bars indicate mean relative mean probability of capture in the core area (left bar), northern Mexican waters (middle bar), and southern Mexican waters (right bar). Where samples occurred so closely spaced that some overlap occurred, samples with the greatest predicted probability of capture are plotted on top.

mixture of geographically offset but overlapping distributions. A drawback of this approach is that the actual geographic centers and relative proportions of the two spawner types likely change through time, and these changes are included in the unexplained variance of the model. However, given the large overlap in spawning behaviors (Fig. 3, D and E) and lack of ability to discriminate between the two spawner types, this may be the only practical way to evaluate habitat effects on their distributions. Latitude also partly reflected the distribution of habitat from north to south. For example, salinity has frequently been used as an indicator of water masses preferred by pelagic fish (e.g., Checkley et al., 2000). Salinity was not used in this model because it had a relatively high correlation with latitude ($r=0.58$).

The core area consistently had greater zooplankton displacement volumes but less appropriate (slower) geostrophic flows for Pacific mackerel larvae than Mexican waters (Fig. 5, B and C). The most favorable average annual temperatures (Fig. 5A) alternated between the core area and Mexican waters. Mexican waters more fully represented the transition zone occupied by both types of spawners: those that were predicted to prefer spawning in April in 15.5°C water, and those predicted to prefer spawning in August in about 22°C water. In contrast, when temperatures departed from the optimum in the core area, usually they were too cold for either group, resulting in better habitat conditions in Mexican waters (e.g., the early to mid 1950s). The greater zooplankton displacement in the core area suggests that greater productivity may have attracted some Pacific mackerel to the SCB that otherwise preferred warmer temperatures. This idea is consistent with data from a tagging study that indicated Pacific mackerel migrated between the two areas seasonally, moving northward in summer and southward in winter (Fry and Roedel, 1949), and that the migration was more pronounced during El Niño events. For Pacific mackerel that prefer warmer water, movement between Mexican waters and the SCB likely represents a trade-off between optimal temperatures and greater feeding opportunities.

The precise mechanism underlying the relation between geostrophic flow and Pacific mackerel larvae in this study is unknown. Geostrophic flow was included as a predictor because it was hypothesized to be related to the productivity field (Mantyla et al., 2008) and has been previously related to abundance of Pacific mackerel (Yatsu et al., 2005). However, geostrophic flow is related to productivity through adjustment of the water column in response to the current, yet no direct relation between larvae and mixed-layer depth was measured in this study. Either the field of geostrophic flows calculated for each year in this study provided a better measure than the calculated mixed-layer depths at each CalCOFI station, or geostrophic flow affected larval distribution through another unknown mechanism.

The CPFV index for the previous year had a larger effect on model predictions than any of the variables re-

lated to habitat (Fig. 5, F–H). After correcting for stock size and sampling time, mean annual differences in predicted probability of capture varied by less than 7%, indicating that habitat quality was much more stable among years than was stock size. The importance of the CPFV index indicates that Pacific mackerel larvae did not fully occupy the suitable habitat during most years. Some of the best habitat for larvae was predicted to occur near Punta Eugenia in the early 1950s, but catches were small, in part, because the stock size was small (cf. Fig. 2 and Fig. 6). Likewise, recent low catches in the 2000s appear related to small stock size and potentially other unknown factors, but the environmental conditions modeled in this study have remained almost as suitable for Pacific mackerel larvae as they were in the 1990s. These results are consistent with previous studies that indicated that the stock-recruit relationship for Pacific mackerel in the Northeast Pacific is not strong (Parrish, 1974; Parrish and MacCall, 1978). The relatively small changes in quality of larval habitat predicted by the model are unlikely to have large effects on future recruitment success or stock size.

Predicted probabilities of capture varied between the core area and Mexican waters when both areas were sampled (Fig. 4), particularly after correcting for day of sampling and stock size (Fig. 6). These results suggest analyses that rely on data from the core area alone as an index of the entire population likely contain some bias. A model such as the one reported here could be used to tune a time series of larval production in the core area by scaling years up or down according to mean habitat conditions. So, for example, larval production would be assumed to be greater than that measured in the SCB during cold years, when a larger proportion of the stock presumably spawns in Mexican waters. However, we do not recommend such an approach given the statistical variability associated with this type of model. It would be much better to include data collected in Mexican waters as part of the IMECOCAL program in future studies and assessments. Although IMECOCAL data were not consistently available for previous U.S. stock assessments (Crone et al., 2009), recent analyses have been conducted with integrated data from both programs (e.g., Lo et al., 2010). We suggest that further analyses with integrated data sets would allow both nations to achieve better assessments with less bias.

The interaction between day of year and latitude was an important predictor in the model, indicating that some samples were more likely to contain larvae than others simply because sampling was conducted when Pacific mackerel were more likely to be spawning at the sample location (Fig. 5D). This problem would also create some bias in estimates of larval production because larval production estimates (Lo et al., 2010) do not contain a correction for the fraction of the adults spawning when sampling occurs (unlike the daily egg production method, cf. Lasker, 1985). In practice, the bias is likely to be small for annual estimates of Pacific mackerel production in the SCB because CalCOFI cruises occur in April and July, near the beginning and

end of the spawning season in the area. Nevertheless, applying a correction such as weighting samples according to sampling time should be considered to improve the accuracy of future estimates of larval production.

The CPFV index and day-of-year variables only partly explain the small or zero catches that have occurred frequently in the 2000s (*cf.* Fig. 4 and Fig. 6). For example, the mean estimated probability of capturing one or more larvae for samples in the core area was 0.04 in 2008 (range <0.01 to 0.18). Although it was unlikely that larvae would be captured at any single station, the predicted probability of capturing no larvae at any of the sixty-six core stations in aggregate was less than 0.001. The model-predicted odds were similar for other recent years when no larvae were captured. Given the extremely small odds that the zero catches would occur by chance alone for several years, these results indicate a lack of model fit. One potential explanation is that stock sizes have recently declined more than the CPFV index has indicated. The most recent stock assessment (Crone et al., 2009) included an alternate model scenario, denoted AB, which included potential changes in gear selectivity and catchability of Pacific mackerel through time. This scenario indicated that Pacific mackerel abundance may have been very low from 2004 through 2007. If the CPFV index did accurately reflect the trend in stock size, one or more unmeasured habitat variables may have had particularly strong effects on the distribution of Pacific mackerel in the 2000s. Another potential explanation is that habitat conditions were even more favorable in Mexican waters or other unsampled areas than in the SCB during this time; therefore most Pacific mackerel may have spawned elsewhere.

The model could discriminate moderately between habitats where larvae would be present or absent, as indicated by an area under curve of 0.80. We note that a model with area under curve of 0.5 would have the same ability as random selection to make correct predictions. The model may be useful for stratifying sampling effort in future cruises if capturing Pacific mackerel is a priority. When the distribution of fish is very patchy, their presence may not be detected in net samples by chance alone, even in habitat where they occur nearby (Mangel and Smith, 1990). The zero catches of Pacific mackerel in the CalCOFI samples in recent years have created a particular problem because the population models used in stock assessment cannot easily incorporate zero estimates for the population during a year as a whole (because zeros would indicate extinction; Dorval et al., 2007). A similar model to this one could be employed adaptively during a cruise by adding additional net tows in areas (and times) where environmental conditions indicate Pacific mackerel larvae are likely to occur. Such an approach would require that zooplankton displacement volumes be measured onboard and the geostrophic flow field calculated by using satellite-derived sea-surface height data during a cruise. Survey estimates could be post stratified into several categories of predicted habitat quality (e.g.,

high-quality versus low-quality habitat as defined by ranges of predicted capture probabilities) to improve estimates.

Conclusions

Presence of Pacific mackerel larvae could be predicted in the California Current as a function of zooplankton displacement volume, geostrophic flow, the interaction between latitude and day of year, the interaction between latitude and water temperature, and the CPFV index as a blocking variable. The model had area under a receiver-operating-characteristic curve of 0.80 but did not completely explain the zero catches that occurred frequently in the 2000s. Two types of spawners overlapped spatially within the survey area: those that exhibited peak spawning during April in the SCB at about 15.5°C and a smaller group that exhibited peak spawning in August near Punta Eugenia, Mexico, at 20°C or greater. The SCB generally had greater zooplankton than Mexican waters but less appropriate (lower) geostrophic flows. Mexican waters generally exhibited greater predicted habitat quality than the SCB in cold years. Predicted quality of the habitat in the SCB was greater in the 1980s to 2008 than in the earlier years of the survey primarily because temperatures and geostrophic flows were more appropriate. However, stock size the previous year had a larger effect on predictions than any environmental variable, indicating that larval Pacific mackerel did not fully occupy the suitable habitat during most years.

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