Corroboration and refinement of a method for differentiating landings from two stocks of Pacific sardine (*Sardinops sagax*) in the California Current

David A. Demer* and Juan P. Zwolinski‡

1Fisheries Resources Division, Southwest Fisheries Science Center (SWFSC), National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Drive, San Diego, CA, 92037, USA
2Ocean Associates Inc. (contracted to SWFSC), 4007 North Abingdon Street, Arlington, Virginia, 22207, USA

*Corresponding Author: tel: +1 858 546 5603; fax: 1 858 546 5652; e-mail: david.demer@noaa.gov

‡Present address: Institute of Marine Sciences, University of California, Santa Cruz, Earth & Marine Sciences Building Rm A317, Santa Cruz, CA 95064


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Efforts to survey, assess and manage Pacific sardine (*Sardinops sagax*) in the California Current may depend on accurate differentiation of the purported two migrating stocks. The southern stock spans seasonally from southern Baja California, México to Point Conception, California; the northern stock spans seasonally from Punta Eugenia, México northwards to southern Alaska (Vrooman, 1964; Smith, 2005). These and other authors have also described a third stock of sardine that resides mostly within the Gulf of California, but it is remote from the northern stock and is therefore not considered further in this paper. Although the northern and southern stocks may not have statistically different characteristics in terms of fish morphometrics, vertebral counts, genetics, parasites, otolith morphometrics or chemistry (see Javor et al., 2011 and references therein), their seasonal north–south migrations are approximately synchronous within their respective domains, resulting in segregated spawning and different identities (Murphy, 1966; Smith 2005; García-Morales et al., 2012).

The northern stock of sardine is annually assessed using an age-structured stock synthesis model (Methot, 2009) fitted with results from acoustic–trawl-method (ATM; Demer et al., 2012) and other fishery-independent surveys, fishery landings data, and many estimated parameters, e.g. fecundity, natural mortality, and growth (Hill et al., 2010, 2011). In these assessments, the landings data from fisheries based at Ensenada, México, multiple ports in

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Introduction

In the California Current, there are two migrating stocks of Pacific sardine (*Sardinops sagax*) (Félix-Uraga et al., 2004, 2005; García-Morales et al., 2012): the southern stock spans seasonally from southern Baja California, México to Point Conception, California; and the northern stock potentially migrates between Punta Eugenia, México (~260 nautical miles, south of Ensenada) northwards to southern Alaska (Vrooman, 1964; Smith, 2005). These and other authors have also described a third stock of sardine that resides mostly within the Gulf of California, but it is remote from the northern stock and is therefore not considered further in this paper. Although the northern and southern stocks may not have statistically different characteristics in terms of...
the USA, and Vancouver Island, Canada (Figure 1), are assumed to be all from the northern stock. Although fishery landings from central California and northwards may be consistently from the migrating northern stock (Zwolinski et al., 2011; Garcia-Morales et al., 2012), the landings at Ensenada and San Pedro may be seasonally from either the southern or northern stock depending on the local presence of suitable habitat (Félix-Uraga et al., 2004, 2005; Smith, 2005; Zwolinski et al., 2011; Garcia-Morales et al., 2012). Inclusion of landings data from the southern stock may serve to overestimate fishing mortality and recruitment for the northern stock, and bias its assessment (Smith, 2005; Hill et al., 2011).

As a case in point, Demer et al. (in press) studied the sardine-length distributions from the ATM surveys and found that the small fish (standard length SL < ~15 cm) landed at Ensenada and San Pedro, California often did not recruit to the northern stock that migrated to, and were fished in, the coastal waters off Oregon and Washington, USA, and Vancouver Island, Canada during summer. Furthermore, often the majority of the assessment-estimated stock abundances were small fish that were not represented in the survey, and the smallest were not represented in fishery catches either. Demer et al. (in press) reasoned that the non-recruiting small fish might comprise a smaller portion of the stock than indicated by the assessments, that they may be virtually completely fished during years of low recruitment, or that they may belong to the southern stock.

Therefore, to more accurately assess the northern stock, a practical method is needed to reject landings data from the Ensenada and San Pedro fisheries if they are likely to be from the southern stock. However, because the fishery landings data are currently reported regionally and monthly, any segregation of the landings data will be inherently coarse spatially and temporally. Consequently, a procedure to reject all of the southern stock landings may inadvertently omit some northern stock landings. Conversely, a procedure that retains all of the northern stock landings may include some southern stock landings. Therefore, the sensitivity of a procedure for differentiating landings should be evaluated.

One practical method for differentiating landings from the northern and southern stocks was proposed by Félix-Uraga et al. (2004, 2005). They used more than 20 years (1981–2002) of commercial catch data from various coastal regions and all monthly periods and identified the ranges of sea-surface temperature (SST) associated with maximum catches of sardine from the putative southern (17°C < SST < 22°C) and northern (SST < 17°C) stocks (see Figure 5 in Félix-Uraga et al., 2004). Although their analyses were based on coarse 2°-latitude by 2°-longitude blocks that did not entirely encompass the Ensenada and San Pedro fishing grounds (Figure 1), they advocated use of the above SST ranges to partition and attribute catch data from within each fishing zone to the northern and southern stocks. Application of their method indicated that sardine landed at San Pedro were likely to be from the northern stock during winter and spring and the southern stock during summer and fall, clearly transitioning during the months of June–July and November–December (Félix-Uraga et al., 2005). This catch pattern is consistent with survey results (e.g. Figure 1) showing that the northern stock has generally resided offshore from southern and central California during winter and spring, and nearshore from central California to Vancouver Island during summer and fall (Lo et al., 2011; Demer et al., 2012; Zwolinski et al., 2012).

Because few sardine were landed at Ensenada or San Pedro when the local SST was in the transitional range between approximately 16.5 and 17.5°C (Figure 3 in Félix-Uraga et al., 2004), both of the fisheries coincidentally and routinely switched effort to another species (e.g. tuna or squid) or, more realistically, the stocks maintained separation. This finding and the general agreement with survey results suggest that the method proposed by Félix-Uraga et al. (2004, 2005) may be robust and could be used to improve the results of integrated stock assessments (Smith, 2005). However, despite the potential benefits of this proposed method, its foundation should be further corroborated.

Building on the results of multiple related studies (e.g. Checkley et al., 2000; Lynn, 2003; Reiss et al., 2008), Zwolinski et al. (2011) developed a non-linear model parameterized with satellite-sensed SST, chlorophyll-a concentration, and the gradient of sea-surface height to characterize and predict the potential habitat of the northern sardine stock. Their model predictions (e.g. see Figure 2) have been corroborated with the results of fishery landings (Zwolinski et al., 2011), and small- (Emmett et al., 2005) and
Figure 2. 2011 monthly average distributions of potential sardine habitat (black line) and sea-surface temperature (SST). The potential habitat model value $= 0.32$ and the range $10.6^\circ C \leq \text{SST} \leq 16.4^\circ C$ include, on average from 1998 – 2009, 90 and 99.9% of the sardine eggs attributed to the northern stock of sardine (Sardinops sagax) in the California Current, respectively (Zwolinski et al., 2011). The maximum SST value related to the northern stock is assumed to correspond to the minimum value related to the southern stock (SST $> 16.4^\circ C$). Regions with SST values $< 10.6^\circ C$ are not associated with either stock.
large-area surveys (e.g. Demer et al., 2012; Zwolinski et al., 2012; Demer et al., in press). In this paper, we use indices of potential northern stock habitat to both corroborate and refine the practical method proposed by Félix-Uraga et al. (2004, 2005). Application of the refined method could enable and improve assessments of multiple sardine stocks (Smith, 2005) and thereby reduce uncertainties in estimations and forecasts of sardine biomasses, exploitation rates, recruitments, and spatial and length distributions.

Methods

Seasonal dynamics of potential sardine habitat

We used satellite-sensed measures of SST (http://coastwatch.pfeg.noaa.gov/erddap/griddap/index.html?page=1&itemsPerPage=1000), chlorophyll-a concentration, and the gradient of sea-surface height to map the monthly average distributions of the optimal and good potential sardine habitat for the northern stock (Zwolinski et al., 2011) during an example year, 2011. These optimal and good regions contained 90% of the Continuous Underway Fish Egg Sampler (CUFES) samples that included sardine eggs during the 1998–2009 spring surveys conducted off California (i.e. the basis of the potential sardine habitat model). To compare this potential habitat with the results of Félix-Uraga (2004, 2005) for the northern stock, we also evaluated the temperature regimes containing 99.9% (9.8°C ≤ SST ≤ 16.7°C) and 100% (9.8°C ≤ SST ≤ 16.7°C) of the CUFES samples that included sardine eggs for the same period (see Figures 4 and 7 in Zwolinski et al., 2011). For the southern stock, we estimated its potential habitat and associated minimum SST as the area outside the potential habitat for the northern stock or its associated maximum SST values (99.9 and 100% confidence intervals; CI values), respectively.

Sardine landings versus potential habitat

Sardine were landed at Ensenada; San Pedro and Monterey, California; Oregon; Washington; and Vancouver Island (Figure 1), each year from 2006–2011. To determine if these landed fish were from the northern versus southern stock, we developed indices based on the potential sardine habitat model (Zwolinski et al., 2011) and associated SST ranges. The SST-based indices are conservative proxies for the potential habitat model. They were evaluated because satellite-sensed sea-surface chlorophyll-a and height data, used to compute the potential sardine habitat model (Zwolinski et al., 2011), were not available for the entire duration of the 2011 assessment model (an anticipated requirement of future

Figure 3. Monthly averages, 2006–2011, of the proportions of each fishing region (see Figure 1) containing optimal or good potential habitat for the northern sardine stock habitat (Zwolinski et al., 2011; grey area) and sea-surface temperature (SST) < 16.4°C (dotted line). The commercial sardine landings (bars; relative within each region) are attributed to the northern stock (black bars) if the SST-based index exceeds 0.5 (i.e. the majority of the fishing region likely contains northern stock habitat), otherwise the landings were attributed to the southern stock (grey bars). There are a couple exceptions to these rules in the Oregon and Washington areas, but fishers there cross regions if sardine are not locally available. The San Pedro fishery was subjected to seasonal closures during and after 2008, resulting in lower catches during summer and fall.
assessments). These indices equal the proportions of each approximated fishing region that contain optimal or good potential habitat for the northern stock or, alternatively, \( \text{SST} \leq 16.4^\circ C \) (99.9% CI) or \( \text{SST} \leq 16.7^\circ C \) (100% CI). Because the analysis regions (Figure 1) approximate but exceed the actual fishing regions, the proportions were normalized to the maximum value within the analysis period. These three indices were evaluated twice per month in \( \sim 10' \times 10' \) blocks spanning each approximated fishing region (Figure 1). For each index, the monthly landings in each fishing region were attributed to the northern stock if the monthly average index was \( \geq 0.5 \) (i.e., the majority of the region contained northern-stock habitat). Otherwise, the monthly landings were attributed to the southern stock.

Landed sardine length distributions

When the northern and southern sardine stocks have different distributions of SL, the sizes of sardine landed at San Pedro may change in concert with the seasonal transitions between their SST-approximated potential habitats. To explore this possibility, monthly average distributions of SL from sardine landed at San Pedro were plotted for the period 2006–2011. Overlaid on this plot are the transitions between the SST-approximated (99.9% and 100% CI values) potential habitat for the northern stock (16.4 and 16.7°C, respectively), which are close to the transition \( \text{SST} = 17^\circ C \) reported by Félix-Uraga et al. (2004, 2005). Because the potential habitat for the northern stock is not only a function of SST, but is generally further constrained in the model by chlorophyll-a concentration and the gradient of sea-surface height (see Figure 4 in Zwolinski et al., 2011), SST alone may provide a conservative boundary for the northern stock (Figure 2). In other words, if sardine from the northern stock are unlikely to reside outside the optimal and good potential habitat (90% CI), they are more unlikely to reside outside the ranges of SST associated with the potential habitat (99.9 and 100% CI values).

From 2006–2011, both the habitat- and SST-based indices for the northern stock show that landings at Monterey and northwards were probably solely from the northern stock (Figure 3). The Monterey region had a large proportion of northern stock habitat year round; the Oregon and Washington regions had northern stock habitat from May–November; and the Vancouver Island region had it from June–October (Figure 3) (see also Zwolinski et al., 2011, and Demer et al., 2012).

In a few instances, the SST–based index in the Oregon and Washington areas fell below the 0.5 cut-off value while the landings remained high (Figure 3). This may have occurred because the Oregon and Washington fleets fished opportunistically off Washington and Oregon, respectively, depending on the availability of sardine to the fisheries. In any case, it is most likely that these landings were from the northern stock. Such events underscore the need

![Figure 4. Monthly average distributions of sardine standard lengths (SL) sampled from landings at San Pedro, California, 2006–2011. The boxes span the first and third quartiles and the whiskers extend to the maximum values not considered outliers. Outliers (circles) are values exceeding the first and third quartiles ± 1.5 times the inter-quartile range. Box widths are proportional to the square root of the sample size. The vertical dotted lines indicate transitions between the northern and southern stock, based on temperature regimes (see Figures 2 and 3). Transitions with significant (Welch’s t-test, \( p < 0.05 \)) changes in the SL distributions are indicated (bold dotted).](attachment:figure4.png)
for finer-scale spatio-temporal matching of the potential-habitat- or SST-based indices and the fishery catches.

In contrast to the northern regions, the indices show that northern-stock habitat was present off Ensenada and San Pedro from December–March and southern-stock habitat was present from May–November (Figure 3). Transitions from northern- to southern-stock habitat and vice versa occurred during April and November–December, respectively.

From 2006–2011, depending on the index used, the percentages of summer landings at Ensenada and San Pedro that were attributed to the southern sardine stock ranged from approximately 63–72% and 32–36%, respectively, depending on the index (Table 1). The higher percentages were for the potential habitat index, which inherently includes an average of 90% of the potential northern stock habitat (Zwolinski et al., 2011). Both of the SST-based indices (including an average of 99.9–100% of the potential northern stock habitat) ascribed 63 and 33.8% of the landings at Ensenada and San Pedro to the southern stock, respectively (Tables 1 and 2; Figure 3). During approximately three-quarters of the transitions between SST ranges associated with the northern and southern stocks (99.9% CI), or vice versa, the distributions of SL changed significantly (Figure 4). Sardine growth or size-dependent seasonal migration is apparent between some, but not all of the periods between transitions.

**Discussion**

Because the assessments of the putative northern stock (e.g. Hill et al., 2010, 2011) included landings at Ensenada and San Pedro during summer when the northern stock had migrated north within its habitat (Murphy, 1966; Félix-Uraga et al., 2005; Zwolinski et al., 2012; Demer et al., 2012; Figure 2), they may have included catch information from two sardine stocks. This could have added uncertainty to assessment estimates of sardine stock biomass, fished abundance, length distributions, and recruitment. To mitigate this potential source of uncertainty, we corroborated and refined a method that Félix-Uraga et al. (2004, 2005) proposed to differentiate northern versus southern stock landings. We based our indices on an extensively corroborated model of potential habitat for the northern stock (Zwolinski et al., 2011) and, alternatively, associated (99.9 and 100% confidence intervals) ranges of SST (Figure 3). The SST–based indices were proposed because the time-series of satellite-sensed SST is much longer than that for satellite-sensed chlorophyll-a concentration, a necessary input to Zwolinski et al.'s (2011) habitat model, and it conservatively includes the northern stock.

**Table 1.** Biomass and proportion of summer landings, 2006–2011, at Ensenada, Mexico and San Pedro, California attributed to the southern stock of sardine (*Sardinops sagax*) versus three indices for the probable absence of the northern stock in the majority of the fishing region.

<table>
<thead>
<tr>
<th>Year/Index</th>
<th>Potential habitat</th>
<th>Ensenada (mt/%)</th>
<th>San Pedro (mt/%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SST ≤ 16.4 °C</td>
<td>SST ≤ 16.7 °C</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>44.697/0.78</td>
<td>46.022/0.80</td>
<td>46.022/0.80</td>
</tr>
<tr>
<td>2007</td>
<td>18.076/0.49</td>
<td>16.928/0.46</td>
<td>16.928/0.46</td>
</tr>
<tr>
<td>2008</td>
<td>50.351/0.75</td>
<td>45.318/0.68</td>
<td>45.318/0.68</td>
</tr>
<tr>
<td>2009</td>
<td>39.862/0.71</td>
<td>31.194/0.56</td>
<td>31.194/0.56</td>
</tr>
<tr>
<td>2010</td>
<td>43.272/0.76</td>
<td>39.745/0.70</td>
<td>39.745/0.70</td>
</tr>
<tr>
<td>2011</td>
<td>55.915/0.80</td>
<td>38.586/0.55</td>
<td>38.586/0.55</td>
</tr>
<tr>
<td>Average</td>
<td>42.029/0.72</td>
<td>36.299/0.63</td>
<td>36.299/0.63</td>
</tr>
</tbody>
</table>

Monthly landings in each region were attributed to the southern stock if the index of optimal or good potential northern stock habitat (Zwolinski et al., 2011), or the indices based on sea-surface temperature (SST) associated with the potential northern stock habitat (99.9 or 100% confidence intervals), were < 0.5 (i.e. a minority of the region contains potential northern-stock habitat).

**Table 2.** Undifferentiated and differentiated northern-stock sardine (*Sardinops sagax*) biomass landed (mt) at Ensenada, Mexico (ENS), and the USA.

<table>
<thead>
<tr>
<th>Year/Index</th>
<th>Undifferentiated landed biomass (mt)</th>
<th>Differentiated landed biomass (mt)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ENS USA</td>
<td>Potential habitat SST ≤ 16.4 °C</td>
</tr>
<tr>
<td>2006</td>
<td>57.237  90.776</td>
<td>12.540  75.079</td>
</tr>
<tr>
<td>2008</td>
<td>66.866  87.175</td>
<td>16.515  76.895</td>
</tr>
<tr>
<td>2009</td>
<td>55.911  67.083</td>
<td>16.049  63.773</td>
</tr>
<tr>
<td>2010</td>
<td>56.821  66.891</td>
<td>13.549  57.529</td>
</tr>
<tr>
<td>2011</td>
<td>70.337  46.745</td>
<td>14.421  41.619</td>
</tr>
</tbody>
</table>

Monthly landings in each region were attributed to the northern stock if the index of optimal or good potential northern stock habitat (Zwolinski et al., 2011), or the indices based on sea-surface temperature (SST) associated with the potential northern stock habitat (99.9 or 100% confidence intervals), were 2 0.5 (i.e. a majority of the region contains potential northern-stock habitat). Although sardine were landed in the USA at San Pedro and Monterey, California, and ports in Oregon and Washington, only the USA landings at San Pedro included some sardine attributed to the southern stock.
Ultimately, the choice of index used to differentiate landings from the northern and southern stocks depends on acceptable risk. For example, if a transition SST = 16.7°C is assumed, all of the landings from the northern stock may be retained, but some of the southern stock landings may be falsely attributed to the northern stock. Depending on the number of misclassified landings, inclusions of southern stock landings could potentially positively bias the estimated fishery exploitation rate, skew the sardine length distribution, and alter the assessed biomass. If a transition SST = 16.4°C is assumed, an average of 0.1% of the northern stock landings may be excluded, but fewer southern stock landings may be included. Depending on the amounts, the inclusion of southern stock landings may positively bias the exploitation rate and perhaps increase the assessed biomass of the northern stock. If the potential habitat index is used, an average of 10% of the northern stock landings may be excluded, but it is less likely that southern stock landings will be included.

We applied each of the alternative indices to the 2006–2011 monthly regional landings data (the finest spatio-temporal scale data available to us). Because sardine landings at Ensenada or San Pedro were often low when the local habitat was transitioning (Félix-Uraga et al., 2004, 2005; Figure 3), these results indicate that the efficacy of the method is insensitive to the choice of index (Tables 1 and 2). For example, both SST-based indices ascribed 63% of the landings at Ensenada and 32% of the landings at San Pedro to the southern stock (Table 2). Note, however, that the San Pedro fishery was seasonally constrained by lower fishing quotas during four of the five years analysed here. If this analysis spanned more years, including the earlier period when the fishery was not so constrained, the long-term estimates would likely be higher than 32%. The increase would depend on both the quotas and the availability of fish to the fishery.

At 73% of the transitions between southern and northern stock habitat (Figure 3), the SL distributions at San Pedro changed significantly (Welch’s t-test, p<0.05; Figure 4). These significant differences could have multiple explanations, e.g. the transition of two stocks within the region, or the timing and extent of the size-dependent sardine migrations of one stock (e.g. Lo et al., 2010; Zwolinski et al., 2011; Demer et al., 2012). When the differences were not significant, the regional landings during transition months may have been comprised of fish from the two stocks, the regional length distributions of the northern and southern stocks may have been similar, or both. Without additional information, this part of our analysis is inconclusive.

Our method for differentiating landings from the two sardine stocks may occasionally be compromised by variations in fish behaviour. For example, sardine may occasionally tolerate waters that are warmer than those associated with their potential habitat (Emmett et al., 2005; Lo et al., 2010; Zwolinski et al., 2011), or exploit patches of their optimal or good potential habitat amidst (e.g. beneath that indicated by the SST), or at the margins of bad or unsuitable habitat (Zwolinski et al., 2011). It is therefore important to know how subsurface sea temperatures differ from the satellite-sensed SST and to match the SST and biological samples (e.g. sardine egg or landings) on finer spatial and temporal scales (e.g. SST at catch). Also, because the landings data are currently only reported regionally and monthly, it may be prudent to omit regional landings data during transition months as there is an increased likelihood during these periods that some landings may not be representative of the assessed stock.

Notwithstanding the remaining uncertainties, Smith (2005) claimed that a method such as ours could now be used to differentiate landings data even before more detailed knowledge is gained of the geographic structures and seasonal migrations of the two stocks. It may serve to improve estimates of northern stock biomass, spatial and length distributions, and mortality.

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