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Original Article

Spatio-temporal associations of albacore CPUEs in the Northeastern Pacific with regional SST and climate environmental variables

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This study investigated the spatial distribution of juvenile North Pacific albacore (*Thunnus alalunga*) in relation to local environmental variability [i.e. sea surface temperature (SST)], and two large-scale indices of climate variability, [the Pacific Decadal Oscillation (PDO) and the Multivariate El Niño/Southern Oscillation Index (MEI)]. Changes in local and climate variables were correlated with 48 years of albacore troll catch per unit effort (CPUE) in 1° latitude/longitude cells, using threshold Generalized Additive Mixed Models (tGAMMs). Model terms were included to account for non-stationary and spatially variable effects of the intervening covariates on albacore CPUE. Results indicate that SST had a positive and spatially variable effect on albacore CPUE, with increasingly positive effects to the North, while PDO had an overall negative effect. Although albacore CPUE increased with SST both before and after a threshold year of 1986, such effect geographically shifted north after 1986. This is the first study to demonstrate the non-stationary spatial dynamics of albacore tuna, linked with a major shift of the North Pacific. Results imply that if ocean temperatures continue to increase, US west coast fisher communities reliant on commercial albacore fisheries are likely to be negatively affected in the southern areas but positively affected in the northern areas, where current albacore landings are highest.

Keywords: albacore, environmental variables, regime shifts, spatial distribution, temporal distribution.

Introduction

North Pacific albacore (*Thunnus alalunga*) is an economically important temperate tuna species distributed across the North Pacific (Sund *et al.*, 1981; Miyake *et al.*, 2004; Ellis, 2008; Laurs and Powers, 2010; Childers *et al.*, 2011). North Pacific albacore account for almost half of all albacore landings worldwide (Laurs and Powers, 2010). They are harvested by a number of countries, but Japan and the USA have landed over 90% of the fish captured since the 1950s (Childers and Aalbers, 2006). Pelagic longline, pole-and-line (bait boat), and troll are the three main gear types used to harvest albacore in the North Pacific. Adult albacore are targeted by several longline fisheries in the Central and Western North Pacific, and juvenile albacore are targeted by various surface fisheries in the Northeastern Pacific.

Along the west coast of North America, juvenile albacore sustain a multi-million dollar troll fishery and are an important contribution to recreational fisheries (PFMC, 2010). This troll fishery has negligible bycatch and has been Marine Stewardship Council (MSC) certified as a sustainable fishery. Albacore is one of the last open access (i.e. no limit on the number of participants) commercial fisheries remaining off the west coast of North America, and anyone can purchase a permit and fish any time of year. North Pacific albacore are highly migratory and distributed throughout the temperate and subtropical regions of the North Pacific (Otsu, 1960; Clemens, 1961; Otsu and Uchida, 1963). Juvenile albacore migrate into coastal waters during the summer months and feed on abundant prey in the California Current (Glaser, 2010).

Juvenile albacore are primarily epipelagic in the North Pacific, spending most of their time above the thermocline with short excursions into deeper water during the day (Domokos *et al.*, 2007; Childers *et al.*, 2011). Although albacore can tolerate temperatures between 7 and 25.2°C (Boyce *et al.*, 2008), juveniles are known to have specific sea surface temperature (SST) preferences ranging from 15–19.5°C, and centred around 17.5°C (Clemens, 1961; Flittner, 1963; Laurs and Lynn, 1977; Boyce *et al.*, 2008; Childers *et al.*, 2011). This preference has been well documented at relatively fine scales, as well as at larger scales over longer periods. At present the reason for this temperature preference in juvenile albacore is not well understood, but we speculate it is related to metabolic constraints.

Most studies that have looked at spatial dynamics of albacore and other tuna distributions have found them sensitive to ocean surface features and climate regime shifts. Sagarminaga and Arrizabalaga (2010) found a close spatio-temporal relationship with a preferred SST window (16–18°C) and seasonal progression of the juvenile Northeast Atlantic albacore fishery. Dufour *et al.* (2010) found the juvenile North Atlantic albacore mean catch latitude trended northward over time, and was correlated with the 17°C SST isotherm. Dufour *et al.* (2010) also determined that the distribution of catch per unit effort (CPUE) of albacore in the Atlantic changed after 1988 following the North Atlantic regime shift. Goñi and Arrizabalaga (2005), also studying albacore in the Atlantic, found regional monthly averaged sea surface agitation and insolation (both related to mixed layer depth) to be the only variables with significant negative relationships to albacore CPUE within season. Surface properties such as SST were found to be important predictors of the spatial distribution of albacore CPUE in the Indian Ocean (Chen *et al.*, 2005). Skipjack tuna (*Katsuwonus pelamis*) in the Southwest Atlantic were found to show a North–South displacement of CPUE, which was strongly associated with seasonal variation in SST (Andrade, 2003). Similarly, the spatio-temporal distribution of Pacific yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna were found to be positively associated with higher SST during both El Niño and La Niña years (Lu *et al.*, 2001).

Evidence from previous studies, both on albacore as well as on other tuna species, suggests that SST and large-scale environmental indices are important drivers of albacore and other tuna spatial distributions in several oceans. Rapid changes in these environmental variables, like those associated with a climate regime shift, have also been shown to affect tuna distribution (Dufour *et al.*, 2010). The impact of large-scale habitat suitability on the distribution of North Pacific albacore is poorly known, and the stock structure is not fully resolved (Barr, 2009; Laurs and Powers, 2010). However, several studies and anecdotal evidence indicate that this species exhibits a large distributional shift in response to changes in the local environmental (Laurs and Lynn, 1977; Barr, 2009; Childers *et al.*, 2011). The West Coast North Pacific albacore troll fishery is an important fishery, with an ex-vessel revenue averaged at over $21 million USD annually (inflation accounted for) between 1981 and 2009 (PFMC, 2010). However, albacore landings are highly variable, both in total numbers and in distribution from year to year. Thus, the economies of numerous local fishing communities along the west coast, which are based on the harvesting of albacore, are likely to be affected in response to climatic changes that may affect the distribution and availability of North Pacific albacore.

This study investigated the spatio-temporal distribution of juvenile (2–5 years old) North Pacific albacore off the US west coast. We examined the interannual changes in albacore distribution in relation to SST, and also in relation to two large scale indices of climate variability [the multivariate El Niño/ Southern Oscillation Index (MEI) and Pacific Decadal Oscillation (PDO)] that are known to influence the productivity and hydrographic features of the northeast Pacific (Lluch-Cota *et al.*, 2001; Chhak and Di Lorenzo, 2007). The effects of geography and environmental variability on the distribution of albacore CPUE were examined by fitting multiple model formulations to account and test for both non-stationary and spatially variable effects of the targeted variables on albacore CPUE. Non-stationarity effects were included because of a major regime shift that occurred in the North Pacific during the late 1970s. This regime shift was characterized by rapid physical and biological changes over a short period, which persisted for decades in the North Pacific ecosystem (Miller *et al.*, 1994; McGowan *et al.*, 2003). This shift brought about changes that resulted in warmer surface temperatures, declines in species populations, changes in species community structure, and/or northward species range shifts over large scales across multiple trophic levels in the eastern North Pacific (Hare and Mantua, 2000; Chavez *et al.*, 2003; McGowan *et al.*, 2003). In addition, several large-scale climate-forcing mechanisms have been shown to affect the productivity of the California Current over yearly and longer time-scales (Schwing *et al.*, 2010; King *et al.*, 2011; Sydeman *et al.*, 2013).

Material and methods

Data

Commercial North Pacific albacore logbook data were provided by the National Oceanic and Atmospheric Administration (NOAA) Southwest Fisheries Science Center (SWFSC). From 1961–2008, monthly CPUE (fish per boat day) was calculated at 1° × 1° spatial resolution (cells hereafter) for troll-caught juvenile albacore in the US coastal fishery. The geographical range of this study was restricted to main fishing areas of the US West Coast albacore fishery (Figure 1) defined as eastward of 130°W to the US west coast and north of 20°N. This region is slightly larger than the US West Coast Exclusive Economic Zone (EEZ), and represents the summer feeding grounds of juvenile North Pacific albacore. Previous research has established this area to represent the majority (99%) of the recorded USA catches, and determined that 130°W was a breakpoint between nearshore and offshore albacore regions (Laurs and Lynn, 1977; Powers *et al.*, 2007; Barr, 2009; Laurs and Powers, 2010). We further restricted the albacore logbook data to the troll fishery by excluding the pole-and-line fishery data for the following reasons: (i) the CPUE standardization between the pole-and-line and troll fisheries was problematic because of a lack of spatio-temporal overlap, (ii) the pole-and-line fishery had a discontinuous time-series that was likely influenced by the US exclusion from Mexican waters in the late 1980s (Laurs and Powers, 2010), and (iii) the troll fishery comprised the vast majority (>85%) of the dataset (Barr, 2009).

To explore albacore spatial distributions in relation to SST and temperature-related anomalies, the following variables were obtained at the monthly scale from January 1961 to December 2008: (i) SST from the International Comprehensive Ocean–Atmosphere Data Set (ICOADS) at 1° × 1° resolution, (ii) the PDO Index (http://jisao.washington.edu, last accessed 7 August 2009), and (iii) the MEI (www.esrl.noaa.gov/psd/people/klaus.wolter/MEI, last accessed 7 August 2009). The ICOADS SST was obtained through the NOAA/OAR/ESRL Physical Science Division (Boulder, Colorado, USA), website (http://www.esrl.noaa.gov/psd/, last accessed 7 August 2009). The ICOADS is derived from surface marine observational records from ships, buoys, and other platform types at 1° latitude by 1° longitude monthly intervals (http://www.icoads.noaa.gov, last accessed 7 August 2010). The general summertime spatial pattern of SSTs in

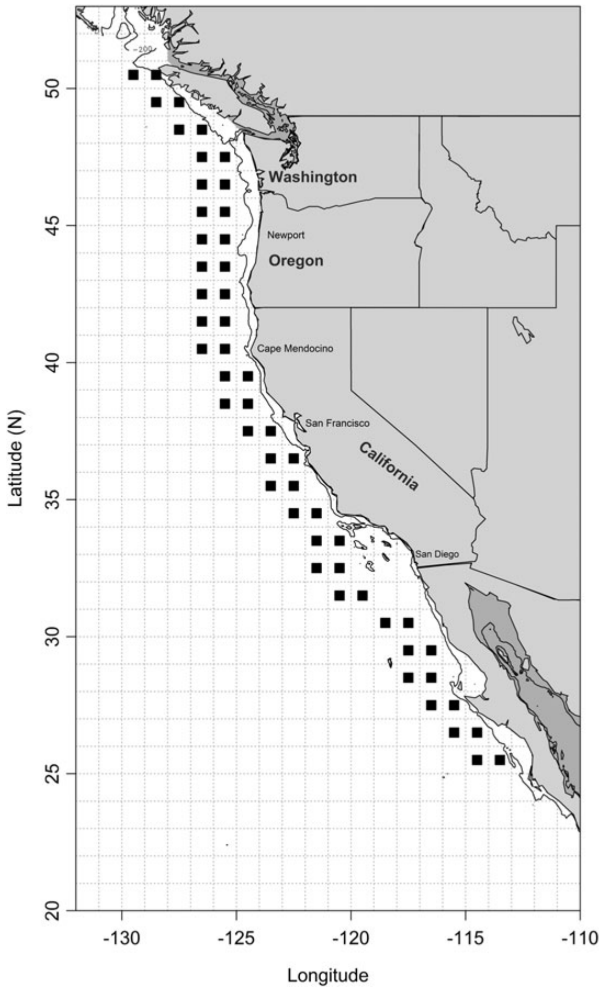

Figure 1. Study region for spatio-temporal analysis. The black squares represent the 1° × 1° cells used to calculate the mean monthly SST and roughly represent the areas with the highest long-term CPUE for each 1° latitude band. The dark blue line is the 200-m isotherm.

our study region decreases to the north and inshore, with the exception of two variable broad cold tongues in the central area (Cape Blanco and Mendocino) that can extend farther offshore (Chelton *et al.*, 2007).

The MEI and PDO were selected because they are indicative of the thermal regime of the subtropical and temperate waters in the North Pacific, which includes the entire geographical range of North Pacific albacore. The ENSO is the most important ocean–atmospheric cycle over the tropical Pacific Ocean, operating on a 2–7 year time-span (Wolter and Timlin, 1998; Hanley *et al.*, 2003). ENSO events have been related to changes in albacore and other fish populations (Ahrens, 1994; Bakun and Broad, 2003). The MEI was selected to represent ENSO-related climate variability. The MEI is the first principal component of the six main observed variables [sea-level pressure (P), zonal (U) and meridional (V) components of the surface wind, SST, surface air temperature, and the total cloud fraction] over the tropical Pacific (Wolter and Timlin, 1993; 1998; available from www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/, last accessed 7 August 2009). The PDO is the leading pattern of North Pacific SSTs, and shows significant variability at interannual and decadal time-scales (Zhang *et al.*, 1997; Mantua *et al.*, 1997; Newman *et al.*, 2003). The PDO is derived as the principle component of monthly SST anomalies in the North Pacific Ocean, pole-ward of 20°N, with records starting January 1900 (Zhang *et al.*, 1997). The PDO index used in this study was updated to include May 2009 (http://jisao.washington.edu/pdo, last accessed 7 August 2009) with monthly mean global average SST anomalies removed to separate the PDO variability from any "global warming" signal. The PDO was selected because of the potential low frequency influences in albacore abundance (Bakun and Broad, 2003).

Average monthly albacore CPUEs in relation to the average underlying water temperature and monthly mean of MEI were plotted to characterize the latitudinal patterns of albacore seasonal and interannual distribution in relation to SST for each 1° latitudinal bin. Monthly albacore CPUEs by 1° latitude bins were calculated by dividing the monthly sum of daily catch by the monthly sum of daily effort (defined as deployment of fishing gear by a vessel during the day) in each bin. Average SST (°C) was calculated by averaging the ICOADS monthly SSTs for each 1° latitude bin. SST was plotted by month with the CPUE overlaid to show trends in latitudinal–temporal shifts in CPUE. The MEI index was also plotted with the CPUE–SST time-series but as a single line, since it has no latitudinal variability. The CPUE (all data including zero CPUE) was binned by 1°C bins, and the differences among these thermal bins were assessed using the Tukey's honestly significant difference test (Ramsey and Schafer, 2002).

Yearly state-space analysis

Threshold generalized additive mixed models (tGAMMs) were used to investigate albacore spatial temporal distributions in relation to SST, MEI and PDO, using the mgcv package in R (v2.10.1) software (Wood, 2006). Albacore CPUE was modelled with four competing formulations: (i) *spatial*, (ii) *spatial and environmental*, (iii) *spatially variant*, and (iv) *non-stationary with spatially variant effects*. Each of these four formulations is reflective of an underlying hypothesis connecting changes of albacore spatial distribution with environmental and geographic forcing. Specifically, the *spatial* GAMM model assumes that albacore distribution along the studied region is only affected by geography, and that CPUE variations are due to interannual changes in albacore stock size. Cells with <6 years of albacore CPUE were removed, resulting in 4561 samples out of the 4704 initial observations. The *spatial* formulation is:

$$x_{y,(\varphi,\lambda)} = S_1(\varphi,\lambda) + e_{y,(\varphi,\lambda)}$$
$$x_y,(\varphi,\lambda) = In\ (CPUE+1)\ at\ (\varphi,\lambda)\ in\ y, \qquad (1)$$

where (φ, λ) = given location by longitude and latitude degrees within the study area, y = given year from 1961–2008, S_1 = 2-dimensional smoothing function [thin plate regression spline (Wood, 2006)] and e = error term with a random component (normally distributed) and a spatially structured component (Gaussian variogram).

The *spatial and environmental* formulation included environmental covariates (SST, PDO and MEI) in addition to the spatial term, and assumes that all the environmental covariates are independently and therefore additively affecting albacore CPUE. We also tested whether the addition of a large-scale climate index improved this model. Therefore, either MEI or PDO, which capture low-frequency environmental variability, were included additively. To confirm the independence assumption had been met, correlations were tested between the variables. The local SST and the PDO were found to be weakly correlated ($R = 0.11$), as was local SST and the MEI ($R = 0.09$). However, both MEI and PDO were not allowed in the same model to avoid collinearity, as they were highly correlated ($R = 0.69$). This resulted in three spatial and environmental models:

$$x_{y,(\varphi,\lambda)} = g_1\left[SST_{y,(\varphi,\lambda)}\right] + S_1(\varphi, \lambda) + e_{y,(\varphi,\lambda)} \quad (2a)$$

$$x_{y,(\varphi,\lambda)} = g_1\left[SST_{y,(\varphi,\lambda)}\right] + g_2\left[PDO_{(y)}\right] + S_1(\varphi, \lambda) + e_{y,(\varphi,\lambda)} \quad (2b)$$

$$x_{y,(\varphi,\lambda)} = g_1\left[SST_{y,(\varphi,\lambda)}\right] + g_2\left[MEI_{(y)}\right] + S_1(\varphi, \lambda) + e_{y,(\varphi,\lambda)} \quad (2c)$$

where g_i = 1-dimensional smoothing function (thin plate regression spline, Wood, 2006).

The *spatially variant* formulation allowed the effect of the environmental covariate that was also spatially variable, namely SST, to smoothly change in relation to the geographical location. Spatially variant effects are modelled locally with a linear function (Bacheler *et al.*, 2009, 2010; Bartolino *et al.*, 2011; Ciannelli *et al.*, 2012). Therefore, the model estimates a landscape of linear slopes, which are indicative of the SST effect on local albacore CPUE (Bartolino *et al.*, 2011). The *spatially variant* formulation was an expansion of the highest ranked model type 2, in which the SST effect was made spatially variable by implementing a variable coefficient formulation. The climate index (PDO or MEI) was treated as a fully additive variable, because it is a large-scale index and not spatially variable.

$$x_{y,(\varphi,\lambda)} = g_1\left[\text{Climate}_{(y)}\right] + s_1(\varphi, \lambda) + s_2(\varphi, \lambda) \cdot SST_{y,(\varphi,\lambda)} + e_{y,(\varphi,\lambda)} \quad (3)$$

The *non-stationary* formulation, as an expansion of model 3, was used to address non-stationary effects, which may be driven by a regime shift. Specifically,

$$x_{y,(\varphi,\lambda)} = g_1\left[\text{Climate}_{(y)} + s_1(\varphi, \lambda) + e_{y,(\varphi,\lambda)}\right] + \begin{cases} s_2(\varphi, \lambda) \cdot SST_{y,(\varphi,\lambda)} \cdot Th1_y \\ s_3(\varphi, \lambda) \cdot SST_{y,(\varphi,\lambda)} \cdot Th2_y \end{cases} \quad (4)$$

where $Th\,1_y = 1$ if $y <$ threshold year else 0, and $Th\,2_y = 1$ if $\geq$ threshold year else 0.

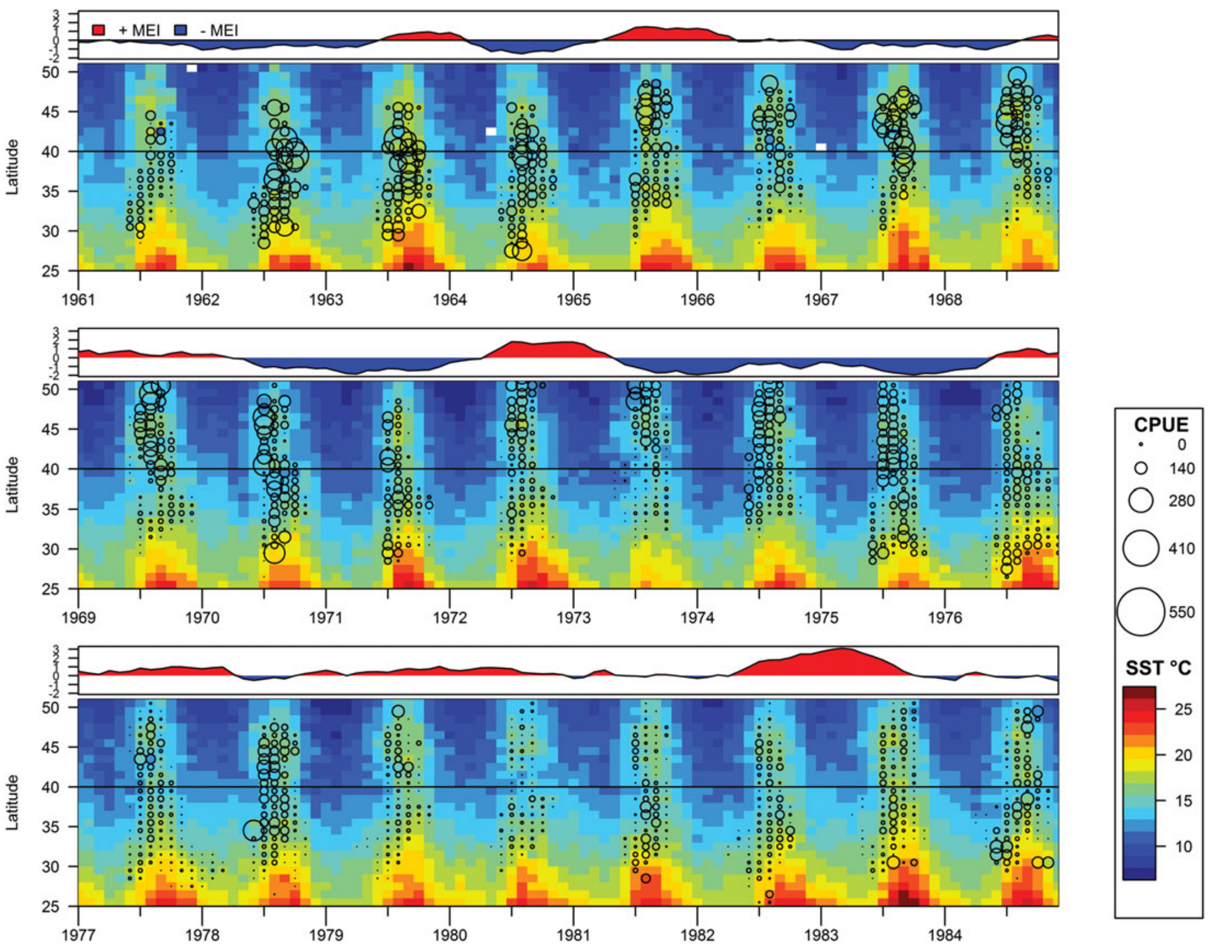

Figure 2. Monthly Sea Surface Temperature vs. CPUE by 1° latitude bins from 1961–2008. Multivariate El Niño/Southern Oscillation Index (MEI) values are also plotted, with positive values shaded in red and negative values shaded in blue.

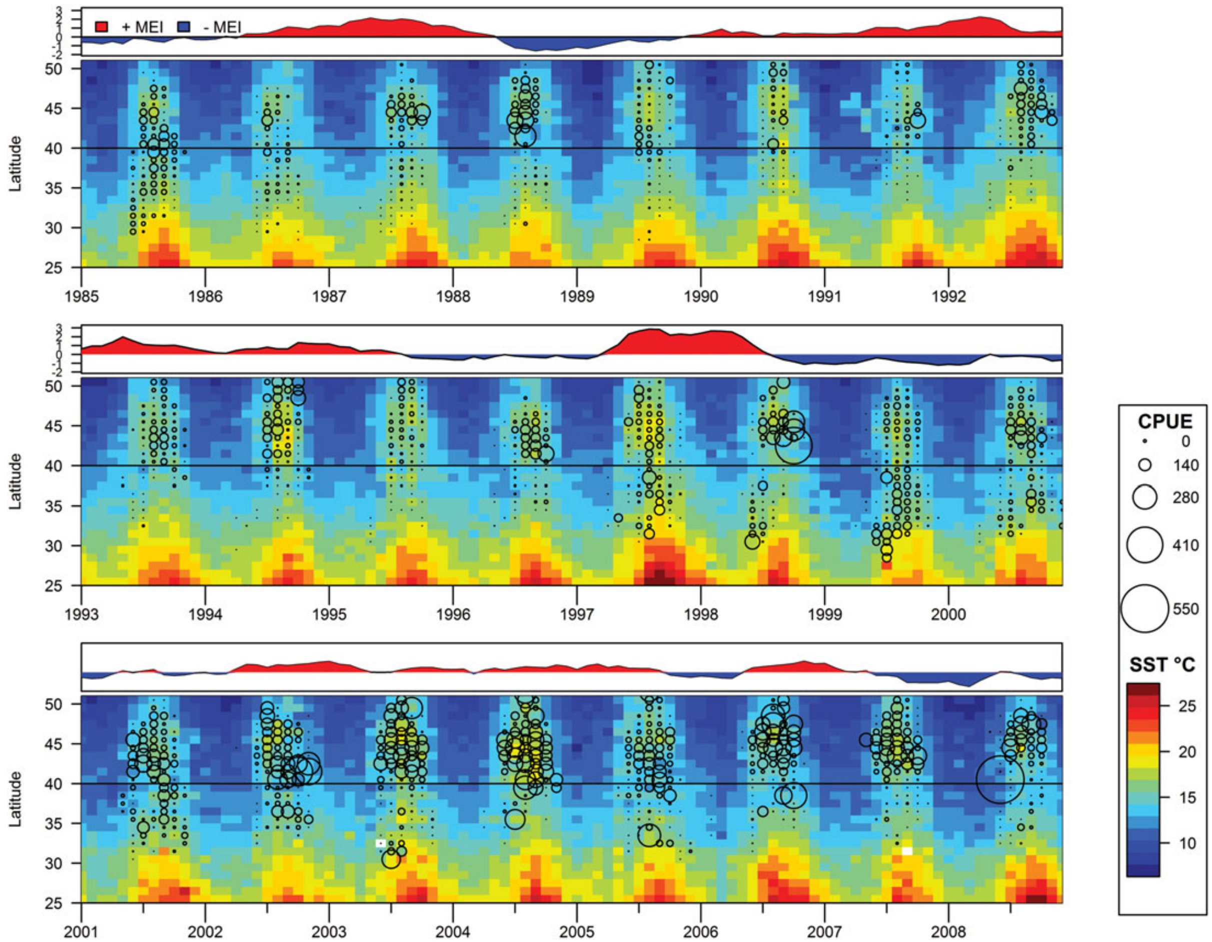

Figure 2. Continued.

The threshold year was estimated by minimizing the model Akaike Information Criterion (AIC) over the entire range (minus the 5 years at either end of the series) of the years considered (Ciannelli *et al.*, 2012). The AIC is the model negative log-likelihood divided by the number of parameters, and models with lower AIC are thought to strike a better balance between complexity (number of parameters) and goodness-of-fit (Burnham and Anderson, 2002). Truncating the time-series by 5 years ensures that even if the threshold year is selected to be either at the start or end of the examined time-span, there is still a small number of years in one of the selected epochs.

In each of the models above, the error term is assumed to have a random component, which is normally distributed, and a spatially structured component, which is modelled with the inclusion of a Gaussian variogram (Bartolino *et al.,* 2011). Model selection was based on AIC. The analysis was restricted to cells with $\geq$6 years of CPUE observations, roughly 10% of the years that had spatial data. This restriction was applied to prevent cells with relatively few years of observations from being overly influential.

Results

Latitudinal temporal mapping of monthly averaged CPUE overlaid with SST cells revealed several spatial trends (Figure 2). The most apparent pattern was a positive association between SST and albacore CPUEs. For approximately half of the years in the time-series, the fishery began in June in the south, and as the season progressed there was a pole-ward shift in latitude of the fishery with increasing CPUE rates. However, this pattern is not observed for the entire duration of the time-series. Some years (e.g. 1970) showed an equatorward shift of the fishery. The mean positive albacore CPUE (zero catches removed) occurred in SST cells of 15.5°C ($\pm$1.69 SD), range 9.8–22.7 °C, and 75% of the positive CPUE occurred in cells with SST ranging from 14.4–16.5°C. When zero catch is included in the CPUE, which was normalized and binned into 1°C intervals, a similar trend to the positive-only CPUE was found (Figure 3). The highest CPUEs (zero catch included) occurred in cells with SST between 14 and 17°C, but these CPUEs were not significantly different ($p > 0.05$; Tukey's honestly significant test) from those of any cells above 14°.

Unlike SST, the MEI values shown in Figure 2 display no clear visual trends in relation to latitudinal CPUE over the entire time-series. During some positive MEI episodes (e.g. 1965, 1972 and 1994), the fishery shifted north and began later (July) than in the previous year. However, other positive MEI episodes (e.g. 1963, 1983, 1991, 1997 and 1998) showed no distributional shift from the previous year's fishery. Inconsistent patterns were also found between the CPUE and negative MEI. For example, southern distributional shifts occurred in some years with negative MEI (e.g. 1964, 1970 and 1999) while other negative MEI episodes (e.g. 2008) did not show a marked change from the previous year.

Yearly spatio-temporal analysis

The yearly averaged cells of CPUE ranged from 0–1093 fish per boat day with a mean CPUE of 50. The best fit model identified from the four competing formulations was the fourth, i.e. *non-stationary* (Table 1), as indicated by adjusted R^2 and AIC scores. Formulation performance decreased with all other models as follows: (iii) *spatially variant*, (ii) *spatial and environmental*, and (i) *spatial*. Model (2b), which included SST and PDO, was determined to be the best spatial and environmental model, as indicated by minimized AIC scores (Table 1). The covariates in all of the formulations were highly significant (p-values < 0.01) (Table 1).

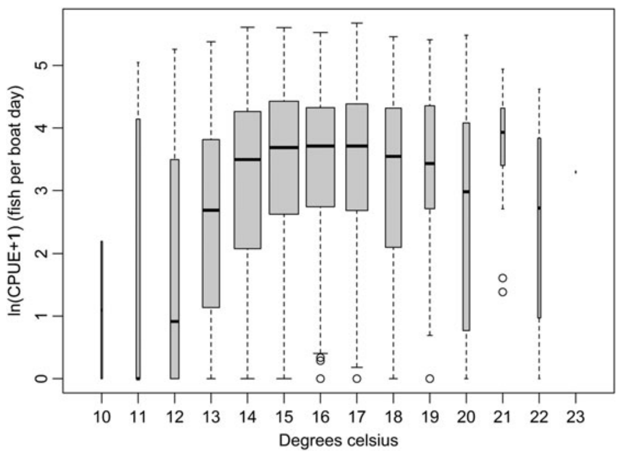

Figure 3. Box plots of the 1° latitude monthly averaged log(CPUE + 1) (fish per boat day) (1961–2008) by 1°C bins, and includes 0 CPUE. The thick black line is the median; the grey box represents the 25th–75th percentiles, the dashed vertical line is 5th–95th percentiles, and the dots outside are potential outliers. The widths of the boxes are proportional to the square roots of the number of observations in the groups.

Based on the (i) *spatial* formulation, the highest densities of albacore CPUEs occurred off the coast of central Oregon at ~45°N, and a secondary density peak occurred off the coast of central California near 35°N (Figure 4). However, in the best fit model, which was non-stationary, the secondary peak off the coast of California was reduced in the spatial distribution after accounting for SST, essentially leaving a single core concentration centred off the coast of central Oregon (Figure 5).

The search for a threshold year resulted in two minima in the AIC profile (Figure 6): one in 1986, the lowest, and another in 1979, the second lowest. Both thresholds resulted in a non-stationary model with lower AIC than any of the stationary models attempted in this analysis (Table 1). Both non-stationary models have comparable spatially variable effects of SST: positive and widespread throughout the sampling range before the threshold year, becoming concentrated north of 40ºN after the threshold (Figure 5). In addition to contracting geographically, the overall effect of SST on CPUE was less influential after 1986, as indicated by a 45% reduction in the mean magnitude of the estimated slopes (Figure 5a and b). The *non-stationary* formulation shows that albacore CPUE was highest off the coast of central Oregon at ~45°N 126°W (Figure 5a).

Table 1. Juvenile troll-caught North Pacific albacore generalized additive mixed models (GAMMs) of yearly averaged catch per unit effort (CPUE) in the Northeast Pacific Ocean (1961–2008).

Model	Model descriptions	Predictor variables				Threshold year	R^2 (%)	AIC
(1)	*Spatial* model based on localized CPUE.	$s_1(\varphi,\lambda)$ 24.99***					14	14 454
(2a)	*Spatial and environmental* model based on spatially localized CPUE and additive effects of SST (e.g. assumes no localized effects of SST on CPUE).	$s_1(\varphi,\lambda)$ 24.46***	$g_1[SST(y)]$ 3.45**				15	14 449
(2b)	*Spatial and environmental* model based on spatially localized CPUE and additive effects of SST and PDO.	$s_1(\varphi,\lambda)$ 24.68***	$g_1[SST_{y(\varphi,\lambda)}]$ 3.16**	$g_2[PDO(y)]$ 2.37***			19	14 342
(2c)	*Spatial and environmental* model based on spatially localized CPUE and additive effects of SST and MEI.	$s_1(\varphi,\lambda)$ 24.57***	$g_1[SST_{y(\varphi,\lambda)}]$ 3.10**	$g_2[MEI(y)]$ 2.23***			18	14 381
(3)	*Spatially variant* model based on spatially localized CPUE and SST, with additive effects of PDO.	$s_1(\varphi,\lambda)$ 24.54***	$s_2(\varphi,\lambda)$ $SST_{y(\varphi,\lambda)}$ 3.03***	$g_1[PDO(y)]$ 2.40***			20	14 346
(4a)	*Non-stationary* model based on spatially localized CPUE and SST, with additive effects of PDO. Assumes an abrupt shift in dynamics between SST and CPUE before (s_2) and after (s_3), a threshold year to be determined from the data.	$s_1(\varphi,\lambda)$ 24.88***	$s_2(\varphi,\lambda)$ $SST_{y(\varphi,\lambda)}$ 3.00***	$s_3(\varphi,\lambda)$ $SST_{y(\varphi,\lambda)}$ 11.425***	$g_1[PDO(y)]$ 2.313***	1986	29	14 086
(4b)	*Non-stationary* model based on spatially localized CPUE and SST, with additive effects of PDO. Assumes an abrupt shift in dynamics between SST and CPUE before (s_2) and after (s_3), a threshold year to be determined from the data.	$s_1(\varphi,\lambda)$ 2 415***	$s_2(\varphi,\lambda)$ $SST_{y(\varphi,\lambda)}$ 3.00***	$s_3(\varphi,\lambda)$ $SST_{y(\varphi,\lambda)}$ 10.88***	$g_1[PDO(y)]$ 1	1979	28	14 138

Four competing model types were tested: (1) spatial, (2) spatial and environmental, (3) spatially variant, and (4) non-stationary. Covariates of the model type (2) with the lowest Akaike Information Criteria (AIC) score were expanded for model types (3) and (4). 1986 was selected as a threshold year for model type (4), but results are also included for the threshold year 1979, which was the second minimum of the AIC profile. Estimated degrees of freedom (or linear coefficient in the case of parametric terms) and statistical significance are shown for each term (*** $p \leq 0.0001$, ** $p \leq 0.001$, *$p \leq 0.05$), and the adjusted R^2. (φ,λ) = position by latitude and longitude degrees, s1–3 = 2-dimensional smoothing functions, g1–2 = 1-dimensional smoothing functions, y = year.

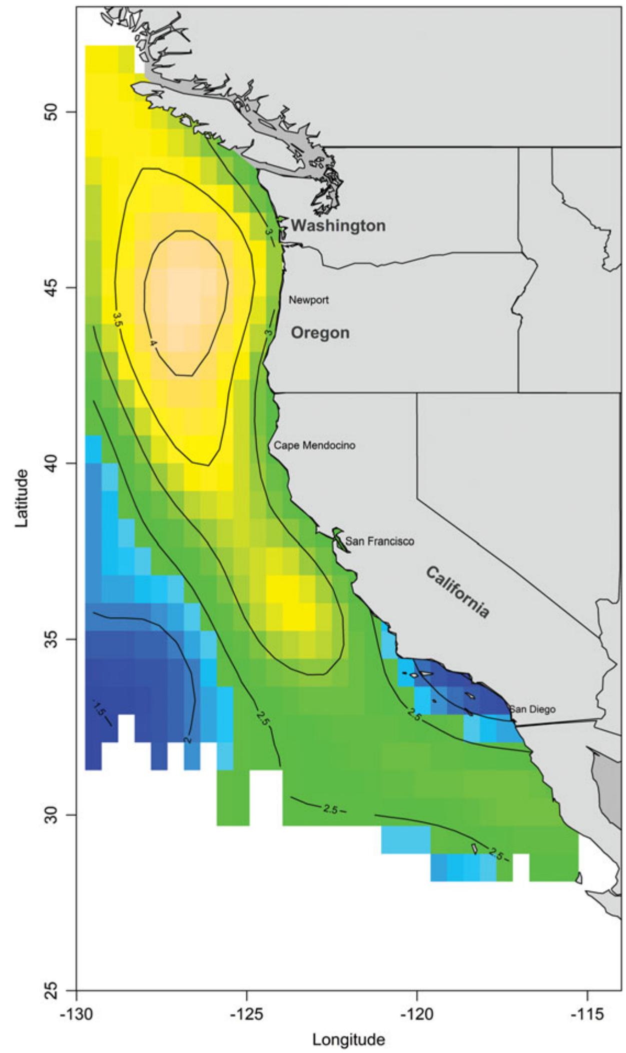

Figure 4. Effect of position yearly averaged log-transformed albacore catch per unit effort (CPUE) (1961–2008) estimated from a generalized additive mixed model. Yellow indicates high predicted yearly CPUE rates, and blue indicates low predicted yearly CPUE rates. The contour lines correspond to predicted yearly log (CPUE + 1).

The effect of the PDO was negative (Figure 5c), as was the case in other models tested that also included a PDO term.

The inspection of the model 4 residuals for spatial autocorrelation (variog function in the geoR library) showed some spatial correlation in each year, which was not always reduced in the best fit model. Temporal (pacf function in R) partial autocorrelation of the yearly averaged residuals showed significant autocorrelation at lag 1 ($r = 0.58$), but this was reduced from the CPUE, which also had an autocorrelation at lag one ($r = 0.68$).

Discussion

This is the first study to characterize how the regional and basin-scale index of environmental and climate variability affect albacore CPUEs in the North Pacific. Results suggest that the positive effect of increase in SST on albacore CPUE have contracted northward since 1986. Our threshold analysis had a second minimum of 1979, which roughly coincides with the North Pacific regime shift (Figure 6). We believe the cannery closure in southern California during the early 1980s was the reason why a threshold occurred in 1986 and not earlier. Between 1982 and 1984, almost 2000 fishermen and 6000 other positions related to the albacore fishery were lost because canneries moved outside the USA and into the global market (Love, 2006). Our underlying hypothesis is that some of these changes were already occurring before 1986, when the canneries were still open. Results with a threshold year of 1979 are very similar to those of 1986, showing a northerly concentrated effect of SST on tuna CPUE. Although our analysis selected 1986 as the year of the threshold some of the changes were already occurring before (i.e. in 1979, when the canneries were still open in California). Dufour *et al.* (2010) concluded that juvenile Atlantic albacore changed their distribution in relation to climatic regime shifts, and this appears to have occurred with North Pacific albacore as well. The PDO switched to a warm phase after 1977. The CPUE trends by latitude and the *non-stationary* model, which outperformed all other models, support the hypothesis that North Pacific albacore distributions are locally influenced by changes in SST over large spatial scales (Figures 2 and 5), and that such effects have changed since 1986.

The local SST effects in the non-stationary model were approximately proportional to the effects of the spatial position, which indicates albacore response to SST is density independent. This apparent preference for SST can most likely be explained as albacore locally occupying areas with an optimal temperature. Childers *et al.* (2011) found that tagged albacore spent most of their time in water temperatures of ~17.5°C. In this study, the latitudinal–temporal pattern of albacore CPUE occurred in cells with temperatures >14°C (Figures 2 and 3). The average temperature albacore appear to occupy in the present study is more variable than that which Childers *et al.* (2011) found, but falls within the range (15–19.5°C) of temperatures that other studies have found (Clemens, 1961; Flittner, 1963; Laurs and Lynn, 1977). It is possible that some of the cells used to calculate SST, especially early and late in the season, were cooler, and albacore were captured further offshore (see Barr, 2009), and/or that the albacore were able to find their preferred temperatures within the averaged 1° cells. It is difficult to say why SST is important to albacore distribution. Most likely it is related to a physiological tolerance, rather than a secondary effect on prey distribution, because in the US west coast during summer we expect forage prey to be abundant in the colder upwelled coastal waters (Brodeur *et al.*, 2005), which are generally void of albacore.

Surprisingly, the PDO showed a negative trend region-wide, while the SST showed a positive relationship (Figure 5c). The negative trend found with PDO can be in part explained by the reduction of the southern peak in CPUE found in the spatially explicit model (Figure 4). Essentially, when the PDO or MEI are included as covariates they account for CPUE in the southern area. Because the PDO and MEI use the same values in every cell for a given year, they were unable to account for smaller-scale variability in the way that SST did. Phillips (2011) used a GAM similar to the *spatially variant* model, but made SST invariant and the PDO spatially variant. Although PDO is not spatially variant, it was found to have stronger negative relationships in southern core CPUE areas. The contrasting results of PDO/MEI and SST can also be reconciled by realizing that the two variables capture temperature effects at two different spatio-temporal scales. The PDO affects albacore CPUEs over an entire year and throughout the spatial domain, thus it is related to the stock productivity or availability in the sampled regions. Conversely, SST tracks changes in local distribution and is related to the

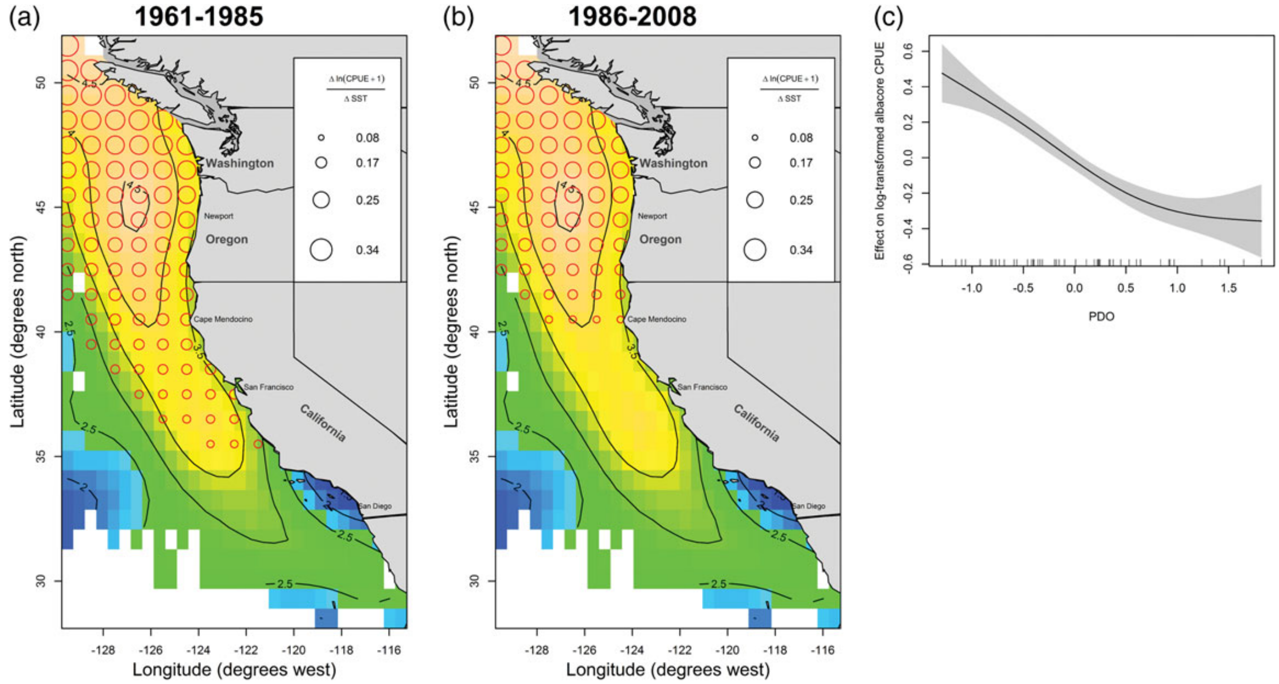

Figure 5. Partial effects of position (1961 – 2008) overlaid with local effects of sea surface temperature (SST) from 1961 – 1985, (b) SST from 1986 – 2008, and (c) Pacific Decadal Oscillation (PDO) on yearly averaged log-transformed albacore CPUE (1961 – 2008) estimated from the threshold spatially explicit variable coefficient generalized additive mixed model. For the positions, yellow indicates high predicted yearly CPUE rates and blue indicates low yearly CPUE rates. The contour line values correspond to predicted yearly log (CPUE + 1). Overlaid on the position plot are red bubbles, which indicate an expected increase in log-transformed albacore CPUE with a 1°C with local SST. Bubble size is scaled to the size of the effect and effects not significantly different from zero (95% C.I.) are excluded. Shaded areas on the PDO plots are 95% confidence intervals, and tick marks on the x-axis indicate sampling intensity.

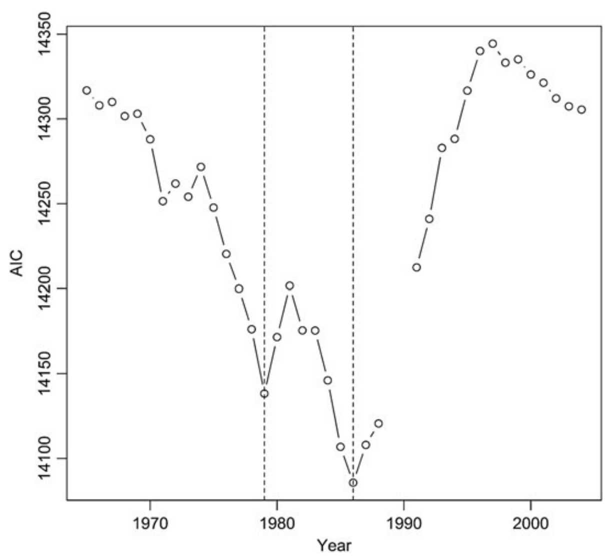

Figure 6. Akaike Information Criterion (AIC) profile in relation to different threshold values of each year for non-stationary models, based on the spatially variable effect of SST and the spatially homogeneous effect of PDO on albacore CPUE.

thermal preferences of albacore tuna. Other studies have found that North Pacific albacore rapidly respond to changes in local SST (e.g. Laurs and Lynn, 1977), but ours is the first to elucidate that juvenile North Pacific albacore are influenced by large-scale climate variability during summer residency off the west coast of North America. It is likely that physical processes acting on smaller scales than we examined (e.g. fronts, eddies, riverine plumes) may be important in regulating local distributions (Pearcy, 1971, Laurs *et al.*, 1984, Zainuddin *et al.*, 2006, 2008), and these features are likely to have indirect effects on albacore through aggregation of their prey resources (Fiedler and Bernard, 1987).

An unresolved issue is whether one or two core subpopulations of albacore are present, with a possible split about 40°N off the US west coast (Otsu and Uchida, 1963; Barr, 2009; Laurs and Powers, 2010). This study provides no conclusive evidence on albacore population structure. Visual inspections of the latitudinal–temporal plots show no obvious split in distribution at about 40°N, but rather in most years, the core concentrations of CPUE appear to follow SST (Figure 2). Andrade (2003) found a similar relationship between skipjack tuna CPUE and SST, in which the skipjack appeared to migrate north and south following preferred SST. When the yearly averages are mapped spatially (Figure 4), two core concentrations of high CPUE are apparent (Barr, 2009). However, when environmental variability is incorporated, it appears that albacore distributions shift north in response to changes in SST (Figure 5a and b). This pattern of change supports a one stock scenario, but cannot rule out the possibility that two substocks could be present. If two substocks are present, their spatial distribution or productivity (via recruitment) could be affected differentially by environmental variability.

Predictions made by the Intergovernmental Panel on Climate Change (IPCC) indicate that SST is expected to continue to increase

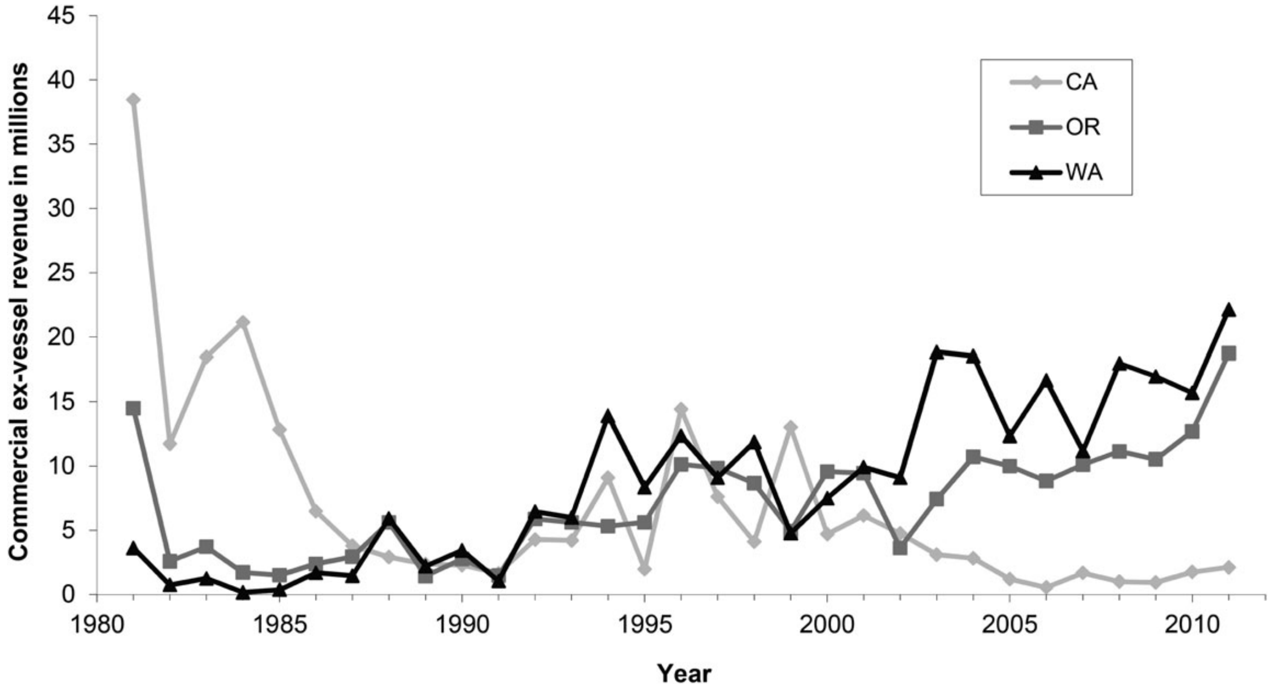

Figure 7. Real commercial ex-vessel revenues (2009 $USD) of the albacore surface hook-and-line (troll and baitboat) fishery in California, Oregon and Washington, 1981–2011. Yearly ex-vessel revenues were acquired from the 2012 Pacific Fishery Management Council report on the Status of the US West Coast fisheries for highly migratory species through 2011. Ex-vessel values were corrected for inflation, and include Canadian landings.

over the next century (IPCC, 2007). Climate change may result in a northern shift in distribution of juvenile North Pacific albacore, as indicated by this study. This scenario could have socio-ecological impacts on fishing communities because albacore can respond rapidly to changing SST. Several west coast fisheries, such as salmon, have closed or been restricted in the last decade (Berkeley *et al.*, 2004; PFMC, 2006), and this may have increased the fishery pressure on albacore as an alternative fishery. If SST continues to increase and albacore distributions continue to move north, they may have reduced availability for harvest unless the fisheries dependent upon them are able to shift at the same rate (Pinsky and Fogarty, 2012). For example, California ex-vessel revenue had declined from an average of 9.7 million USD/year in 1981–1994 to an average of 4.4 million USD/year in 1995–2009 (PFMC, 2006) (Figure 7). Additionally, the average ex-vessel revenue had been <2 million USD/year from 2005–2009. In contrast Oregon ex-vessel revenue had increased from 4 million USD/year in 1981–1994 to 8.6 million USD/year in 1995–2009. Washington also had ex-vessel revenue increases from 3.3 to 12.2 million USD/year during the same time-spans, but effort has increased in recent years because fish have become more available to smaller vessels with more limited range. Economic conditions (e.g. California cannery closures) probably influenced changes in revenue, but a changing marine climate may have also been a factor. Regardless of stock structure, this study implies that if ocean temperatures continue to increase, west coast communities reliant on commercial albacore fisheries are likely to be negatively affected in the southern areas but positively affected in the northern areas, where current albacore landings are highest.

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