DYNAMIC HABITAT USE OF ALBACORE AND THEIR PRIMARY PREY SPECIES IN THE CALIFORNIA CURRENT SYSTEM

BARBARA MUHLING, STEPHANIE BRODIE,
OWYN SNODGRASS, DESIREE TOMMASI

University of California, Santa Cruz
Institute for Marine Science
Santa Cruz, CA
ph: (858) 546-7197
Barbara.Muhling@noaa.gov

BARBARA MUHLING, OWYN SNODGRASS,
HEIDI DEWAR, DESIREE TOMMASI, JOHN CHILDERS
NOAA Southwest Fisheries Science Center
San Diego, CA

STEPHANIE BRODIE, MICHAEL JACOX
NOAA Southwest Fisheries Science Center
Monterey, CA

MICHAEL JACOX
NOAA Earth System Research Laboratory
Boulder, CO

CHRISTOPHER A. EDWARDS
Ocean Sciences Department
University of California, Santa Cruz, CA

YI XU
Department of Fisheries and Oceans
Delta, British Columbia, Canada

STEPHANIE SNYDER
Thomas More University,
Crestview Hills, KY

ABSTRACT

Juvenile north Pacific albacore (*Thunnus alalunga*) forage in the California Current System (CCS), supporting fisheries between Baja California and British Columbia. Within the CCS, their distribution, abundance, and foraging behaviors are strongly variable interannually. Here, we use catch logbook data and trawl survey records to investigate how juvenile albacore in the CCS use their oceanographic environment, and how their distributions overlap with the habitats of four key forage species. We show that northern anchovy (*Engraulis mordax*) and hake (*Merluccius productus*) habitat is associated with productive coastal waters found more inshore of core juvenile albacore habitat, whereas Pacific sardine (*Sardinops sagax*) and boreal clubhook squid (*Onychoteuthis borealijaponica*) habitat overlaps more consistently with that of albacore. Our results can improve understanding of how albacore movements relate to foraging strategies, and why prey-switching behavior occurs. This has relevance for the development of ecosystem models for the CCS, and for the eventual implementation of ecosystem-based fishery management.

INTRODUCTION

Ecosystem-based fishery management (EBFM) aims to account for environmental and ecosystem factors within fisheries assessment and management frameworks (Link 2017). This goal can be achieved through many possible approaches of varying complexity; including explicit consideration of processes such as climate variability and change, habitat quality, predator-prey relationships in models of species productivity, distribution, and trophic structure (Pikitch et al. 2004; Link 2017). Optimal management strategies may involve trade-offs, as managers balance a desire to maximize sustainable catch of target species while preserving ecosystem function, particularly for major forage species such as clupeiods, krill, and some cephalopods (Smith et al. 2011). Many of these forage species are fished commercially, but also support higher-order predators further up the food chain, such as other exploited species (e.g., tunas, billfish) and protected resources (e.g., marine mammals and seabirds) (Pikitch et al. 2004; Link and Browman 2014). Effectively managing marine ecosystems to preserve these trophic linkages, and improve robustness of management strategies to environmental variability, thus requires knowledge of food web structure.

Food webs of the California Current System (CCS) are comparatively well studied (e.g. Field et al. 2006; Kaplan et al. 2013; Rose et al. 2015; Koehn et al. 2016). However, it is not yet clear how the dynamic nature of the CCS in space and time impacts trophic structure and predator-prey relationships, which presents a challenge for building ecosystem models (Hunsicker et al. 2011). The diets of many large pelagic predators may vary both temporally and spatially, reflecting opportunistic feeding strategies. Some studies in the CCS have shown a near-exclusive reliance of pelagic predators such as tunas on one prey species, particularly coastal pelagic fishes such as anchovy (*Engraulis mordax*), while others show a much more diverse diet including crustaceans and cephalopods (Pinkas et al. 1971; Bernard et al. 1985; Glaser 2010). Existing studies have typically been snapshots, providing limited information on how predator-prey interactions vary at higher temporal and spatial scales. However, such variability has implications for how energy flows through the food web, as well as foraging costs and net energy gain in predators, some of which migrate long distances to reach the CCS (Childers et al. 2011; Fujioka et al. 2018). Prey-switching behavior in predators may be triggered by changes in dominant species in the ambient prey assemblage, or by active targeting of preferred or high-energy prey when these are more available (Begoña Santos et al. 2013). The importance of these behaviors to
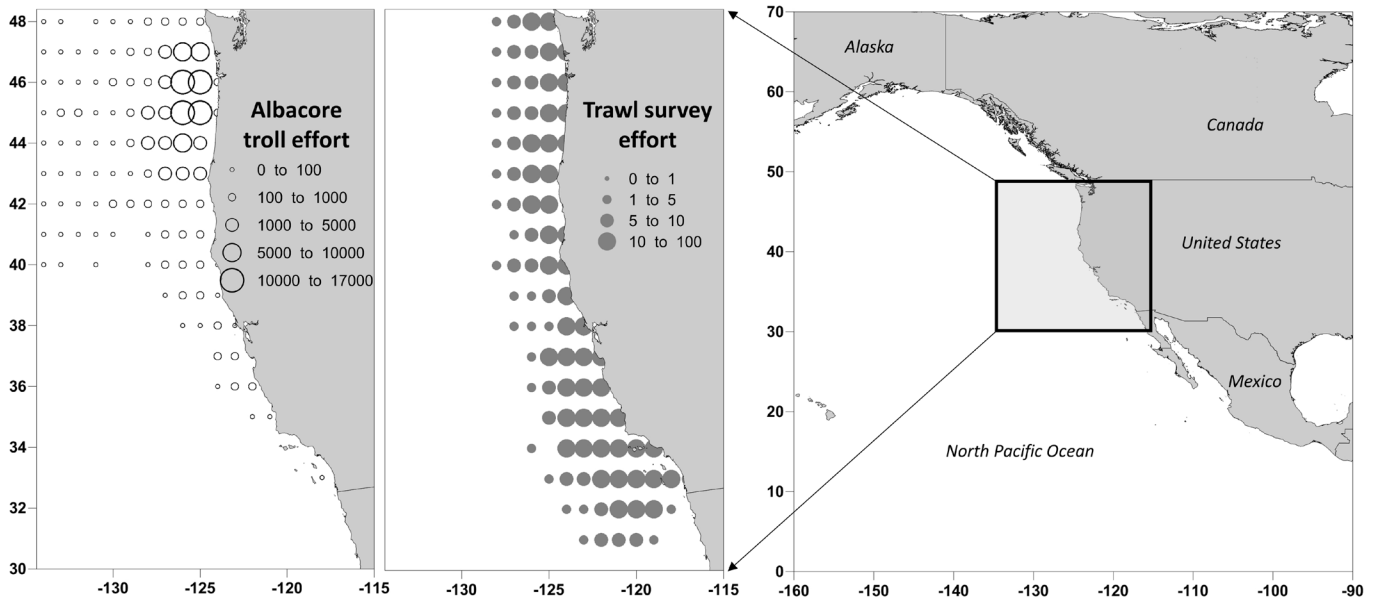
Figure 1. Map of the study area and ROMS domain. The total number of sets in the albacore surface fishery 2002–15 (left), and hauls in the NOAA SWFSC trawl surveys 2003–16 (right) are also shown. Locations with < 3 vessels reporting data for the troll fishery are not shown.

pelagic predators in the CCS is not yet well known. A first step to understanding foraging ecology is therefore to define the spatial and environmental niches occupied by interacting predator and prey species, and to assess how the degree of overlap between these varies in space and time.

Foraging behaviors in commercially important predators have implications for the fisheries that target them. Switching between shallow-living prey species and those that live deeper in the water column, or undertake diel vertical migrations, may impact the availability of predators to fishing gear. For example, commercial and recreational tuna fisheries in the CCS mostly use surface gear, which is largely deployed during daylight hours (Teo 2017; Runcie et al. 2018). Consequently, shifts in the vertical distribution of tuna in response to forage will impact gear vulnerability and catch. Improving understanding of spatiotemporal predator-prey relationships between commercially important species thus has the potential to benefit fishers, future management strategies in the CCS, and to contribute to the implementation of EBFM.

In this study, we used statistical species distribution models (SDMs) to predict the distribution of a top predator (albacore: *Thunnus alalunga*) and five key prey species (northern anchovy: *Engraulis mordax*; hake: *Merluccius productus*; boreal clubhook squid: *Onychoteuthis borealijaponica*; Pacific sardine: *Sardinops sagax*; and Pacific saury: (*Cololabis saira*) in the CCS. Environmental predictors were sourced from a high-resolution, data-assimilative CCS configuration of the Regional Ocean Modeling System (ROMS), allowing examination of the impor-

tance of subsurface water column structure in species distributions. We compared results between three contrasting years with different environmental conditions: a weak El Niño year (2004), a cool La Niña year (2012), and a very warm El Niño/marine heat wave year (2015). Overall, we aimed to provide a better understanding of how these species overlap in space and time, and how environmental variability impacts their distributions.

METHODS

Biological data sources

Albacore catch per unit effort (CPUE) was defined as the number of fish recorded per vessel-day in the US pole-and-line and troll fisheries. These were obtained from logbooks from US vessels submitted to the National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS). Data were available throughout the central and eastern North Pacific Ocean from 1961 through the end of 2015. However, we limited records used for SDM training to those contained within the ROMS domain (fig. 1, and see further description below), and within the time period covered by the MODIS Aqua and VIIRS ocean color missions (mid-2002 onwards). This ensured that at least two of the three ocean color satellites (Sea-WiFS, MODIS Aqua, VIIRS) were available to source surface chlorophyll for most of the sets, limiting observations lost to clouds. To account for varying degrees of accuracy in fishing locations reporting in the logbooks, we removed records where fishing latitude and longitude were both reported in whole degrees (n = 2,937),

assuming that these were approximate locations. Locations of all remaining records were then coarsened to show catch per vessel/day at 0.25° resolution, to align with expected accuracy in location reporting, and vessel movements while fishing (see Nieto et al. 2017). These filtering criteria resulted in 129,693 spatially explicit, daily data points for environmental data extraction.

A fishery-independent data set was also available to validate albacore habitat predictions. Since 2001, NMFS and the American Fishermens Research Foundation (AFRF) have collaborated to tag albacore in the CCS with archival tags (see Childers et al. 2011 and Snyder 2016 for more details). To date, 30 tags have been recovered; 22 between 2003 and 2008, and a further 8 from 2012 to the present. Location data for all recovered tags was processed using an unscented Kalman filter (Lam et al. 2008). 4,624 daily estimated tagged albacore locations were available within the ROMS domain, covering 11 years between 2003 and 2016. Although positional error from this type of tag can be substantial (>1 degrees), we extracted environmental variables at all daily archival tag locations in the same way as for the troll fishing locations. As a comparison, we also extracted environmental variables for the same dates as the tag locations, but at random locations throughout the ROMS domain ("pseudo-absences"). Random locations were generated using "spsample" in the "sp" package in R (Pebesma and Bivand 2005). Predicted habitat quality from the albacore SDM (see description below) was then compared between the tag locations, and the pseudo-absence locations. In addition, as tagged albacore were sometimes located in regions outside the main area of fishing operations, tag locations were added to maps of predicted albacore CPUE as a means of qualitative validation.

We used the Glaser (2010) comparative study of albacore diets to choose key prey species to model. The most important prey taxa were defined as those which had contributed >20% energetic contribution to diets in any region of the CCS, defined as north (>44°N), central (34°–44°N), and south (<34°N), in any of the four studies examined covering years 1949–2006. These criteria resulted in the selection of northern anchovy, Pacific saury, hake, and cephalopods for further analysis. We also included sardine, which is a key CCS forage species that showed moderate energetic contribution (15.3%) to albacore diets in the southern CCS in 2005–06, but was of surprisingly little importance in the other feeding studies. We narrowed the cephalopod group further by examining the results of the two studies that found them to be of greatest importance: Pinkas et al. (1971), and Glaser et al. (2015). Both studies showed that boreal clubhook squid (clubhook squid hereafter) contributed the most to albacore diets, in terms of % energetic contribution. We there-

fore proceeded with anchovy, saury, hake, sardine, and clubhook squid as the five prey species for which to construct SDMs.

Occurrence records for prey species were obtained from trawl surveys conducted by the NOAA Southwest Fisheries Science Center (SWFSC), with 1,486 hauls completed between 2003 and 2016. Sampling effort was primarily concentrated in spring (April: 460 hauls) and summer (July–August: 691 hauls), but some samples were also available from other months between March and October. The trawl net was towed near the surface at night, at a target speed of 3.5–4.0 knots. The net was fitted with an 8 mm mesh liner in the codend (more details are contained in Zwolinski and Demer 2012; Zwolinski et al. 2012, and Weber et al. 2018). Sampling was concentrated on the continental shelf and slope.

Environmental variables

Environmental predictors for the SDMs were sourced from a data assimilative CCS configuration of ROMS, with 42 terrain-following vertical levels, and a domain covering 30°–48°N, inshore of 134°W at 0.1° horizontal resolution (http://oceanmodeling.ucsc.edu/ccsnrt version 2016a; Veneziani et al. 2009; Neveu et al. 2016). The temporal scale of the biological data covered two ROMS iterations; a historical reanalysis (1980–2010; Neveu et al. 2016) and a near real-time product (2011–present). Environmental variables used in the SDMs were limited to those that were consistent across the reanalysis products (Becker et al. 2018; Brodie et al. 2018).

The predictors extracted from the data assimilative CCS model for use in the SDMs were similar to those used previously to model distributions of large pelagic fishes and mammals in the CCS (Scales et al. 2017; Becker et al. 2018; Brodie et al. 2018) (table 1). Variables included sea surface temperature (SST), measures of mesoscale oceanographic features (sea surface height, eddy kinetic energy), and measures of current flow and wind stress (northward and eastward wind stress and current velocities, wind stress curl). These were extracted as 0.3 by 0.3 degree means for albacore fishing locations, and at 0.1 degree native resolution for trawl sampling locations, to best align with the spatial resolution of the biological data. The exception was wind stress curl, which was extracted at 0.5 degree resolution for all data sets, to account for the coarser resolution of wind forcing used to force the historical reanalysis. In addition to the surface-associated predictors, we included two indicators of subsurface water column structure, as Brodie et al. (2018) found them to be useful predictors of the distribution of other large pelagic fishes. These were isothermal layer depth, and bulk buoyancy frequency, which represents stratification and stability in the upper water column. Isothermal

TABLE 1
Environmental variables used as predictors in SDMs for all species. "st.dev" denotes standard deviation.

Variable Name	Measured Unit	Source
Sea surface temperature	°C	ROMS
Sea surface temperature st.dev.	°C	Derived from ROMS
Sea surface height	m	ROMS
Sea surface height st.dev.	m	Derived from ROMS
Surface eastward current velocity	m/s	ROMS
Surface eastward wind stress	N/m^2	ROMS
Surface northward current velocity	m/s	ROMS
Surface northward wind stress	N/m^2	ROMS
Wind stress curl	N/m^3	ROMS
Eddy kinetic energy (log)	m^2/s^2	Derived from ROMS
Isothermal layer depth	m	Derived from ROMS
Bulk buoyancy frequency	/s	Derived from ROMS
Surface chlorophyll (4th root)	mg/m^3	SeaWiFS, MODIS Aqua, VIIRS
Moon phase	%	"lunar" R package

layer depth was calculated as the depth at which temperature deviates by 0.5°C relative to the surface, while bulk buoyancy frequency was calculated as the mean buoyancy frequency in the upper 200 m of the water column (or to the bottom in shallower water). The spatial standard deviation of both sea surface temperature and sea surface height at 0.7 degree resolution were also included as predictors, to highlight areas of high variability such as frontal zones (Hazen et al. 2018). The percent of the moon illuminated on the troll fishing or trawl sampling date was also included as a predictor, as some prey and predators have been shown to alter their vertical distributions depending on moon phase (e.g., Sepulveda et al. 2010; Drazen et al. 2011).

Surface chlorophyll concentration was extracted from the SeaWiFS (1997–2010), MODIS Aqua (2002–16), and VIIRS (2012–16) sensors, using the SWFSC Environmental Research Division's ERDDAP server. Chlorophyll was extracted at 0.25 degree spatial resolution for albacore fishing, tagged albacore, and trawl survey locations, from 8-day composites, to minimize the number of observations lost to cloud cover. Where more than one chlorophyll product was available (64.8% of troll locations, and 77.6% of trawl locations), a mean between the two was taken. Troll locations with no chlorophyll information due to clouds were removed, leaving a total of 111,984 points for SDM training. Similarly, removing daily archival tag positions with no chlorophyll information left 3,695 locations for model validation. The trawl survey data set was much smaller than the fishery-dependent logbook data set, and so to preserve as much data as possible, monthly chlorophyll was used at sampling locations with no 8-day chlorophyll available. This impacted 65 observations, or 4.4% of the data set. A comparison of 8-day and monthly chlorophyll at the remaining 1421 stations showed them to be closely correlated (r = 0.83), and so this substitution likely did not impact the results substantially.

Eddy kinetic energy and surface chlorophyll were strongly right-skewed, and so as a result were $\log_e$ and 4th root transformed, respectively, before further analysis. Cross-correlation matrices were then used to identify any collinear predictors, across all biological locations for which environmental data were extracted. Sea surface temperature was moderately and positively correlated with bulk buoyancy frequency (r = 0.70). However, leaving both variables in the SDMs resulted in stronger models for all species (determined by comparisons of R^2 for the albacore SDM and area under the receiver operating curve (AUC) for the prey species SDMs), and so we elected to keep both in the suite of predictors. All other correlations among variables were < r = 0.6.

Forage fish species may show dramatic fluctuations in stock biomass over short periods of time, and may also restrict their migration patterns at low population sizes (MacCall 1990; Demer et al. 2012; Zwolinski et al. 2012). As a result, theoretically suitable environmental habitat may be unoccupied when stocks are at low levels, impacting the probability of occurrence in trawl surveys, and potentially model performance (Weber et al. 2018). To account for these interactions, we included annual biomass indicators in the hake, sardine, and anchovy SDMs, as additional predictors. Estimates of hake biomass (in metric tons) were sourced directly from the stock assessment (Edwards et al. 2018). Recent estimates of sardine spawning biomass were also sourced from the most recent stock assessment, however this assessment model only includes output for 2006 through 2016 (Hill et al. 2018). Values for years prior to 2006 were sourced from a prior stock assessment, and should be considered more uncertain (Hill et al. 2014). As there is no current stock assessment for anchovy, we followed Zwolinski and Demer (2012) by estimating biomass from three-year running mean larval abundances from CalCOFI surveys. We calculated these by averaging larvae per m^2 across stations which were sampled between January and

June using standard oblique bongo net tows. We only included "core" sampling stations between 30°–40°N, east of 130°W, which were sampled in at least 15 of the 20 years between 1997–2016. We note that CalCOFI larval abundance indices are most applicable to the central anchovy stock, and that the sardine stock assessment covers only the northern sardine stock. However, trawl surveys likely capture anchovy and sardine from other subpopulations (particularly the more northern anchovy stock) at certain times of year. Saury larvae and clubhook squid paralarvae are only rarely recorded in CalCOFI surveys, and so no biomass indicators were included in the SDMs for these two species.

Similarly, the overall abundance of juvenile albacore in the CCS each year could theoretically be influenced by stock-wide recruitment strength several years earlier. We therefore included annual recruitment estimates from the North Pacific albacore stock assessment in the albacore SDM (ISC 2017). As the majority of albacore caught by the surface fleet are 2–3 years old, we used recruitment estimates from 2 and 3 years prior as two separate predictor variables. As North Pacific albacore recruitment is strongly variable from year to year, these two recruitment time series were not strongly correlated (r = 0.19), and so both were included in the SDM.

SDMs

SDMs were built and visualized using boosted regression trees (BRTs) in the "dismo" and "gbm" packages for R Version 3.3.2 (Elith et al. 2008; Ridgeway 2017). The BRT for albacore CPUE was constructed using a Gaussian distribution, with CPUE values transformed using $\log_{10}(x+1)$ beforehand to reduce skewness. The BRTs predicting the probability of presence for the five prey species were built using a Bernoulli distribution. The optimum tree complexity and learning rate for each SDM, to maximize skill and minimize overfitting, was determined largely following the guidelines in Elith et al. (2008). BRTs were built using 50% of the available training data, selected randomly, and then scored on the remaining 50% of the data. The configuration with the lowest error on the unseen validation data set, and which also resulted in a model with at least 2,000 trees, was assumed to be the best. This exercise resulted in a tree complexity value of 7 for the albacore SDM, and 5 for each of the prey species, with a learning rate of 0.1 for the albacore SDM, 0.0008 for the anchovy SDM, 0.0006 for the hake SDM, 0.00005 for the saury SDM, and 0.0002 for the sardine and clubhook squid SDMs, with a bag fraction of 0.6 in all cases. Overall model skill was determined using R^2 between predicted and observed values for the albacore CPUE SDM, and AUC for the prey species presence/absence SDMs. These skill metrics were calculated using only the validation data

not used for building the models. The relative influence of each predictor in the model is scored out of 100 based on the number of times each variable is used for tree splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees (Elith et al. 2008).

SDMs were visualized using one- and two-dimensional partial plots. The marginal effect of each predictor in each SDM was shown by plotting observed and predicted abundance (for albacore) or occurrence (for prey species) against binned environmental variables, integrated across all other predictors. Additionally, two-dimensional partial relationships were visualized using plot.gbm in the "gbm" package, which shows the predicted marginal effects of two predictors simultaneously.

Initial tests of the albacore SDM showed that the model did not resolve the lower temperature limit of favorable habitat in a biologically reasonable way, with surface temperatures of <9°C predicted to be suitable. These predictions are contrary to current knowledge on the physiology of albacore, and were caused by there being very few troll sets completed in cold waters. This bias is a common issue with building SDMs using fishery-dependent data, as fishers rarely fish in strongly unsuitable habitat (Jones et al. 2012). We thus followed Muhling et al. (2017) by adding 54 "dummy" zero catch locations to the data set, located at whole degree locations from 43°–48°N, and 134°–126°W, in January and February, for each year from 2003–15. Albacore have never been recorded in this region in January and February by commercial or recreational fishers, or by archival tag locations, and we therefore assumed that these locations represented strongly unfavorable habitat. A total of 984 of these dummy locations had all environmental variables available (including chlorophyll), and were added to the 111,988 true catch records, giving 112,972 total points. The addition of this relatively small number of dummy locations forced a more biologically realistic lower temperature limit in the SDM, with negligible effect on predictions at surface temperatures >10°C. However, this should be noted as a source of uncertainty in the albacore SDM.

RESULTS

Bulk buoyancy frequency was the most important variable in the albacore CPUE SDM, with a score of 17.57 (table 2). Sea surface temperature (11.70) and surface chlorophyll (10.90) were also influential to the model. Notably, recruitment strength 2 and 3 years prior were not particularly important to the albacore SDM, ranking 14th and 16th, respectively, out of the 16 total predictors. The coefficient of determination (R^2) between observed and predicted CPUE in the unseen validation portion of the data set was 0.31.

TABLE 2
Predictor variable importance to all 5 SDMs. The top three most important variables for each SDM are shaded in gray.

| Variable Name	Albacore	Anchovy	Hake	Sardine	Clubhook
Sea surface temperature	11.70	6.98	4.92	14.04	10.46
Sea surface temperature st.dev.	5.06	6.97	6.53	6.73	6.56
Sea surface height	6.00	6.23	10.53	6.19	5.92
Sea surface height st.dev.	4.62	3.59	7.46	3.45	5.56
Surface eastward current velocity	3.85	3.31	5.60	4.09	2.28
Surface eastward wind stress	4.86	4.03	3.42	6.31	7.60
Surface northward current velocity	4.17	6.66	3.16	4.95	3.24
Surface northward wind stress	4.78	15.82	3.70	5.1	9.4
Wind stress curl	4.81	2.72	4.31	5.86	7.29
Eddy kinetic energy (log)	3.73	7.27	4.37	5.37	3.64
Isothermal layer depth	6.34	9.52	9.03	3.41	10.65
Bulk buoyancy frequency	17.57	5.74	10.03	8.27	8.34
Surface chlorophyll (4th root)	10.90	12.51	17.89	10.41	6.58
Moon phase	4.83	5.01	6.86	4.78	11.44
Albacore recruits 2 years ago	3.83	—	—	—	—
Albacore recruits 3 years ago	2.93	—	—	—	—
Anchovy SSB index	—	3.64	—	—	—
Hake SSB index	—	—	2.2	—	—
Sardine SSB index	—	—	—	11.03	—
SDM AUC or R^2	$R^2 = 0.31$	AUC = 0.82	AUC = 0.79	AUC = 0.78	AUC = 0.71
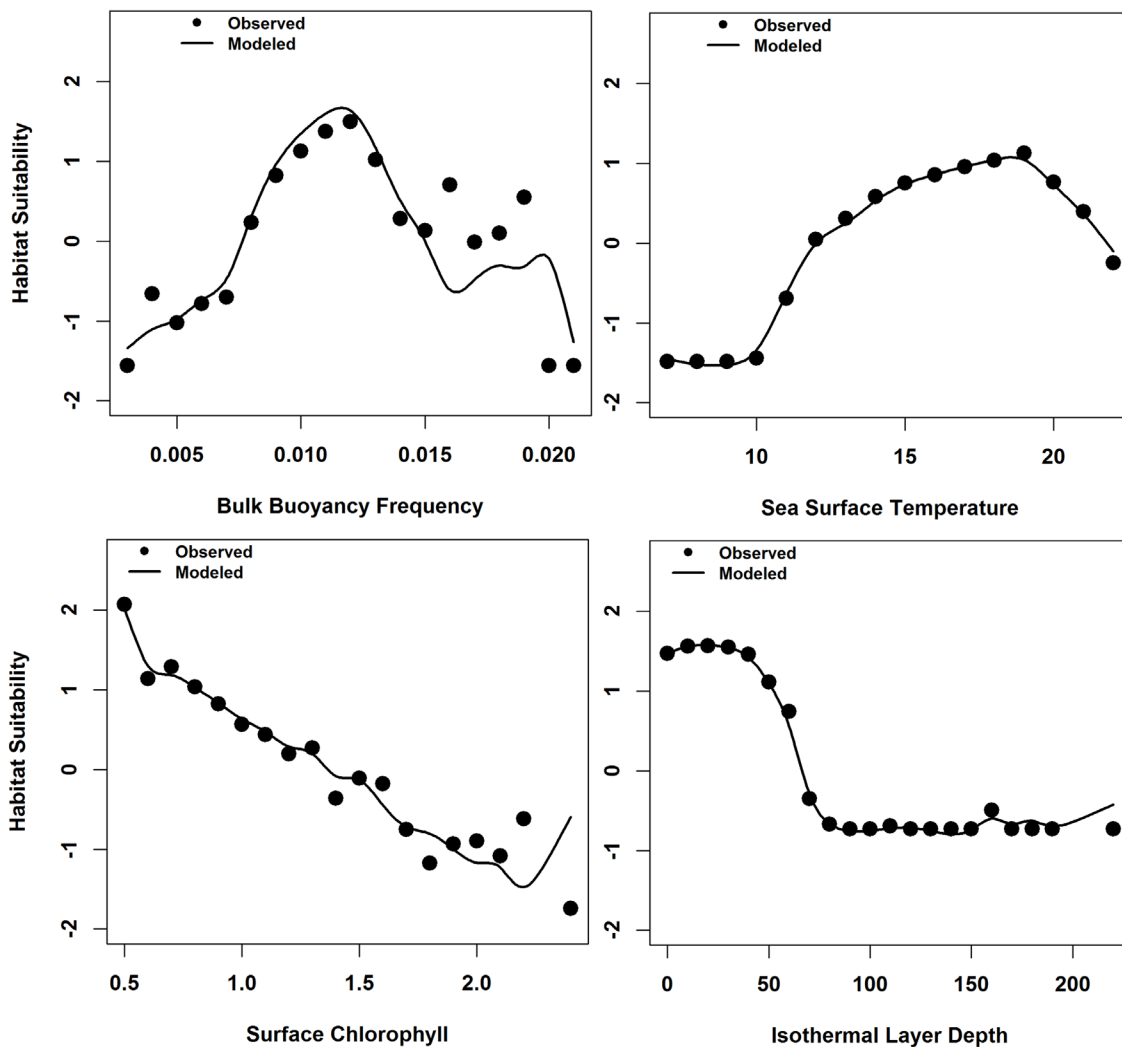
Figure 2.   Partial response curves from binned observations and the SDM for albacore, for the four most influential predictors in the model.
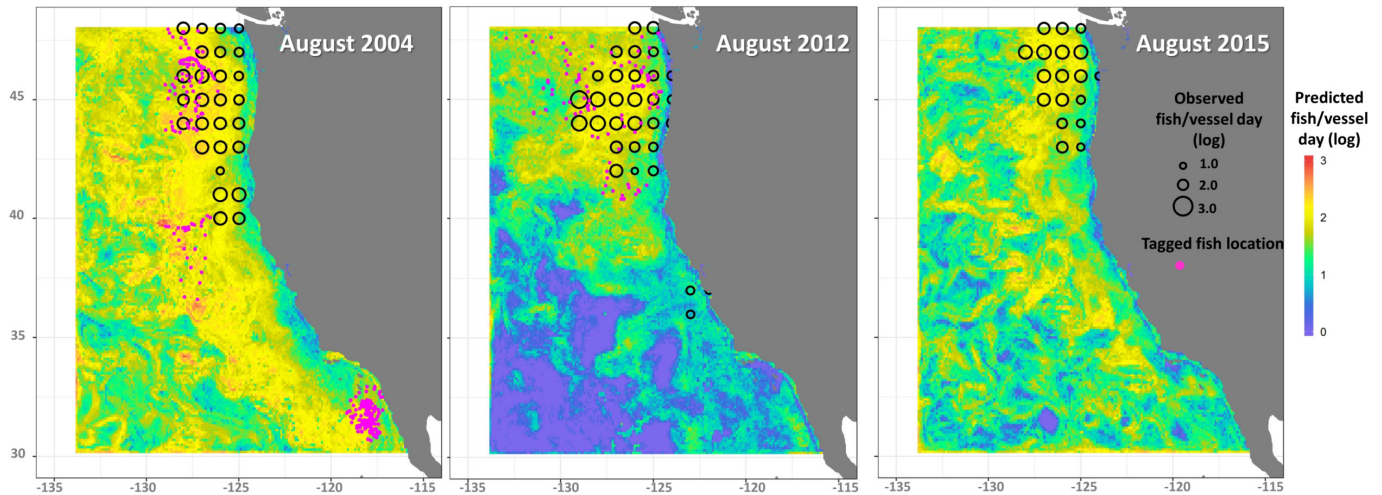
Figure 3. Predicted catch per unit effort (log CPUE) in fish/vessel/day in the albacore surface fishery during August for three example years: 2004, 2012 and 2015. Monthly means of the daily ROMS outputs are shown. Observed CPUE is shown in the black circles, with daily locations from albacore tagged with archival tags shown in pink, for the same month and year as the SDM predictions.

Partial plots suggested that albacore CPUE was generally highest at moderate values of bulk buoyancy frequency (~0.012 /s) and surface temperature (~15°–20°C), and at lower values of surface chlorophyll and isothermal layer depth (fig. 2).

Predictions from the albacore SDM for 2004, 2012, and 2015 during the month of August (around the typical peak of the fishing season) showed some variability in habitat extent among years (fig. 3). In August 2004, predicted suitable habitat was located throughout the latitudinal extent of the study region, between Baja California in the south (30°N), and the US–Canada border in the north (48°N). In contrast, August 2012 had lower predictions of albacore habitat south of ~40°N, with August 2015 showing an intermediate situation. There was little fishing effort south of 40°N in all three years, making it difficult to validate the interannual variability in predictions; however some albacore tagged with archival tags were located off Baja California in August 2004, suggesting that there may have been some favorable habitat present during this year (fig. 3). In all years, the extreme inshore region close to the coast was predicted to be less favorable for albacore, as was the offshore, southwestern portion of the study area (south of 37°N, west of 123°W).

Predicted albacore CPUE was higher at the daily archival tag locations than it was at the random pseudo-absence locations in the winter and summer, but differences were minimal during spring and fall (fig. 4). Overall habitat suitability was highest during summer and lowest during winter at points throughout the ROMS model domain. However, predictions were markedly higher at the true tag locations. This result suggests that even though there is large uncertainty in

location estimates of tagged fish, making migrating versus foraging behavior difficult to distinguish, tagged fish were preferentially located in habitat predicted to be more suitable by the SDM.

The anchovy SDMs performed strongly on the unseen validation data (AUC = 0.82), while the hake, sardine, and clubhook squid AUCs were good to fair (0.79, 0.78, and 0.71, respectively) (Pearce and Ferrier 2000; Weber and McClatchie 2010). The saury SDM AUC (0.69) indicated the weakest model of the five. This result was likely due to the low proportion of positive occurrences of saury in the trawl data (45/1373 stations), which limited the power of the SDM for this species. As spatial predictions from the saury SDM were also patchy, and biologically implausible, this model was not considered further.

SDMs for the remaining four prey species were strongly influenced by surface chlorophyll (table 2). Surface temperature was the most important variable in the sardine SDM, and also influential in the clubhook squid SDM, where it ranked 3rd of 14 predictors. The sardine biomass index was strongly important to the sardine SDM, suggesting that sardine were more likely to be present when overall biomass was higher. In contrast, the anchovy biomass index was much less influential to the anchovy SDM (ranking 12th out of 15 predictors), and the hake biomass index was the least important of all predictors in the hake SDM.

Partial plots for the three strongest predictors in each of the prey SDMs showed that hake and anchovy were associated with moderate to high surface chlorophyll concentrations, while sardine were associated with moderate to low chlorophyll areas (fig. 5). Anchovy were also most likely to be present at weak (near-zero) north-
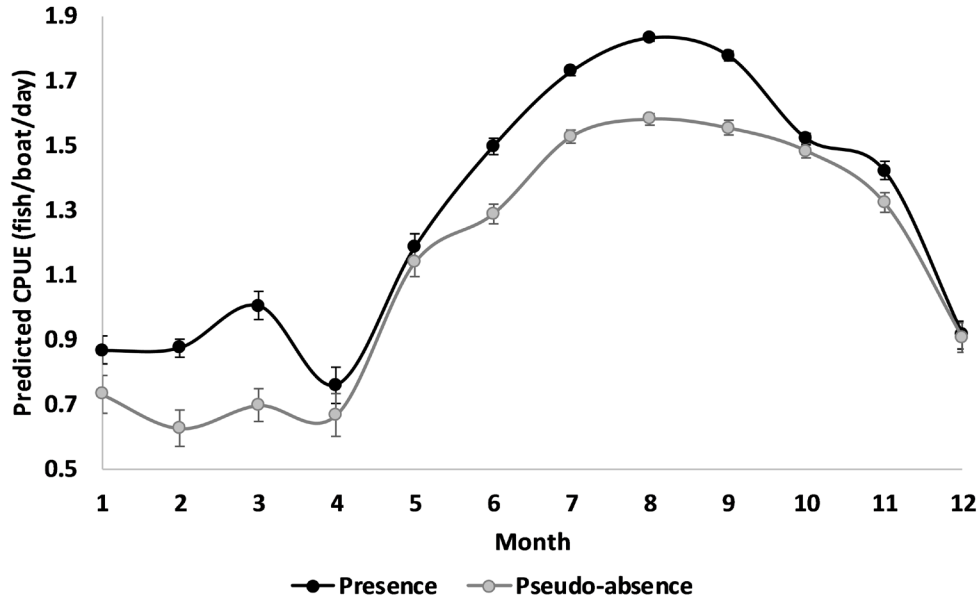
Figure 4.   Predicted catch per unit effort (log CPUE) from the albacore SDM at 3,695 daily locations of tagged albacore in the ROMS domain by month, between 2003 and 2016. Predicted CPUE at 3,695 random locations in the ROMS domain sampled on the same dates as the tag locations are also shown. Error bars denote standard errors.
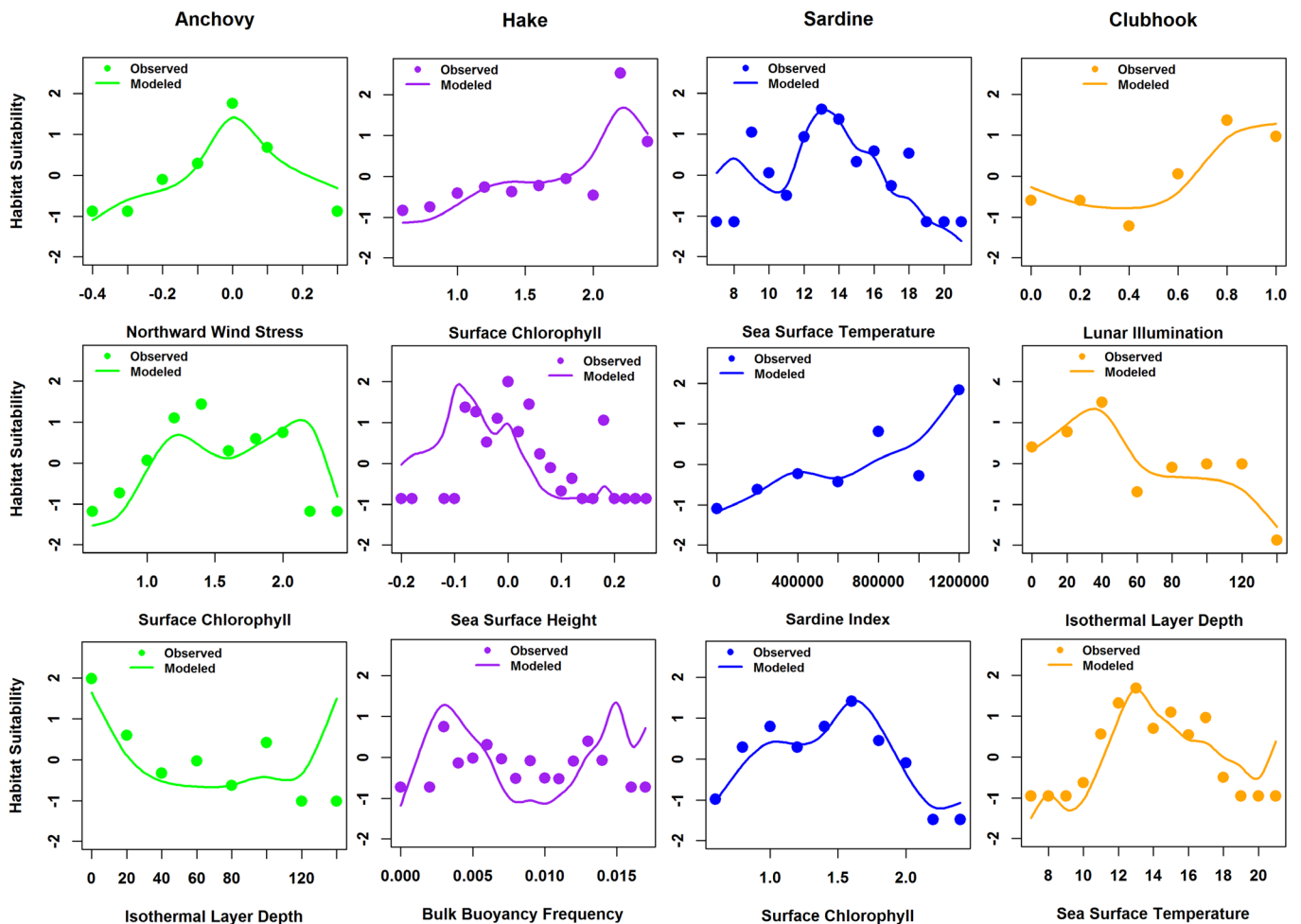

Figure 5.   Partial response curves from binned observations and the SDM for four prey species, for the three most influential predictors in each model.
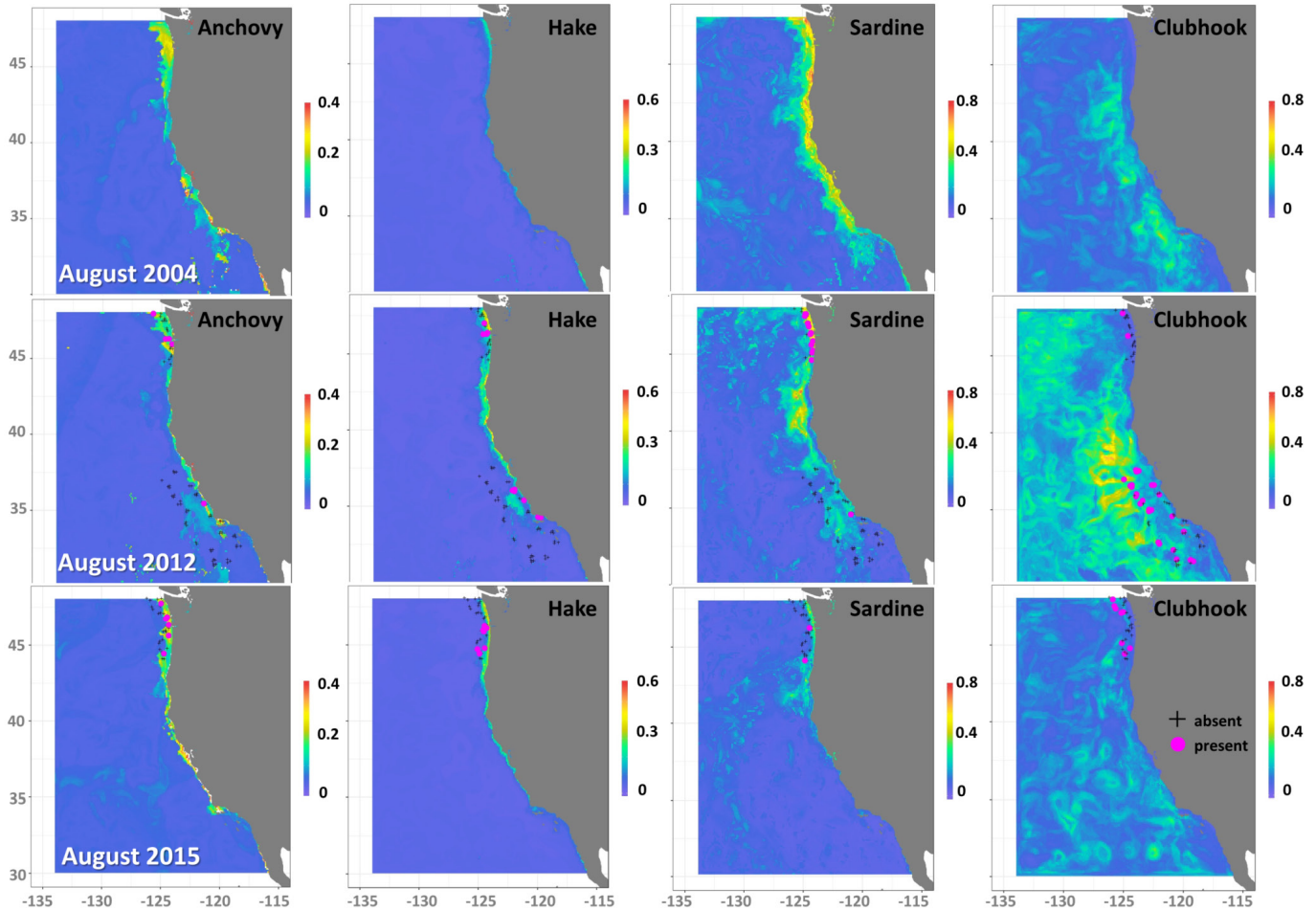
Figure 6.   Predicted probability of occurrence (/1) of four prey species in the SWFSC trawl surveys during August for three example years: 2004, 2012 and 2015. Monthly means of the daily ROMS outputs are shown. Observed positive catch locations are shown in pink, with observed negative catch locations shown in black crosses, for the same month and year as the SDM predictions.

ward wind stress. Sardine were most likely to be present at moderate (~10°–17°C) sea surface temperatures, and during times of higher overall biomass. Clubhook squid were more commonly present in trawl surveys near to the full moon, at moderate to low isothermal layer depths, and moderate sea surface temperatures (~11°–18°C) (fig. 5).

Predictions of suitable habitat for the four prey species in August 2004, 2012, and 2015 highlighted the strong association of anchovy and hake with near-coastal environments (fig. 6). In contrast, sardine were associated with both inshore and continental shelf environments, while clubhook squid were associated with continental shelf and offshore mesoscale features. Favorable habitat for hake appeared to extend further south in 2012, but it was difficult to validate predictions with so few survey data available. During the "blob" marine heat wave in 2015, anchovy and hake habitat was not predicted to be strongly different from the other two years examined. However, conditions appeared less favorable over-

all for clubhook squid (fig. 6). The probability of sardine occurrence was also predicted to be low, likely driven by the low biomass of sardine during 2015, and the high importance of the sardine biomass index to the SDM for this species.

Previous studies have shown that anchovy and hake can be important to the diets of albacore. However, predictions from the SDMs (fig. 3, fig. 6) suggested somewhat minimal spatial overlap of these species with albacore. Two-dimensional representations of SDMs, showing partial relationships with surface chlorophyll and sea surface temperature averaged across all other predictors, also highlighted this separation in environmental space (fig. 7). Although surface chlorophyll and sea surface temperature were moderately to strongly important to the SDMs for albacore, anchovy, hake, sardine, and clubhook squid (table 2), the partial relationships were quite different. While albacore CPUE was predicted to be highest at low surface chlorophyll and moderate sea surface temperatures, anchovy and hake were most likely
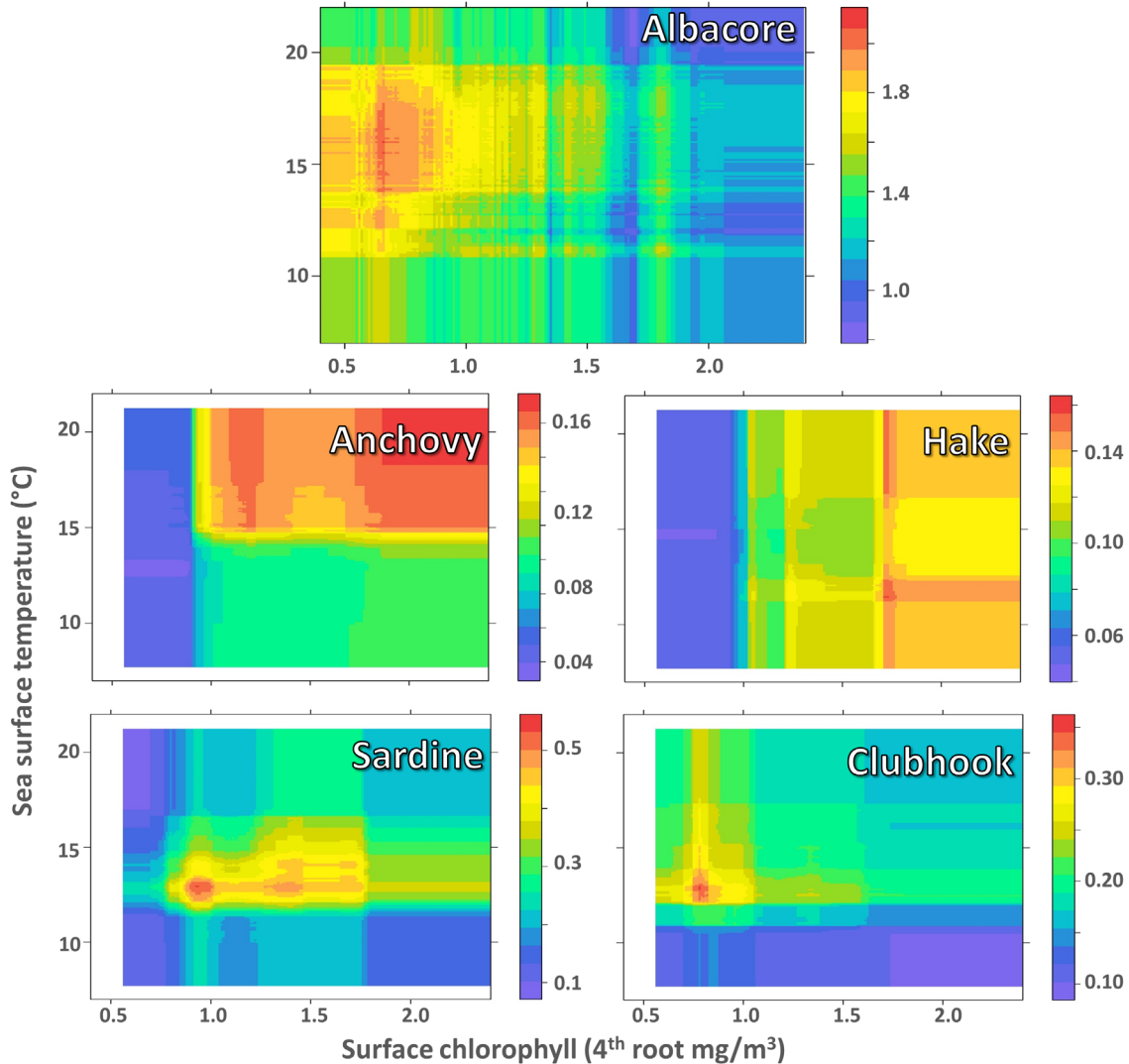
Figure 7.   Two-dimensional representations of SDMs for albacore, anchovy, hake, sardine, and clubhook squid, showing the marginal effects of sea surface temperature (°C), and surface chlorophyll (4th root transformed). Colors show predicted CPUE in catch/vessel/day (albacore), or probability of occurrence /1 (anchovy, hake, sardine, clubhook squid)

to be collected where surface chlorophyll was higher, characteristic of the productive inshore waters in which they were most abundant. In contrast, sardine and clubhook squid occupied similar environmental space to albacore, reflecting the occupation of the continental shelf and slope waters by both species.

DISCUSSION

Results from the albacore SDM are generally consistent with the findings of previous habitat modeling studies that used satellite variables as predictors (e.g., Nieto et al. 2017; Xu et al. 2017). Our model outputs showed that the highest catch rates for this species were located in the transitional area offshore of the coastal upwelling zone. However, the use of data assimilative CCS ocean model output provided the advantages of relatively long,

gap-free environmental time series, and the availability of variables describing subsurface water column structure. Two of the four most influential variables in the albacore SDM were subsurface variables not available from satellite sensors: bulk buoyancy frequency and isothermal layer depth. Albacore CPUE was highest at moderate values of bulk buoyancy frequency. This variable is a measure of water column stability, with higher values indicating a more stable, stratified water column, and low values indicating highly mixed, less stable waters typical of recent upwelling (Brodie et al. 2018). In practice, habitats with moderate BBV were those located just offshore of the upwelling zone, and may provide access to a transition zone between upwelled waters richer in prey, and more stable waters offshore where fish can recover from vertical movements (Snyder et al. 2017).

Isothermal layer depth approximates the thickness of the mixed layer, below which temperature and oxygen decline sharply. Albacore CPUE was higher at shallower isothermal layer depths less than around 70 m. These conditions were mostly found in the warmer summer months, when albacore are most abundant in the CCS, and particularly off Oregon and Washington. Shallower isothermal layer depths may concentrate prey nearer to the surface, providing favorable feeding conditions for albacore, but may also concentrate albacore themselves in the upper water column, where they are more vulnerable to surface fishing gear.

Albacore CPUE was also higher at lower values of surface chlorophyll, suggesting avoidance of both colder nearshore upwelled waters, and mesoscale features moving new productivity offshore. Predictions from the SDM trained on fishery-dependent data were consistent with fishery-independent observations of tagged albacore, providing a rare opportunity to validate a distribution model with independent data. Tagged fish occupied habitat that was markedly more favorable than random during summer, the season when they are relatively resident in the CCS (Childers et al. 2011). During spring and fall, when many albacore are migrating between the CCS and the open North Pacific, they were located in habitat not much more favorable than random, likely reflecting rapid movements between seasonal foraging areas (Childers et al. 2011; Snyder 2016).

Bulk buoyancy frequency and isothermal layer depth from the ocean model were also shown to be useful for predicting swordfish (*Xiphias gladius*) habitat in the CCS in a previous study (Brodie et al. 2018). However, swordfish spend much more time at depth than albacore, particularly during the day (Sepulveda et al. 2010; Childers et al. 2011). As a result, close relationships between their occurrence and the subsurface environment may be expected. Results from the current study suggest that dynamic subsurface predictors can also be useful for modeling distribution of more epi-pelagic species such as albacore, providing a useful complement to the more widely used surface environmental variables.

Observed catch rates of albacore from the troll fishery were concentrated in the northern CCS during our study time period, just offshore of Oregon and Washington. Although our results may be partially confounded by factors such as cannery closures in southern California in the 1980s, the northern CCS also had consistently favorable spring–summer albacore habitat, as predicted by the SDM. In contrast, predicted habitat suitability off California and Baja California appeared to be more ephemeral, being highly favorable in August 2004, but much less so in 2012 and 2015. Albacore catches off southern California are strongly variable interannually, and have been so for at least the past 100 years (Clemens and

Craig 1965; Childers et al. 2011). Although larger-scale migration patterns (Childers et al. 2011; Snyder 2016) and potentially stock structure (Laurs and Lynn 1977) likely influence the availability of albacore off southern California, results from the present study suggest that habitat suitability in the southern CCS may also contribute to interannual variability in north-south catch distributions. Despite relatively high variability in recruitment in the years since 2002 (ISC 2017), we found no strong influence of year class strength on CPUE in the CCS. This apparent lack of influence of recruitment suggests that regional-scale environmental conditions may be more influential for determining catch rates, but additional examination of migration and movement patterns is likely needed to confirm this.

The 2013–16 northeast Pacific marine heat wave (including the "blob" and the 2015–16 El Niño event) resulted in much warmer waters than usual in the study region, with lower primary productivity except for within a narrow band of strong upwelling near the coast (Jacox et al. 2016; Zaba and Rudnick 2016). In August 2015, most of the CCS was at least 1°C warmer than usual, with positive temperature anomalies of >2°C off California (Gentemann et al. 2017). In contrast, summer 2012 was cooler than average in the CCS after several La Niña years, while 2004 temperatures were slightly above normal (Goericke et al. 2005; Bjorkstedt et al. 2012; Runcie et al. 2018). Anomalously warm conditions in 2015 did not result in a marked northward shift in predicted albacore habitat within the ROMS model domain. Predictions from the SDM suggested that suitable habitat was available from northern Baja California to the northern limit of the study area (48°N) during this year. However, albacore are known to extend their range northwards as far as southeast Alaska during warm years, as was observed in 2005 and in 2015 (Cavole et al. 2016; Christian and Holmes 2016). Although temperature is known to be an important determinant of albacore habitat in the North Pacific (Snyder 2016; Nieto et al. 2017; Xu et al. 2017), the ocean circulation model domain covered a relatively small portion of their geographic range, which is usually within tolerable limits from spring through fall. The study domain would therefore need to be extended northwards to best capture changes in habitat and range extensions for albacore resulting from marine heat waves and future warming. This may also be the case for the four prey species, which are also found well outside the ROMS domain (Lluch-Belda et al. 1991; Bigelow 1994; Gustafson et al. 2000).

A somewhat unexpected result of the study was the general lack of spatial overlap between albacore and some of their main prey species, particularly anchovy and hake. While albacore catch was low in highly productive coastal waters, anchovy and hake showed a strong

affinity for these areas, while sardine were most common on the continental shelf. These results are consistent with previous work on the distribution of these species (Zwolinski et al. 2012; Weber et al. 2018). Some historical diet studies conducted when anchovy biomass was high show a near-exclusive reliance of albacore on anchovy in some parts of the CCS (Glaser 2010). The spatial separation between albacore's preferred habitat and that of their prey suggests that albacore may need to move back and forth across the front separating productive coastal waters from offshore waters to feed on anchovy. Studies of tagged albacore have shown that they can employ precisely this behavior when conditions are favorable (Fiedler and Bernard 1987; Snyder et al. 2017), and that these movement patterns are likely to confer physiological advantages (Kirby et al. 2000). These observations may explain why catch rates of albacore can be higher near thermal fronts and Lagrangian coherent structures (Nieto et al. 2017; Xu et al. 2017; Watson et al. 2018). We included spatial standard deviation of sea surface temperature as an indicator of frontal activity in the SDMs, but although this variable was moderately influential to the albacore model (ranked 6th of 16), the partial relationship was negative (result not shown). However, Nieto et al. (2017) and Xu et al. (2017) show that the distance of fishing activity from thermal fronts, and the distance of the front from the coast, may be better predictors of CPUE than temperature gradient metrics, such as those used in this study. Studies on albacore (Watson et al. 2018) and other large pelagic predators (Abrahms et al. 2018; Scales et al. 2018) suggest that Lagrangian Coherent Structures, identified from surface velocity fields using finite-time or finite-size Lyapunov exponents (FTLE, FSLE), may act as hotspots of distribution and foraging activity. Further studies of how albacore forage across fronts could thus examine different indicators of frontal activity across multiple spatiotemporal scales to find the most ecologically relevant predictors, and potentially improve the modest predictive power of the albacore SDM from this study.

In contrast to targeting coastal species such as anchovy, albacore can potentially feed on sardine or cephalopods such as clubhook squid while remaining further offshore. Clubhook squid habitat, in particular, showed strong spatial and environmental overlap with albacore habitat. While sardine habitat was also spatially accessible to albacore, they were absent from albacore diets in the 1950s–60s and contributed only 5%–15% of energetic contribution by region in 2005–06 (Glaser 2010). However, sardine populations were at very low levels from the early 1950s, before recovering somewhat in the late 1990s and declining again more recently (Zwolinski and Demer 2012). Future foraging studies during periods of higher sardine abundance may provide more accurate information on the potential importance of sardine to albacore diets.

Although saury have been shown to be important to albacore diets (Glaser 2010), the SDM for this species had poor skill, due to the rarity of this species in the trawl and larval surveys. However, the low number of positive occurrences was most likely due to low vulnerability of saury to these fishing gears, rather than an absence of saury in the region. Previous studies using more neustonic gears have recorded saury in greater numbers (e.g., Moser 2002; Brodeur et al. 2005), and so future efforts to model saury distributions should use catch records from surveys targeting near-surface environments.

It is not yet clear how albacore feeding on ecologically distinct prey species may alter their degree of aggregation near fronts, or their diel vertical distribution, depending on the species targeted. While anchovy and sardine are generally distributed in the upper water column (Robinson et al. 1995; Kaltenberg and Benoit-Bird 2009), clubhook squid may undertake more extensive diel vertical migrations, occupying much deeper depths during the day (Watanabe et al. 2006). As the main fishing methods in the US fishery are surface-based troll and pole-and-line, and fishing takes place mostly during the day, there is the potential for different foraging behaviors to impact availability of albacore to fishers.

By switching between coastal and offshore-associated prey species, albacore may exert spatiotemporally variable predation pressure on forage species, with implications for the CCS pelagic food web (Wade et al. 2007; Glaser 2010; 2011). Trophic links are dynamic, and anomalous environmental conditions can cause unexpected predator–prey relationships. For example, Glaser (2010) shows that hake formed an important component of albacore diets in 2005–06, but not in earlier studies from the 1950s–60s. This discrepancy may arise from unusually warm conditions in the mid-2000s leading to hake spawning further north than previously recorded, resulting in high abundances of young-of-the-year (YOY) in the central–northern CCS during spring and summer (Phillips et al. 2007). Spatiotemporal overlap between core albacore habitat and juvenile hake may therefore only occur sporadically under warm conditions, as hake spawning in the northern CCS was recorded again during the marine heat wave years of 2015–06 (Auth et al. 2018). However, it provides an example of an unanticipated trophic connection between an epipelagic predator and a prey species which is largely mesopelagic once mature (Childers et al. 2011; Gustafson et al. 2000), facilitated by spawning phenology responding to anomalous environmental conditions.

Previous studies of albacore diets in the CCS have shown that while they can take fish larger than 10 cm in

length, they rely strongly on YOY and juvenile life stages of prey (Glaser 2010). This preference may relate to ease of capture, maximum mouth gape in the age classes of albacore in the CCS (mostly 2–3-year-olds), or some other unknown factor (Menard et al. 2006). Although offshore samples are rare, available evidence suggests that juveniles of the four prey species examined here likely occupy similar spatial habitats to mature adults (Bigelow 1994; Gustafson et al. 2000; Demer et al. 2013; Rose et al. 2015). However, they only occur as the size classes apparently targeted by albacore for part of the year, depending on their spawning dates, and growth rates. The prey SDMs constructed in this study predicted the presence of any life stage catchable by the trawl gear, which likely includes some juveniles and some adults, depending on the species (Demer et al. 2013). Narrowing predictions of available albacore prey fields to include only the prey sizes targeted will thus require consideration of spawning phenology and growth rates for each prey species, which also likely vary interannually and spatially with oceanographic conditions (Weber and McClatchie 2010; Auth et al. 2018; Weber et al. 2018). For example, Daly et al. (2013) show that although both sardine and anchovy can occur in the northern CCS as adults, larval anchovy are collected much more commonly than larval sardine. This may result in distinct latitudinal ranges of YOY anchovy versus sardine, even though their distributions as adults are quite similar.

Additional future work should also include more consistent sampling of albacore diets and trophic ecology at higher spatial and temporal resolution, to improve understanding of the bioenergetic implications of prey switching. As albacore do not spawn in the CCS, they presumably migrate into the area as juveniles to build condition. Reliance on prey with different energy contents (Glaser 2010) may therefore have implications for trade-offs between energy spent migrating, and energy gained on foraging grounds (Kitagawa and Aoki 2017). Albacore have the potential to exert significant predation pressure on forage species (Glaser 2011), but these trophic links are likely to be highly dynamic. To advance the goals of EBFM in the CCS, a better understanding of spatiotemporal overlap and trophodynamics of predators and prey is required. In addition, improved knowledge of how oceanographic conditions and prey fields interact to influence availability of albacore to surface fisheries in the region could help industry adapt to environmental variability and future change.

ACKNOWLEDGEMENTS

LITERATURE

Abrahms, B., K. L. Scales, E. L. Hazen, S. J. Bograd, R. S. Schick, P. W. Robinson, and D. P. Costa. 2018. Mesoscale activity facilitates energy gain in a top predator. Proc. Royal Soc. B. 285: http://doi.org/10.1098/rspb.2018.1101.

Auth, T. D., E. A. Daly, R. D. Brodeur, and J. L. Fisher. 2018. Phenological and distributional shifts in ichthyoplankton associated with recent warming in the northeast Pacific Ocean. Global Change Biol. 24:259–272.

Begoña Santos, M., I. German, D. Correia, F. L. Read, J. Martinez Cedeira, M. Caldas, A. Lopez et al. 2013. Long-term variation in common dolphin diet in relation to prey abundance. Mar. Ecol. Prog. Ser. 481:249–268.

Becker, E. A., K. A. Forney, J. V. Redfern, J. Barlow, M. G. Jacox, J. J. Roberts, and D. M. Palacios. 2018. Predicting cetacean abundance and distribution in a changing climate. Divers. Distrib. https://doi.org/10.1111/ddi.12867.

Bernard, H. J., J. B. Hedgepeth, and S. B. Reilly, S. B. 1985. Stomach contents of albacore, skipjack, and bonito caught off southern California during summer 1983. Calif. Coop. Oceanic Fish. Invest. Rep. 26:175–183.

Bigelow, K. A. 1994. Age and growth of the oceanic squid *Onychoteuthis borealijaponica* in the North Pacific. Fish. Bull. 92:13–25.

Bjorkstedt, E. P., S. J. Bograd, W. J. Sydeman, S. A. Thompson, R. Goericke, R. Durazo, P. Warzybok et al. 2012. State of the California Current 2011–12: Ecosystems respond to local forcing as La Niña wavers and wanes. Calif. Coop. Oceanic Fish. Invest. Rep. 53:41–76.

Brodie, S., M. G. Jacox, S. J. Bograd, H. Welch, H. Dewar, K. L. Scales, K. L., S. M. Maxwell et al. 2018. Integrating dynamic subsurface habitat metrics into species distribution models. Front. Mar. Sci. 5:https://doi.org/10.3389/fmars.2018.00219.

Brodeur, R. D., J. P. Fisher, R. L. Emmett, C. A. Morgan, and E. Casillas. 2005. Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. Marine Ecology Progress Series 298:41–57.

Cavole, L. M., A. M. Demko, R. E. Diner, A. Giddings, I. Koester, C. M. Pagniello, M. L. Paulsen et al. 2016. Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: winners, losers, and the future. Oceanography 29:273–285.

Childers, J., S. Snyder, and S. Kohin, S. 2011. Migration and behavior of juvenile North Pacific albacore (*Thunnus alalunga*). Fish. Oceanogr. 20:157–173.

Christian, J. R. and J. Holmes. 2016. Changes in albacore tuna habitat in the northeast Pacific Ocean under anthropogenic warming. Fish. Oceanogr. 25:544–554.

Daly, E. A., T. D. Auth, R. D. Brodeur, and W. T. Peterson. 2013. Winter ichthyo-plankton biomass as a predictor of early summer prey fields and survival of juvenile salmon in the northern California Current. Marine Ecology Progress Series 484:203–217.

Demer, D. A., J. P. Zwolinski, K. A. Byers, G. R. Cutter, J. S. Renfree, T. S. Sessions, and B. J. Macewicz. 2012. Prediction and confirmation of seasonal migration of Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem. Fish. Bull. 110:52–70.

Demer, D. A., J. P. Zwolinski, G. R. Cutter Jr, K. A. Byers, B. J. Macewicz, and K. T. Hill. 2013. Sampling selectivity in acoustic-trawl surveys of Pacific sardine (*Sardinops sagax*) biomass and length distribution. ICES J. Mar. Sci. 70:1369–1377.

Drazen, J. C., G. Lisa, and R. Domokos. 2011. Micronekton abundance and biomass in Hawaiian waters as influenced by seamounts, eddies, and the moon. Deep Sea Res Part 1 Oceanogr Res Pap. 58:557–566.

Edwards, A. M., I. G. Taylor, C. J. Grandin, and A. M. Berger. 2018. Status of the Pacific hake (whiting) stock in U.S. and Canadian waters in 2018. Prepared by the Joint Technical Committee of the U.S. and Canada Pacific Hake/Whiting Agreement, National Marine Fisheries Service and Fisheries and Oceans Canada. 222 p.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77:802–813.

Fiedler, P. C. and H. J. Bernard. 1987. Tuna aggregation and feeding near fronts observed in satellite imagery. Cont. Shelf Res. 7:871–881.

Field, J. C., R. C. Francis, and K. Aydin. 2006. Top-down modeling and bottom-up dynamics: linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. Prog. Oceanogr. 68:238–270.

Fujioka, K., H. Fukuda, Y. Tei, S. Okamoto, H. Kiyofuji, S. Furukawa, J. Takagi et al. 2018. Spatial and temporal variability in the trans-Pacific migration of Pacific bluefin tuna (*Thunnus orientalis*) revealed by archival tags. Prog. Oceanogr. 162:52–65.

Gentemann, C. L., M. R. Fewings, and M. García-Reyes. 2017. Satellite sea surface temperatures along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat wave. Geophys. Res. Lett. 44:312–319.

Glaser, S. M. 2010. Interdecadal variability in predator–prey interactions of juvenile North Pacific albacore in the California Current System. Mar. Ecol. Prog. Ser. 414:209–221.

Glaser, S. M. 2011. Do albacore exert top-down pressure on northern anchovy? Estimating anchovy mortality as a result of predation by juvenile north pacific albacore in the California current system. Fish. Oceanogr. 20:242–257.

Glaser, S. M., K. E. Waechter, and N. C. Bransome. 2015. Through the stomach of a predator: regional patterns of forage in the diet of albacore tuna in the California Current System and metrics needed for ecosystem-based management. J. Mar. Syst. 146:38–49.

Goericke, R., E. Venrick, A. Mantyla, R. Hoof, C. Collins, G. Gaxiola-Castro, S. J. Bograd et al. 2005. The state of the California current, 2004–05: still cool? Calif. Coop. Oceanic Fish. Invest. Rep. 46:32–71.

Gustafson, R. G., W. H. Lenarz, B. B. McCain, C. C. Schmitt, W. S. Grant, T. L. Builder, R. D. Methot. 2000. Status review of Pacific hake, Pacific cod, and walleye pollock from Puget Sound, Washington. NOAA Technical Memorandum NMFS-NWFSC-44.

Hazen, E. L., K. L. Scales, S. M. Maxwell, D. K. Briscoe, H. Welch, S. J. Bograd, H. Bailey et al. 2018. A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. Sci. Adv. 4: DOI: 10.1126/sciadv.aar3001.

Hill, K. T., P. R. Crone, D. A. Demer, J. P. Zwolinski, E. Dorval, and B. J. Macewicz. 2014. Assessment of the Pacific sardine resource in 2014 for U.S.A. management in 2014–15. US Department of Commerce. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-531.

Hill, K. T., P. R. Crone, and J. P. Zwolinski. 2018. Assessment of the Pacific sardine resource in 2018 for U.S. management in 2018–19. US Department of Commerce. NOAA Technical Memorandum NMFS-SWFSC-600. https:// doi.org/10.7289/V5/TM-SWFSC-600.

Hunsicker, M. E., L. Ciannelli, K. M. Bailey, J. A. Buckel, J. Wilson White, J. S. Link, T. E. Essington et al. 2011. Functional responses and scaling in predator–prey interactions of marine fishes: contemporary issues and emerging concepts. Ecol. Lett. 14:1288–1299.

International Scientific Committee (ISC). 2017. Stock assessment of albacore tuna in the North Pacific Ocean in 2017. In: Report of the Albacore Working Group Stock Assessment Workshop. International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean, Vancouver, Canada, pp. 103.

Jacox, M. G., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bograd. 2016. Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. Geophys. Res. Lett. 43:7072–7080.

Jones, M. C., S. R. Dye, J. K. Pinnegar, R. Warren, and W. W. Cheung. 2012. Modelling commercial fish distributions: Prediction and assessment using different approaches. Ecol. Model. 225:133–145.

Kaltenberg, A. M. and K. J. Benoit-Bird. 2009. Diel behavior of sardine and anchovy schools in the California Current System. Mar. Ecol. Prog. Ser. 394:247–262.

Kaplan, I. C., C. J. Brown, E. A. Fulton, I. A. Gray, J. C. Field, and A. D. Smith. 2013. Impacts of depleting forage species in the California Current. Environ. Conserv. 40:380–393.

Kirby, D. S., O. Fiksen, and P. J. B. Hart. 2000. A dynamic optimisation model for the behaviour of tunas at ocean fronts. Fisheries Oceanography 9:328–342.

Kitagawa, T. and Y. Aoki. 2017. Viewpoints of high migratory tuna species ecology. Comment on; Physics of metabolic organization; by M. Jusup et al. Phys. Life Rev. 20:54–56.

Koehn, L. E., T. E. Essington, K. N. Marshall, I. C. Kaplan, W. J. Sydeman, A. I. Szoboszlai, and J. A. Thayer. Deceloping a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current ecosystem. Ecol. Modell. 335:87–100.

Lam, C. H., A. Nielsen, and J. R. Sibert. 2008. Improving light and temperature based geolocation by unscented Kalman filtering. Fish. Res. 91:15–25.

Laurs, M. R. and J. Lynn. 1977. Seasonal migration of North Pacific albacore, *Thunnus alalunga,* into North American coastal waters: distribution, relative abundance, and association with Transition Zone waters. Fish. Bull. 75:795–822.

Link, J. 2017. A Conversation about NMFS' Ecosystem-Based Fisheries Management Policy and Road Map. Fisheries 42:498–503.

Link, J. S. and H. I. Browman. 2014. Integrating what? Levels of marine ecosystem-based assessment and management. ICES J. Mar. Sci. 71:1170–1173.

Lluch-Belda, D., D. B. Lluch-Cota, S. Hernandez-Vazquez, C. Salinas-Zavala, and R. A. Schwartzlose. 1991. Sardine and anchovy spawning as related to temperature and upwell in the California current system. Calif. Coop. Oceanic Fish. Invest. Rep. 32:105–111.

MacCall, A. D. 1990. Dynamic geography of marine fish populations. Seattle, WA: Washington Sea Grant Program.

Ménard, F., C. Labrune, Y. J. Shin, A. S. Asine, and F. X. Bard. 2006. Opportunistic predation in tuna: a size-based approach. Mar. Ecol. Prog. Ser. 323:223–231.

Moser, H. G. 2002. Distributional atlas of fish larvae and eggs from Manta (surface) samples collected on CalCOFI surveys from 1977 to 2000 (Vol. 35). California Dept. of Fish and Game, Southwest Fisheries Science Center.

Muhling, B. A., R. Brill, J. T. Lamkin, M. A. Roffer, S. K. Lee, Y. Liu, and F. Muller-Karger. 2017. Projections of future habitat use by Atlantic bluefin tuna: mechanistic vs. correlative distribution models. ICES J. Mar. Sci. 74:698–716.

Neveu, E., A. M. Moore, C. A. Edwards, J. Fiechter, P. Drake, W. J. Crawford, M. G. Jacox et al. 2016. An historical analysis of the California Current circulation using ROMS 4D-Var: System configuration and diagnostics. Ocean Model. 99:133–151.

Nieto, K., Y. Xu, S. L. Teo, S. McClatchie, and J. Holmes. 2017. How important are coastal fronts to albacore tuna (*Thunnus alalunga*) habitat in the Northeast Pacific Ocean? Prog. Oceanogr. 150:62–71.

Pearce, J. and S. Ferrier, S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecol. Model. 133:225–245.

Pebesma, E. R. and R. S. Bivand. 2005. Classes and methods for spatial data in R. R news 5 (2), ttps://cran.r-project.org/doc/Rnews/.

Phillips, A. J., S. Ralston, R. D. Brodeur, T. D. Auth, R. L. Emmett, C. Johnson, and V. G. Wespestad. 2007. Recent pre-recruit Pacific hake (*Merluccius productus*) occurrences in the northern California Current suggest a northward expansion of their spawning area. Calif. Coop. Oceanic Fish. Invest. Rep. 48:215–229.

Pikitch, E., C. Santora, E. A. Babcock, A. Bakun, R. Bonfil, D. O. Conover, P. A. Dayton et al. 2004. Ecosystem-based fishery management. Science 305:346–347.

Pinkas L., M. S. Oliphant, and I. L. K. Iverson. 1971 Food habits of albacore, bluefin tuna, and bonito in California waters. Fish. Bull. 152:2–83

Ridgeway, G. 2017. gbm: Generalized Boosted Regression Models. R package version 2.1. 1. 2015. URL: https://CRAN. R-project. org/package= gbm.

Robinson, C. J., F. V. Arenas and G. J. Gomez. 1995. Diel vertical and offshore-inshore movements of anchovies off the central Baja California coast. J. Fish Biol. 47:877–892.

Rose, K. A., J. Fiechter, E. N. Curchitser, K. Hedstrom, M. Bernal, S. Creekmore, A. Haynie et al. 2015. Demonstration of a fully-coupled end-to-end model for small pelagic fish using sardine and anchovy in the California Current. Prog. Oceanogr. 138:348–380.

Runcie, R. M., B. Muhling, E. L. Hazen, S. J. Bograd, T. Garfield, and G. DiNardo. 2018. Environmental associations of Pacific bluefin tuna (*Thunnus orientalis*) catch in the California Current system. Fish. Oceanogr. https://doi.org/10.1111/fog.12418.

Scales, K. L., E. L. Hazen, M. G. Jacox, C. A. Edwards, A. M. Boustany, M. J. Oliver, and S. J. Bograd. 2017. Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. Ecography 40:210–220.

Scales, K. L., E. L. Hazen, M. G. Jacox, F. Castruccio, S. M. Maxwell, R. L. Lewison, and S. J. Bograd. 2018. Fisheries bycatch risk to marine megafauna is intensified in Lagrangian coherent structures. Proc. Natl. Acad. Sci. USA 115:7362–7367.

Sepulveda, C. A., A. Knight, N. Nasby-Lucas, and M. L. Domeier. 2010. Fine-scale movements of the swordfish *Xiphias gladius* in the Southern California Bight. Fish. Oceanogr. 19:279–289.

Smith, A .D., C. J. Brown, C. M. Bulman, E. A. Fulton, P. Johnson, I. C. Kaplan, H. Lozano-Montes et al. 2011. Impacts of fishing low–trophic level species on marine ecosystems. Science 333:1147–1150.

Snyder, S. M. (2016). Navigating a seascape: physiological and environmental motivations behind juvenile North Pacific albacore movement patterns. Doctoral dissertation, University of California–San Diego.

Snyder, S., P. J. Franks, L. D. Talley, Y. Xu, and S. Kohin. 2017. Crossing the line: Tunas actively exploit submesoscale fronts to enhance foraging success. Limnol. Oceanogr. Lett. 2:187–194.

Teo, S. L. H. 2017. Relative abundance indices of juvenile albacore tuna for the US surface fishery in the north Pacific Ocean. ISC/17/ALBWG/09.

Veneziani, M., C. A. Edwards, J. D. Doyle, and D. Foley. 2009. A central California coastal ocean modeling study: 1. Forward model and the influence of realistic versus climatological forcing. J. Geophys. Res. Oceans 114: https://doi.org/10.1029/2008JC004774.

Wade, P. R., V. N. Burkanov, M. E. Dahlheim, N. A. Friday, L. W. Fritz, T. R. Loughlin, T. R., S. A. Mizroch et al. 2007. Killer whales and marine mammal trends in the North Pacific—a re-examination of evidence for sequential megafauna collapse and the prey-switching hypothesis. Mar. Mammal Sci. 23:766–802.

Watanabe, H., T. Kubodera, M. Moku, and K. Kawaguchi. 2006. Diel vertical migration of squid in the warm core ring and cold water masses in the transition region of the western North Pacific. Mar. Ecol. Prog. Ser. 315:187–197.

Watson, J. R., E. C. Fuller, F. S. Castruccio, and J. F. Samhouri. 2018. Fishermen Follow Fine-Scale Physical Ocean Features for Finance. Front. Mar. Sci. 5: https://doi.org/10.3389/fmars.2018.00046.

Weber, E. D. and S. McClatchie. 2010. Predictive models of northern anchovy *Engraulis mordax* and Pacific sardine *Sardinops sagax* spawning habitat in the California Current. Mar. Ecol. Prog. Ser. 406:251–263.

Weber, E. D., Y. Chao, and F. Chai. 2018. Performance of fish-habitat classifiers based on derived predictors from a coupled biophysical model. J. Mar. Syst. 186:105–114.

Xu, Y., K. Nieto, S. L. Teo, S. McClatchie, and J. Holmes. 2017. Influence of fronts on the spatial distribution of albacore tuna (*Thunnus alalunga*) in the Northeast Pacific over the past 30 years (1982–2011). Prog. Oceanogr. 150:72–78.

Zaba, K. D. and D. L. Rudnick (2016). The 2014−2015 warming anomaly in the Southern California Current System observed by underwater gliders. Geophys. Res. Lett. 43:1241–1248.

Zwolinski, J. P. and D. A. Demer. 2012. A cold oceanographic regime with high exploitation rates in the Northeast Pacific forecasts a collapse of the sardine stock. Proc. Natl. Acad. Sci. USA 109:4175–4180.

Zwolinski, J. P., D. A. Demer, K. A. Byers, G. R. Cutter, J. S. Renfree, T. S. Sessions, and B. J. Macewicz. 2012. Distributions and abundances of Pacific sardine (*Sardinops sagax*) and other pelagic fishes in the California Current Ecosystem during spring 2006, 2008, and 2010, estimated from acoustic–trawl surveys. Fish. Bull. 110:110–122.