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Environmental associations of Pacific bluefin tuna (*Thunnus orientalis*) catch in the California Current system

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Abstract

We investigate the impact of oceanographic variability on Pacific bluefin tuna (*Thunnus orientalis*: PBF) distributions in the California Current system using remotely-sensed

environmental data, and fishery dependent data from multiple fisheries in a habitat-modeling framework. We examined the effects of local oceanic conditions (sea surface temperature, surface chlorophyll, sea surface height, eddy kinetic energy), as well as large-scale oceanographic phenomena, such as El Niño, on PBF availability to commercial and recreational fishing fleets. Results from Generalized Additive Models showed that warmer temperatures of around 17 - 21°C with low surface chlorophyll concentrations (< 0.5mg/m^3) increased probability of occurrence of PBF in the Commercial Passenger Fishing Vessel (CPFV) and purse seine fisheries. These associations were particularly evident during a recent marine heatwave (the "Blob"). In contrast, PBF were most likely to be encountered on drift gillnet gear in somewhat cooler waters (13 - 18°C), with moderate chlorophyll concentrations (0.5 - 1.0 mg/m^3). This discrepancy was likely a result of differing spatiotemporal distribution of fishing effort among fleets, as well as the different vertical depths fished by each gear, demonstrating the importance of understanding selectivity when building correlative habitat models. In the future, monitoring and understanding environmentally-driven changes in the availability of PBF to commercial and recreational fisheries can contribute to the implementation of ecosystem approaches to fishery management.

Keywords: Pacific bluefin tuna; dynamic habitat models; commercial fisheries; recreational fisheries; Eastern Pacific Ocean; California Current; Large Marine Ecosystem

Introduction

The ocean environment responds to climate variability and change across multiple time scales, from intra-seasonal to centennial. These dynamic ocean states drive variability in habitat use, catchability, recruitment potential and sustainability of managed fish stocks (Hazen et al., 2013; Link et al., 2011; Kaplan et al., 2013). However, most stocks are currently managed with environmentally invariant reference points and catch limits. This can cause problems for the management of highly mobile, environmentally-sensitive species. Distribution and habitat use can vary spatially in response to unusual environmental conditions, impacting availability to fishing fleets (Perry et al., 2005; Maxwell et al., 2015). A more dynamic understanding of species-habitat relationships is therefore required, to provide context to catch data and inform spatial management approaches (Dunn et al., 2016).

The California Current system is highly productive, fueled by seasonal upwelling of cold, nutrient-rich water. Upwelling is a significant determinant of the local coastal conditions, impacting nutrient supply, oxygen concentration and ocean acidity (Doney et al., 2012), as well as a forage community of copepods, krill, and small fishes such as Pacific sardines (*Sardinops sagax*), northern anchovies (*Engraulis mordax*) and Pacific herring (*Clupea pallasii*). These in turn serve as food for larger species (Lehodey et al., 2006; Fisher et al., 2015). Between 2013 and 2016, unusually high catches of several fish species that are typically found in warmer water to the south and west were recorded off California. These included dorado (*Coryphaena hippurus*), wahoo (*Acanthocybium solandri*), blue marlin *(Makaira nigricans*), and hammerhead sharks (*Sphyrna* spp) (Cavole et al., 2016). Other species, such as Pacific bluefin tuna (*Thunnus orientalis*: PBF), were seen in unusually large numbers, and earlier in the year than is typical (Leising et al., 2015; Feeney and Lea, 2016). These unusual biological occurrences appear to be associated with the 'Blob' marine heatwave (Bond et al., 2015; Zaba and Rudnick, 2016), and subsequent 2015-6 El Niño. Anomalously warm sea surface temperatures associated with these events first appeared in the Gulf of Alaska during winter of 2013, and the majority of the California Current region was >2°C warmer than usual by late 2014 (Bond et al., 2015; Di Lorenzo et al., 2016; Peterson et al., 2017). The strongest sea surface temperature anomalies of up to 3°C occurred in summer and fall 2015, and unusually warm conditions extended thousands of kilometers offshore (Peterson et al., 2017). The Blob, in combination with El Niño conditions, affected the distribution and abundance of many local marine organisms, with effects radiating throughout the food web (Bond et al., 2015; Leising et al., 2015; Jacox et al., 2016).

The overall range of PBF covers most of the North Pacific Ocean south of 50°N (Bayliff, 1994; Fujioka et al., 2015), and only a small portion of this habitat is available to fishers based on the west coasts of the U.S. and Baja California. Spawning takes place in two locations in the western north Pacific Ocean, near the Nansei Islands, and in the Sea of Japan (Shimose and Farley, 2015). A portion of immature 1- 2 year olds then migrate from the western to the eastern north Pacific, before returning to the western Pacific as mature adults (Bayliff, 1994; Fujioka et al., 2015). PBF are considered to start maturing at age 3, with 100% mature by age 5 (ISC, 2018). As a result, most PBF in the eastern North Pacific are immature juveniles. PBF of this age are associated with a broad range of surface temperatures between around 10 - 25°C (Fujioka et al., 2018), which corresponds to conditions with minimal metabolic costs (Blank et al., 2007).

However, within the broader California Current system, PBF make seasonal north and south migrations, likely taking advantage of both optimal physiological conditions and seasonal patterns of prey availability (Boustany et al., 2010; Whitlock et al., 2015). Gut contents studies have shown that PBF feed on species associated with highly productive conditions (e.g. anchovy), as well as species associated with oligotrophic waters (e.g. pelagic red crabs, *Pleuroncodes planipes*) (Boustany et al., 2010; Craig et al., 2017).

PBF are targeted by both commercial and recreational fisheries off the west coast of North America. They are of particular concern to regional fisheries managers, as the most recent stock assessment found that the stock was overfished, and subject to overfishing, with spawning biomass at an estimated 3.3% of unfished levels (ISC, 2018). The anomalously high catches off the U.S. west coast thus occurred during a period of near-historic lows in spawning biomass, at a time when catch and bag limits were being reduced to limit fishing mortality on juveniles in the eastern Pacific. PBF are targeted in recreational fisheries in both U.S. and Mexican waters, and by a purse seine fishery which operates primarily out of Mexico, with occasional effort in U.S. waters. They are also encountered as bycatch in the large mesh drift gillnet (DGN) fishery. The DGN fishery was developed in the late 1970s off southern California for pelagic sharks and swordfish (X*iphias gladius*) (Hanan et al., 1993). Historically, fishing effort was concentrated in the Southern California Bight during spring and shifted northward and offshore as the season progressed (Hanan et al., 1993). However, since 2001, the DGN fishery has been subject to a time/area closure north of Point Conception from 15 August through 15 November to protect leatherback turtles (*Dermochelys coriacea*). An additional season/area closure south of Point Conception is effective from June - August during El Niño years to protect loggerhead turtles (*Caretta caretta*) (Caretta et al., 2004), and was implemented for the first time in 2014. The number of fishing vessels participating in the DGN fleet has declined since the mid-1990s, with less than 1,000 total sets per year in recent years.

Recreational catch of PBF is separated into private vessels, and the Commercial Passenger Fishing Vessel (CPFV) fleet, which are usually larger vessels taking on several paying fishers. These vessels target multiple species, including PBF, yellowfin tuna (*Thunnus albacares*), albacore tuna (*Thunnus alalunga*), dorado, yellowtail (*Seriola lalandi*) and rockfish (*Sebastes* spp.). In contrast to the DGN fishery, which operates primarily mid-summer to early winter, the

CPFV fishery operates all year, but peak tuna fishing season is spring and summer. While Mexican purse seine fisheries in the equatorial eastern Pacific Ocean mainly target yellowfin tuna, there is some targeted catch of PBF for ranching off Baja California (Farwell, 2001; Dreyfus-Leon et al., 2017). A smaller U.S. based fishery also takes PBF when they are available in U.S. waters. Historically, fishing for PBF off Baja California was primarily incidental. However, since the mid-1990s there has been greater interest in ranching activities.

Each of these fisheries uses different gear, fishes at different times of year and in different areas, and has different selectivity for PBF. The influence of environmental variability on the catches of each fleet may therefore be different, depending on how oceanographic features drive spatial distribution of PBF. In this study, we quantify the links between oceanographic variability and PBF distributions, in light of recent anomalous conditions, using dynamic habitat models. We identify core habitat for PBF off the U.S. west coast, using data from three different fisheries, and show how the extent of the overlap between suitable conditions and fishing grounds varies with oceanographic events.

Methods

Fishery-dependent data

We investigated the impact of environmental variability on PBF availability to fishers in the California Current system using the fishery-dependent datasets described in Table 1, and shown in Figure 1. Each fishery fishes with different gear and targets different species, with different spatiotemporal coverage (Figure 2). A separate habitat model was therefore built for each fishery. Measures of effort are not comparable across fisheries, and are difficult to calculate for the CPFV and purse seine fisheries, as is common for these types of fisheries in other parts of the world (e.g. Maunder & Punt, 2004; Maunder et al., 2006). In addition, it is difficult to identify CPFV trips specifically targeting PBF, since no clear distinction is made in the CPFV logbooks (Stohs, 2016). Data from the CPFV and DGN fisheries are also strongly zero-inflated (see Supplementary Figure 1). We therefore built habitat models predicting the presence or absence of PBF at each location fished by each fishery, rather than the total catch, or catch per unit effort.

The habitat model for the DGN fishery was built using records from the observer program, which was initiated in the 1980s to record detailed catch data, and bycatch by taxon for fish, mammals and turtles (Hanan et al., 1993). Although logbook data across spatially aggregated reporting blocks are also available for this fishery, these data are less useful for constructing habitat models, as the reporting blocks become larger with distance from shore, reaching a size of approximately 111 km^2 at the seaward extent of the fishery. In contrast, the observer data are recorded at the exact locations of each set.

Detailed catch data are available for the CPFV fleet, with little information on smaller private vessels. We therefore used the CPFV data from California to build the second PBF habitat model. California CPFV operators submit mandatory logbooks to the California Department of Fish and Wildlife, containing information on locations fished, ports of landing, number of anglers, hours fished, species and number of fish kept. Logbook data from CPFVs fishing in the U.S. Exclusive Economic Zone are available from 1980 to present, by reporting blocks approximately 10 x 10 nautical miles in size. Data are also available from Mexican waters off Baja California, but reporting blocks for this region are more than ten times larger than those in U.S. waters, preventing the meaningful association of catch records with environmental data. We therefore used only data from U.S. waters in this study, despite the considerably higher catch and effort in Mexican waters. From mid-2014 through the end of 2015, U.S. flagged recreational vessels were not permitted to fish for PBF in Mexican territorial waters, potentially resulting in a shift of effort to U.S. waters.

PBF catch data from purse seine vessels were taken from at-sea observer reports and fishing logbooks. When data from both sources were available, the observer data was used. The fishing season usually runs from May to October. However, the introduction of quotas for the purse seine fishery targeting PBF has resulted in an earlier end to the season in more recent years. For example, the quota was reached and the fishery closed in July 2014, and by June in 2015.

Environmental data

We selected four environmental variables to include in habitat models for PBF, based on known relationships with PBF physiology, biology (e.g. Boustany et al., 2010; Hahlbeck et al., 2017), and availability (Table 2, Supplementary Figure S2). Temperature drives physiological processes, such as cardiac output and metabolic rate (Blank et al., 2004; 2007), while surface

chlorophyll-*a* is a proxy for ocean productivity and thus feeding conditions (Longhurst et al., 1995). Sea surface height and eddy kinetic energy help to determine eddy fields, and the positions of regional current systems. Surface chlorophyll-*a* and eddy kinetic energy were natural log-transformed before analysis, to reduce skewness.

Values were extracted for the location and date of each fishery-dependent record, using the MGET toolbox in ArcGIS (Roberts et al., 2010), and the Xtractomatic package in R 3.3.2 (R Core Team 2016), which extracts data from the Environmental Research Division's Data Access Program (ERDDAP) (Simons, 2017). To construct Hövmöller plots of spatiotemporal changes in oceanographic conditions, and habitat suitability for PBF, we also extracted all four environmental variables on a monthly timescale, across a 1 x 1 degree grid of locations covering the California Current system (20 – 49°N). To account for the shape of the coastline, the grid of locations extended to 7° offshore of the nearest land at each latitude. This region covered the spatial extent of all three fisheries, and was also well within the extent of the region impacted by the blob heatwave.

Dynamic Habitat Models

Habitat models predicted the presence or absence of PBF for each fishing fleet, and were built using Generalized Additive Models (GAMs) with the 'mgcv' package in R 3.3.2 (R Core Team 2016; Wood, 2006). GAMs are conceptually similar to Generalized Linear Models, but they incorporate smoothing functions of predictors to allow non-linear relationships between predictors and response variables. As chlorophyll-*a* data were only available from mid-1997 onwards, we restricted the input data for the habitat models to cover the years 1997 – 2015, as 2015 was the most recent year in which fishery-dependent data were available from the three fisheries. To ensure biologically plausible results, the number of knots ('k') in each GAM was restricted to 5 after model selection (e.g. Keele, 2008). Each GAM included the four environmental variables (sea surface temperature, surface chlorophyll, sea surface height, eddy kinetic energy). A receiver-operator-characteristic curve (ROC) was fit as an indicator of model performance (Hanley and McNeil, 1982). The area under the ROC curve (AUC) typically ranges between 0.5 and 1 (Elith et al., 2006; Parisien and Moritz, 2009). An AUC value of 0.5 indicates that the model predictions are no better than random and a value of one indicates perfect discrimination of probabilities between presence (1) and absence (0) values (Elith et al., 2006;

Parisien and Moritz, 2009; Froeschke and Drymon, 2013). Models with AUC values greater than 0.6 are considered informative and useful (Parisien and Moritz, 2009), values greater than 0.7 are considered good, values greater than 0.8 very good, and greater than 0.9 excellent (Lane et al., 2009). As the three fisheries examined in this study were not comparable in terms of selectivity, catchability, or spatiotemporal extent, we built separate GAMs for each fishery. The presence or absence of PBF at each date and location was predicted using a binomial response distribution and logit link function. Since we were most interested in the spatial availability of PBF to each fishery, rather than their distribution throughout the broader Pacific Ocean, we restricted the spatial extent of predictions from each GAM. This was completed by adding several "dummy" negative catch locations to each fishery-dependent dataset, at locations 2 degrees offshore of the most distant recorded fishing locations, in all months where each particular fishery recorded effort. This had the effect of constraining predictions from each GAM to the spatiotemporal extent of fishing effort. Of the four predictor variables, adding the dummy points to the observed data had the largest impact on partial responses to sea surface temperature (see Supplementary Figure 3). While the partial response for the CPFV data did not change markedly, the addition of the dummy points more strongly constrained the lower temperature limit for the DGN fishery, and the upper and lower limits for the purse seine fishery.

Results were visualized by applying each GAM to monthly climatological means (1998 – 2015) of each of the four environmental variables across the California Current system. Predicted probabilities of occurrence were then interpolated using kriging in Surfer 9 (Golden Software, Golden, Colorado), and observed probabilities of occurrence aggregated to rounded 1x1° spatial locations were overlaid. Locations with < 20 sets recorded in a particular month, across all years, were mapped as presence or absence only, as this was considered insufficient effort to determine the overall probability of PBF occurrence. This corresponded to less than 0.5% of the total sets recorded in all three fisheries.

Results

Generalized Additive Models:

All GAMs provided useful predictions of PBF presence/absence, as indicated by AUCs of 0.79 (DGN), 0.71 (CPFV), and 0.76 (purse seine) (Table 3). All four environmental variables were strongly significant to each GAM, at $p < 0.01$.

Partial relationships between environmental variables and probability of PBF occurrence showed some similarities among the different fisheries (Figure 3). PBF were more likely to be present at moderate to low surface chlorophyll concentrations (0.1 - 0.5 mg/m^3 in the CPFV and purse seine fisheries, 0.3 - 1.5 mg/m^3 in the DGN), and at low to moderate sea surface heights (< 0.7 m). Relationships with eddy kinetic energy suggested that moderate values (~3.4e-4 - 1.8e-2 m^2/s^2) were most associated with PBF, but uncertainty was high, particularly at lower values. In contrast, while all three GAMs showed parabolic responses of PBF occurrence to surface temperature, the values associated with maximum probabilities were different among fisheries. The DGN GAM predicted highest probability of PBF occurrence at 13 - 18°C, while the CPFV and purse seine GAMs showed maximum values at 17 - 21°C.

Two-dimensional plots of modeled responses to the four environmental predictors show that the oceanographic environments fished by each fleet were markedly different (Figure 4). Fishing effort in the DGN fishery primarily took place where sea surface temperature was 12 – 23°C, and where surface chlorophyll was 0.06 – 19.87 mg/m^3 (note log scale in figure), and in contrast to the other fleets, recorded the most PBF in the coldest waters (<18°C). The CPFV fleet fished a similar temperature range to the DGN fleet (10 – 24°C), but showed the highest probabilities of occurrence in moderately warm, low chlorophyll waters (18 – 22°C, < 0.4 mg m^{-3}). The purse seine fishery largely occurred at higher surface temperatures between 15 – 24°C in moderately oligotrophic waters < 1.0 mg/m^3 surface chlorophyll.

Sea surface height characteristics of water fished by each fleet were similar, ranging from 0.39 – 0.72 m, 0.36 – 0.76 m, and 0.43 – 0.74 m in the DGN, CPFV, and purse seine fisheries respectively (Figure 4). However, while the DGN and CPFV models showed maximum probabilities of occurrence at low to moderate values (< 0.65m), the purse seine GAM predicted highest probabilities of occurrence at low values (< 0.55m). In contrast, the models showed a relatively weak influence of EKE, consistent with the partial plots in Figure 3, with high probabilities of occurrence across most of the range fished.

Monthly climatologies

The six months with highest historical fishing effort (1998 – 2015) in the DGN were January, and August through December (Figure 5). Modeled probabilities of PBF occurrence using environmental climatologies for this fishery showed a wider latitudinal range than the CPFV and purse seine fisheries. PBF were encountered in this fishery from the offshore Southern California Bight in the south to the U.S. – Canadian border in the north. The GAM captured the overall distribution of positive catch locations reasonably well, but may have somewhat overestimated the offshore movement of suitable habitat in winter. In contrast to the DGN, effort in the CPFV fishery was highest from spring through fall (Figure 6). Core habitat for PBF from this fishery was largely restricted to the Southern California Bight, with 95.5% of all PBF records from this fishery occurring south of 34°N. This was reflected in climatological predictions from the GAM, with highest probabilities of occurrence centered around the U.S. - Mexico border. Some suitable habitat was also predicted to occur offshore of central California (Figure 6). Throughout the six months with highest fishing effort (May through October), highest modeled probabilities of occurrence in the purse seine fishing region were located in the Southern California Bight, and the north-central coast of Baja California (Figure 7). Suitable habitat appeared to extend most of the length of the Baja California peninsula in spring, but contracted northwards in the summer and fall. These predictions coincided strongly with observed catch locations. Comparison of probabilities of occurrence by rounded 1x1° latitude - longitude location and month, averaged across all years, showed strong agreement between observed and predicted values. Correlation coefficients (for all latitude/longitude/month combinations with >20 records between 1998 and 2015) were 0.74 for the CPFV fishery, 0.70 for the DGN, and 0.87 for the purse seine fishery.

Both fishery-dependent catch data and habitat models thus suggested that PBF were located as far north as San Francisco Bay (~37-38°N) in winter (January – March), where they were sometimes recorded in the DGN fishery. As the purse seine fishery has minimal effort before March, their southern extent during winter is less certain. By spring, PBF were encountered along Baja California north of ~20°N, and occasionally up to around Point Arena (39°N) in the CPFV fishery. In summer and early fall, both catches and predicted suitable habitat reached their most northern extent, as far as the latitude of the Columbia River (~46°N) in the DGN fishery. The purse seine GAM suggested that favorable habitat in summer could extend as far south as

25°N, resulting in a particularly broad extent of suitable habitat along the North American coast during this season (> 2,500 km from north to south).

Environmental variability

The oceanographic environment within the California Current system varied across the 17 year time series, particularly with respect to sea surface temperature and sea surface height (Figure 8). The strong positive temperature anomalies associated with the Blob marine heatwave in 2014 – 2015 are clearly evident, as are weaker warm anomalies associated with El Niño events. However, while unusually warm temperatures from the Blob extended throughout much of the region, those from El Niño events were more spatially heterogeneous. Surface chlorophyll was generally inversely related to sea surface temperature, with negative anomalies during warm events, and positive anomalies when water temperatures were cooler. Variability in sea surface height was related to temperature, but also showed the impact of mesoscale oceanographic features on spatiotemporal anomalies. Eddy kinetic energy was more variable through the time series, both among years, and spatially (Figure 8).

Hövmöller plots of predicted probabilities of PBF occurrence highlighted some similarities among fishing fleets (Figure 9). All three GAMs predicted a northward displacement of suitable PBF habitat in 2014 and 2015, associated with the Blob phenomenon. Due to the different partial responses to surface temperature among models, however (Figure 3), this resulted in increased probabilities of occurrence in the Southern California Bight in the CPFV and purse seine fisheries, but decreased probability in the DGN. Predicted probabilities of occurrence in the purse seine fishery were generally higher off southern Baja California during La Niña events than during El Niños, but no clear association with the El Niño cycle was obvious for the other two fisheries (Figure 9).

2015 showed the strongest environmental anomalies (warmer temperatures, high sea surface height, low chlorophyll, low eddy activity) across the study region, particularly off northern Baja California and in the Southern California Bight (~ 30 - 35°N, Figure 8). This coincided with the main fishing regions for the CPFV and purse seine fisheries, which recorded the majority of the PBF occurrences out of the three fisheries. In contrast, water temperatures during 2010 were cooler than usual throughout the California Current system, with moderate positive chlorophyll anomalies north of 30°N (Figure 8). The GAMs suggested that this resulted in higher

probabilities of PBF occurrence off southern Baja California and lower probabilities in the Southern California Bight in 2010, with the reverse situation in 2015 (Figure 9). To examine these two contrasting years in more detail, we compared observed and predicted catches for all three fisheries in 2010 and 2015 (Figure 10). Predicted probability of PBF occurrence in the Southern California Bight in months fished by the CPFV fishery (June through November) was higher in 2015 than in 2010, primarily due to warmer temperatures (a mean of 16.8°C in 2010 versus 20.1°C in 2015), lower surface chlorophyll (0.86mg/m^3 in 2010 versus 0.30mg/m^3 in 2015), and higher sea surface height (0.53m in 2010 versus 0.66m in 2015). Observations showed that PBF were more likely to be encountered by the CPFV fleet in 2015 than in 2010, with a higher proportion of positive catch locations in the area. This comparison is somewhat complicated by the displacement of U.S.-based CPFV effort from Mexican waters into the U.S. exclusive economic zone in 2015, with the 2014 closure of Mexican waters to U.S. fishers to the direct targeting of PBF. However, the total of 21,345 PBF recorded from the CPFV fleet in 2015 was higher than the 1998 - 2015 average of 20,847, even though the most historically favorable fishing grounds off Baja California were inaccessible. In contrast, a total of 8,437 PBF were caught by the CPFV fleet in 2010, across both U.S. and Mexican waters (CDFW, 2011).

Predictions from the purse seine GAM for the same two years (May - October) showed a northwards contraction of PBF habitat along Baja California (Figure 10). This was consistent with a potential northward displacement of PBF towards the far northern Baja peninsula, and into the Southern California Bight. Recorded catches of PBF in the purse seine fishery showed a much broader region of occurrence in 2010, with catches in 2015 restricted to a small area north of 30°N. Monthly mean surface temperatures off southern Baja California were as warm as 30.4°C in August 2015 at 110°W and 20°N, which is much warmer than any of the fished locations in the fishery-dependent datasets, and thus results in considerable extrapolation of the purse seine GAM. In contrast, the surface temperature at the same month and location in 2010 was 26.0°C. Total catches in the purse seine fishery in Mexican waters were 7,694 metric tons in 2010, and 3,082 in 2015 (Inter-American Tropical Tuna Commission). However, catches in this fishery are primarily determined by quota limits, which were imposed in 2012, and tightened in 2013 (to 5,000 metric tons per year) and 2015 (to 3,300 metric tons per year) (IATTC, 2014).

Fishing effort in the DGN has declined through time, and was low in the California Current system by 2010. Only 4 PBF from 70 sets were recorded in 2010, and 7 PBF from 74 sets in 2015 (compared to 114 from 691 sets in 1998). Predictions from the DGN GAM (August - January) suggest that this fishery was more likely to encounter PBF in the central and northern California Current from summer through fall of 2015, and in the central and southern study region in 2010. However, the lack of effort in these years precludes validation of the model predictions. Overall, comparison of predicted and observed presence of PBF in 2010 versus 2015 suggests a general northward movement of suitable habitat associated with the warmer conditions in 2015 (Figure 10). This may have improved accessibility to the CPFV fishery in the Southern California Bight, and restricted the purse seine fishery to northern Baja California.

Discussion

Results from this study showed that PBF were encountered by multiple fisheries throughout most of the California Current system. Catch locations varied substantially in time, space, and by fishery. These patterns are broadly consistent with those documented by Domeier et al. (2005), Kitagawa et al. (2007), Boustany et al. (2010) and Fujioka et al. (2018), using satellite-tagged PBF. These studies showed that winter PBF habitat was highly variable, with some fish remaining off far southern Baja California, while others migrated offshore of the northern California Current. Both these movement patterns would result in low availability of PBF to all three fisheries examined in our study during winter. In spring, tagged fish moved closer inshore to the northern Baja California peninsula and into the Southern California Bight as temperatures warmed, coinciding with the approximate start of the CPFV and purse seine fisheries. However, the timing and extent of these movements appeared to vary interannually (Boustany et al., 2010). During summer, tagged fish were located from near Vancouver Island in the north, to southern Baja California in the south (Fujioka et al., 2018), with core habitat concentrated in the Southern California Bight, and off northern Baja California (Boustany et al., 2010). In fall, some tagged animals moved farther north and sometimes offshore, before returning southwards again around December. Taken together, results from Domeier et al. (2005) Kitagawa et al. (2007), Boustany et al. (2010), Fujioka et al. (2018) and our study suggest that core juvenile PBF habitat is maximally available to the CPFV and purse seine fleets during summer. In addition, the

geographic range of these fisheries can allow exploitation of a relatively high proportion of this core habitat, depending on environmental conditions.

A broad thermal tolerance for PBF is supported by results from tagging and laboratory studies. Age-0 PBF tagged at ~40 – 80cm length in the East China Sea occupied waters with ambient temperatures of around 14 – 22°C in their first year (Kitagawa et al., 2006a). Larger juvenile PBF in the California Current system were primarily found where surface temperatures were ~14 – 22°C, with ambient temperatures of as low as 11°C experienced during subsurface foraging movements (Kitagawa et al., 2007; Boustany et al., 2010). A recent synthesis of 12 years of data from juvenile PBF showed that they associated with surface temperatures of ~11 - 25°C across the North Pacific, with highest frequencies of occurrence at ~ 15 - 21°C (Fujioka et al., 2018). The endothermic capabilities of PBF increase with size (Kitagawa et al., 2006b), so larger juveniles which remain in the eastern North Pacific for several years (Madigan et al., 2017) are likely able to occupy cooler waters of <14°C.

The upper thermal limits of juvenile PBF are less clear. Mature adult PBF can tolerate very warm water temperatures of > 25°C on their spawning grounds in the western Pacific, (Ashida et al., 2015). However, this tolerance of extreme temperatures may not be present in smaller fish such as those generally occurring in the California Current, which have endothermic capabilities, but are still immature (Kitagawa et al., 2006b). In both PBF and the closely related Atlantic bluefin tuna (*T. thynnus*), only the largest mature adults migrate to the most distant, and warmest, spawning grounds (Okochi et al., 2016; Richardson et al., 2016). Fujioka et al. (2018) recorded the maximum surface temperature encountered by juvenile PBF across the entire North Pacific to be 25.3°C. Similarly, Hazen et al. (2013) found that tagged PBF utilized habitats where sea surface temperature was as warm as ~25°C, with generally increasing probabilities of occurrence with temperature. In our study, PBF were caught in waters as warm 24.4°C in the CPFV fishery, 21.7°C in the DGN, and 24.5°C in the purse seine fishery. Both lower and upper temperature limits of occurrence for PBF were therefore generally consistent between our data, and previous tagging and physiological studies (e.g. Blank et al., 2007). This suggests that even though our study relied on fishery-dependent information, using data from across the three different fisheries still sampled a broad range of environmental conditions.

However, although thermal environments occupied by PBF from our study were within the overall ranges reported by previous studies, the partial relationships among the three GAMs were different. In particular, while peak probabilities of occurrence in the CPFV and purse seine fisheries were similar (at ~ 17 - 21°C), those from the DGN fishery were somewhat cooler (13 - 18°C). There are two potential drivers of this discrepancy. Firstly, warmer waters (> 19°C) fished by the DGN fleet were located primarily in the Southern California Bight between August and November (Figure 2), as a result of spatial management measures imposed on this fishery, and availability of their target species (primarily swordfish: Scales et al., 2017). Data from the CPFV fleet, which is not bound by these spatial restrictions, suggest that peak catches of bluefin tuna in this region occur between June and August. As a result, the DGN fleet is spatially mismatched with the warmer waters which are most likely to contain PBF. Secondly, studies of tagged bluefin tuna suggest that they occupy shallower depths in the water column (upper 20m) when conditions are warm and stratified, and dive deeper as stratification breaks down in cooler seasons (e.g. Kitagawa et al., 2000; Marcinek et al., 2001; Tanaka et al., 2007). Drift gillnets are required to be set with the top of the net at a minimum depth of 11 - 20m to avoid turtle bycatch (Caretta & Barlow, 2011). In warm, stratified conditions, catchability of bluefin tuna may therefore be greater on surface gears, such as pole-and-line as used by the CPFV fleet, while in cooler, less stratified conditions, they may overlap vertically more with sub-surface drift gillnets. It is not possible to address these hypotheses in more depth with the data available, but we note that more detailed analysis of large tagging datasets, such as initially described in Fujioka et al. (2018), may allow questions of oceanographic influences on selectivity to be more closely examined. However, these findings highlight the importance of considering the bias inherent in fishery-dependent data when using them to build species distribution models. It is not common for habitat modeling studies to use data from more than one source to model spatiotemporal distributions, but our results suggest that this is a useful practice. Moving towards habitat models with stronger mechanistic underpinnings, which consider habitat use in three dimensions, can also provide a more useful understanding of how environmental conditions mediate the susceptibility of different species to different fishing gears.

Although PBF may preferentially occupy water of particular temperatures, data from our study, and previous work, suggests that their overall thermal tolerances are very broad. This suggests that other environmental characteristics may be driving finer-scale PBF distributions in the

California Current system, within their broader physiological thermal limits. For example, previous studies have proposed that availability of prey species is particularly important to PBF movements within the region (e.g. Whitlock et al., 2015). Kitagawa et al. (2007) noted that north-south seasonal movements of tagged PBF coincided with seasonal availability of potential sardine prey off California, and Boustany et al. (2010) suggested that migratory patterns targeted areas of highest primary productivity between spring and fall. Results from our study were generally consistent with these conclusions, in terms of seasonal latitudinal movements. However, the longer time series examined here (1997 – 2015 vs. 2002 – 2005 in Boustany et al. (2010) and Kitagawa et al. (2007)) highlighted strong interannual variability in PBF catch locations with season. For example, PBF were encountered farthest north during late summer and fall, consistent with tagging studies. In many years though, PBF were also caught in one or more fisheries in the Southern California Bight, and sometimes off Baja California in September and October. The GAMs also showed that PBF were caught in both oligotrophic waters (~0.1 – 0.2 mg/m^3), as well as much more productive waters (> 4 mg/m^3). Highest probabilities of occurrence were at <0.5 mg/m^3 in the CPFV and purse seine fisheries, and 0.5 - 1.0mg/m^3 in the DGN fishery. During the Blob heatwave and subsequent El Niño, surface chlorophyll was lower than usual in some parts of the California Current (Gómez-Ocampo et al., 2017, Figure 8 this study), and PBF were caught in the CPFV fishery in the Southern California Bight at levels as low as 0.1 – 0.15 mg/m^3. However, surface chlorophyll-*a* is not necessarily a good proxy for abundance or distribution of PBF prey, which may vary in response to thermal conditions, migration patterns, or inshore-offshore transport (Brodeur et al., 2003).

The lack of correspondence with surface primary productivity is likely due to the tendency of PBF, and other tunas, to feed opportunistically and prey on a diverse forage base, including fish, cephalopods, and crustaceans (Pinkas et al., 1971; Shimose et al., 2013; Madigan et al., 2016). Early studies of PBF diets showed a predominance of anchovy in stomach contents, with this species comprising up to 86% of the prey assemblage (Pinkas et al., 1971). However, this work was conducted during a time when anchovy were particularly abundant in the California Current system (Zwolinski and Demer, 2012). More recent analyses show strong interannual variability in PBF diets, with anchovy prevalent in stomach contents during years when they are generally abundant in the region, and other taxa such as squid, jack mackerel (*Trachurus symmetricus*), and pelagic red crabs more prevalent in other years (Craig et al., 2017; Snodgrass et al.,

unpublished data). Despite being present at relatively high biomass in the mid-2000s (Zwolinski and Demer, 2012), sardine were not prominent in PBF diets, comprising less than 10% in all years examined since 2007. Pelagic red crabs were a particularly high proportion of PBF diets in 2015 and 2016, contributing > 50% in both years (Craig et al., 2017). Red crabs are usually associated with warm waters off southern Baja California, but may be transported further northwards in some years (Longhurst, 1967), as appeared to have occurred during the recent anomalous period (Cavole et al., 2016). In contrast, anchovy are more abundant in cooler productive waters (Weber and McClatchie, 2010). PBF may therefore be associated with water masses of widely varying characteristics, and may switch prey resources opportunistically, rather than targeting only regions with high primary productivity.

Relationships with sea surface height suggested that low to moderate values of <0.65m were most favorable for PBF occurrence. This generally corresponded to waters offshore of cold, newly upwelled water next to the coast, but inshore of North Pacific Gyre waters, which were characterized by particularly high sea surface heights, and very low chlorophyll concentrations (see Supplementary Figure S2). PBF occurrence was not as well predicted by eddy kinetic energy as it was by the other environmental variables, but partial plots suggested that moderate values of 0.01 to 0.05 m^2/s^2 were generally favorable in the CPFV and DGN fisheries. This range is characteristic of moderate strength mesoscale oceanographic features, which are usually located offshore of the continental shelf break. These results thus suggest that within favorable temperature limits, PBF may be targeting habitat of low to moderate chlorophyll concentration and moderate mesoscale eddy activity, located offshore of the summer upwelling zone. Habitat associations shown in this study may have been complicated by size-specific migration patterns. PBF are mostly encountered as 1-3 year olds off the west coast of North America, with older fish assumed to return to the western Pacific to spawn starting around age three to five years (Sund et al., 1981; Bayliff, 1994). However, in 2014-2015, some larger PBF up to 7 years old were encountered by anglers in the California Current (Madigan et al., 2017), and this trend has continued through 2017 (L. Heberer, pers. comm.). Larger PBF > 100kg were also briefly present off California in the late 1980s (Foreman and Ishizuka, 1990). Drivers of variability in PBF age composition in our study region are not currently known. However, if unidentified environmental or biological conditions are leading to longer residence times of PBF in the California Current, this may complicate modeling of suitable habitat using the methods

employed in this study, which considered only presence or absence of PBF of any size. In addition, overall abundance of PBF in the California Current is also likely to be impacted by their population levels, age structure, and migration rates. These are not represented in the habitat models, and so predictions from the GAMs should be taken to represent overall suitable environmental habitat, rather than any proxies for abundance.

While our results showed that PBF are caught where sea surface temperatures are as warm as ~25°C off Baja California, future warming due to climate change will not necessarily lead to increased habitat suitability in the rest of the region. The eastern North Pacific may warm by 2-3°C by the end of the 21st century (Woodworth-Jefcoats et al., 2012), and upwelling may weaken in the southern California Current system (Rykaczewski et al., 2015). Conditions similar to those generated by the Blob and coincident El Niño in recent years could thus become more common in the future. However, the potential effects of climate change on food web structure are more complex (Woodworth-Jefcoats et al., 2012; Fiechter et al., 2015), and will likely be more influential for determining PBF distribution in the eastern North Pacific, given their broad physiological tolerances.

Overall, our results show that PBF in the California Current system are associated with a broad range of surface temperatures within approximate limits of ~10 - 25°C, low to moderate surface chlorophyll concentrations, and moderate levels of mesoscale eddy activity. Modeled partial relationships with environmental variables were somewhat different among fisheries, particularly for surface temperature, highlighting the importance of understanding bias in fishery-dependent data when using them to build habitat models. The blob marine heatwave may have improved habitat for PBF within the Southern California Bight, leading to higher catches in this region during recent years. In addition, areas where PBF were caught during the blob years moved northwards in all three fisheries, compared to climatologies. However, given their broad thermal tolerances, it is likely that relationships defined by the GAMs partially reflect prey distributions for PBF, and so the effects of the blob on PBF habitat suitability overall may have been a response to temperature, prey distributions, or both. El Niño events appeared to result in slightly more favorable habitat accessible by some fisheries in some years, but the effect was much weaker than that of the combined Blob / El Niño in 2014-15. Our results suggest that monitoring of oceanographic conditions in the California Current system may allow the prediction of PBF

habitat, and thus their vulnerability to regional fisheries. However, improved understanding of the mechanistic drivers of PBF habitat suitability, primarily prey dynamics, is required to better assess their potential responses to environmental variability and climate change.

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Table 1. Fishery-dependent datasets available for developing habitat models. Southwest Fisheries Science Center (SWFSC), California Department of Fish and Wildlife (CDFW), Inter-American Tropical Tuna Commission (IATTC), Drift Gillnet (DGN), Commercial Passenger Fishing Vessel (CPFV).

Data	Fishery	Data Source	Dates	Catch PBF As:

Holder				
SWFSC	DGN	Observer	July 1990 - Present	Bycatch
CDFW	CPFV	Logbook	May 1986 - Present	Target
IATTC	Purse Seine	Logbook	Feb. 1985 - Present	Target

Table 2. Environmental datasets used for developing habitat models.

Variable	**Product/Sensor**	**Resolution**	**Temporal coverage**	**Source**
Surface temperature	AVHRR Pathfinder	0.0129 deg	1981 - 2007	NOAA/NESDIS
	MODIS/Aqua	0.0125 deg	2002 - present	NASA/GSFC
Chlorophyll-*a*	SeaWiFS	0.05 deg	1997 - 2010	NASA/GSFC
	MODIS/Aqua	0.0125 deg	2002 - present	NASA/GSFC
Sea surface height	Multiple altimetry sensors	0.25 deg	1993 - present	AVISO
Eddy kinetic energy	Sea Level Anomalies	0.25 deg	1993 - present	AVISO

Table 3: Results of GAMs predicting presence of PBF in three fisheries. SST denotes sea surface temperature, Chl denotes surface chlorophyll-*a* (log transformed), SSH denotes sea surface height, and EKE denotes eddy kinetic energy (log transformed). '*' indicates the variable was significant at $p < 0.05$, '**' at $p < 0.01$, '***' at $p < 0.001$. The area under the Receiver Operating Curve (AUC) is also shown for each model.

Fishery	**SST**	**Chl**	**SSH**	**EKE**	**AUC**
DGN	***	***	***	***	0.79
CPFV	***	***	***	***	0.71
Purse Seine	***	***	***	**	0.76

Figure captions

Fig. 1: Spatial extent of data sources from the three different fisheries used in this study.

Fig 2: Seasonal and spatial distribution of effort in the three fisheries. Seasons are defined as January, February and March being winter, April, May and June being spring, and so on. Zones are shown at bottom right, and were stratified based on overall effort from all fisheries

Fig. 3: Partial response plots from each of the GAMs showing the modeled probability of PBF occurrence for the three fisheries. Solid lines show the centered smooth for each environmental variable (sea surface temperature, surface chlorophyll, sea surface height, and eddy kinetic

energy), while dashed lines show ± 2 standard deviations. DGN refers to the drift gillnet observer data, and CPFV to the Commercial Passenger Fishing Vessel data. Histogram bars show the frequency distributions of environmental variables across all locations fished by each fishery, regardless of whether PBF were recorded or not.

Fig. 4: Modeled probability of PBF occurrence by fishery in two-dimensional space. Colors show predicted probability from the GAMs. Upper row: sea surface temperature versus surface chlorophyll (log). Lower row: sea surface height versus eddy kinetic energy.

Fig. 5: Monthly climatologies (1998 – 2015) of predicted probability of PBF occurrence (%) in the DGN fleet from the GAM, for the six months with highest fishing effort. Colors show predicted probability from the GAM, and points shown are mean observed probabilities of occurrence from the fishery-dependent data. “Low effort” denotes less than 20 sets within a month/location over all years of the time series (1997 – 2015). Areas further than 2 degrees offshore of the most distant historical fishing locations (1997 – 2015) are masked in white.

Fig. 6: Monthly climatologies (1998 – 2015) of predicted probability of PBF occurrence (%) in the CPFV fleet from the GAM, for the six months with highest fishing effort. Colors show predicted probability from the GAM, and points shown are mean observed probabilities of occurrence from the fishery-dependent data. “Low effort” denotes less than 20 records within a month/location over all years of the time series (1997 – 2015). Areas further than 2 degrees offshore of the most distant historical fishing locations (1997 – 2015) are masked in white.

Fig. 7: Monthly climatologies (1998 – 2015) of predicted probability of PBF occurrence (%) in the purse seine fleet from the GAM, for the six months with highest fishing effort. Colors show predicted probability from the GAM, and points shown are mean observed probabilities of occurrence from the fishery-dependent data. “Low effort” denotes less than 20 sets within a month/location over all years of the time series (1997 – 2015). Areas further than 2 degrees offshore of the most distant historical fishing locations (1997 – 2015) are masked in white.

Fig. 8: Hövmöller plot showing anomalies of the four environmental predictor variables in the California Current system (132 – 110°W, 20 – 49°N), across all months of the year. Approximate El Niño and La Niña periods are also shown.

Fig. 9: Hövmöller plot of predicted probability of occurrence of PBF by month and latitude for the Commercial Passenger Fishing vessel (CPFV), Drift Gillnet (DGN) and Purse Seine (PS) fisheries. Anomalies from each degree of latitude are shown, averaged across the six months for each fishery where historical effort has been highest (see Figures 5 – 7). Regions not fished by each fishery, based on Figure 1, are masked. Horizontal lines denote regions shown in Figure 2: South Baja (SB), North Baja (NB), Southern California Bight (SCB), Central Coast (CC), and North Coast (NC). Environmental data were sourced from monthly climatologies of the four environmental predictor variables (1998 – 2015).

Fig. 10: Mean predicted probability of PBF occurrence in the CPFV (top row), purse seine (middle row), and DGN (bottom row) fisheries from the GAMs, comparing from 2010 versus 2015. Mean values across the 6 months shown in Figures 5 through 7 are shown. Points are mean observed probabilities of occurrence from the fishery-dependent data. Areas further than 2 degrees offshore of the most distant historical fishing locations (1997 – 2015) are masked in white.

Supplementary Materials:

Fig. S1: Frequency distribution of CPUE in the Commercial Passenger Fishing Vessel (CPFV), Drift Gillnet (DGN) and Purse Seine (PS) fisheries.

Fig. S2: Winter (January – March) and summer (July – September) climatologies of sea surface temperature, sea surface height, surface chlorophyll and eddy kinetic energy, across the study region. Surface temperature and chlorophyll were obtained from the MODIS Aqua sensor (2003 – 2015), while sea surface height and eddy kinetic energy were from AVISO altimetry (1998 – 2015).

Fig. S3: Partial relationships between probability of occurrence of PBF in the Commercial Passenger Fishing Vessel (CPFV: red), Drift Gillnet (DGN: blue) and Purse Seine (PS: green) fisheries, with respect to sea surface temperature. Series are shown for observations with no "dummy" locations included (circles), with "dummy" locations included (open triangles), as well as predictions from the three Generalized Additive Models.

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Chlorophyll-a	SeaWiFS	0.05 deg	1997 - 2010	NASA/GSFC
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Fishery	**SST**	**Chl**	**SSH**	**EKE**	**AUC**
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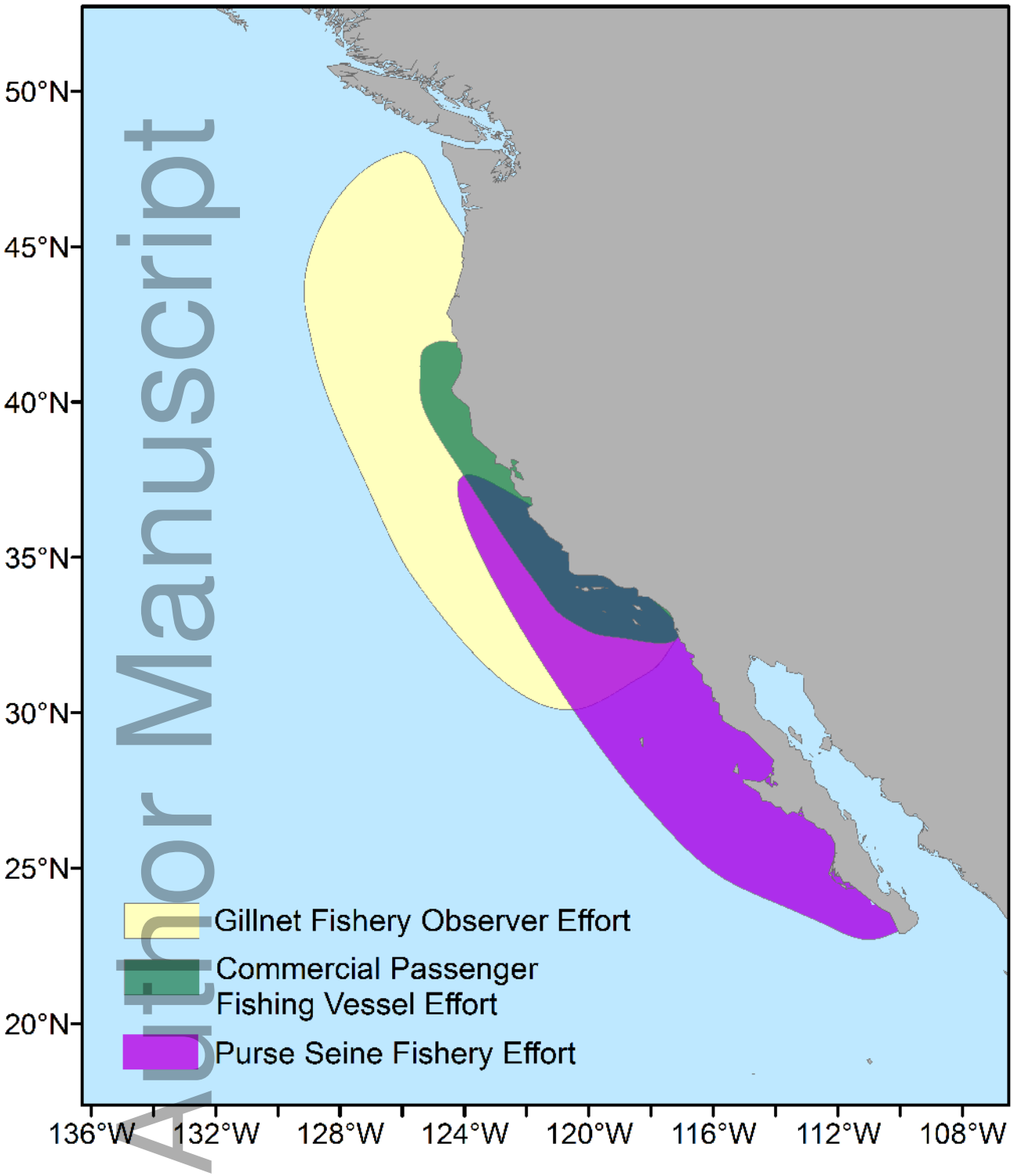
CPFV	***	***	***	***	0.71
Purse Seine	***	***	***	**	0.76



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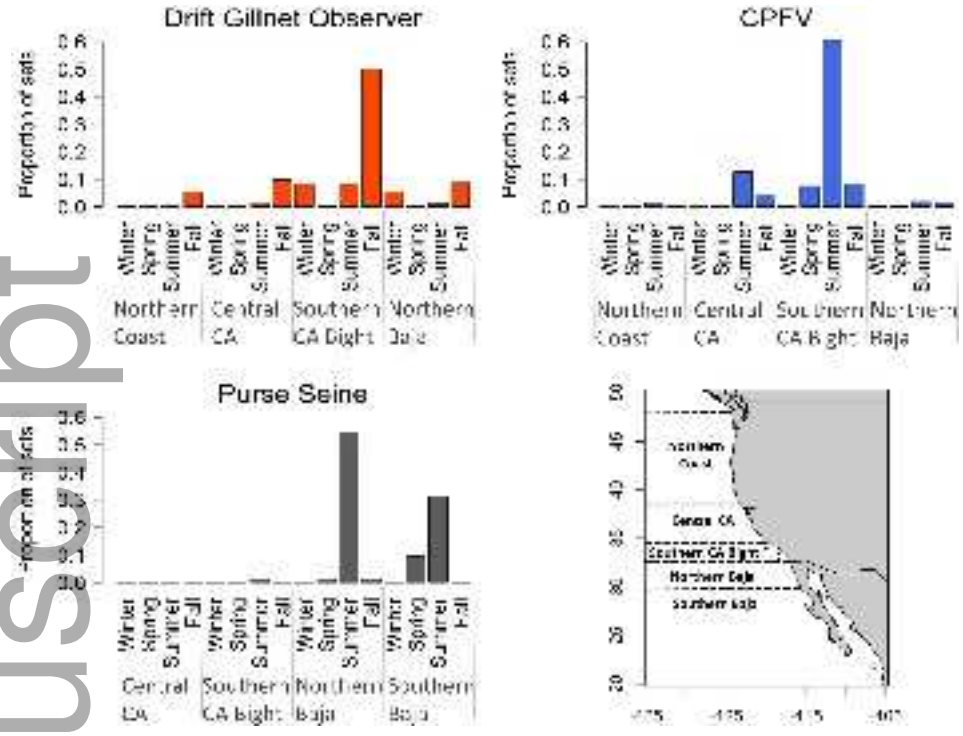

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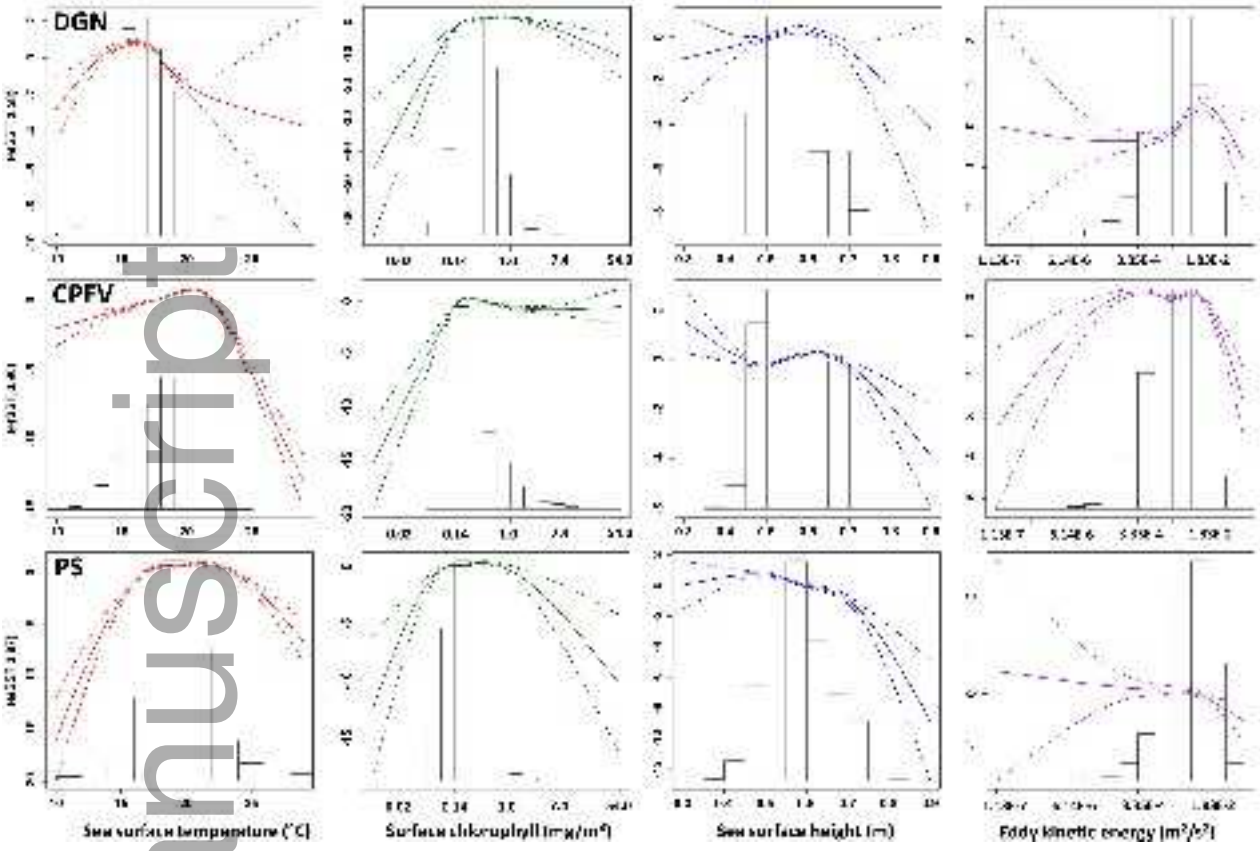

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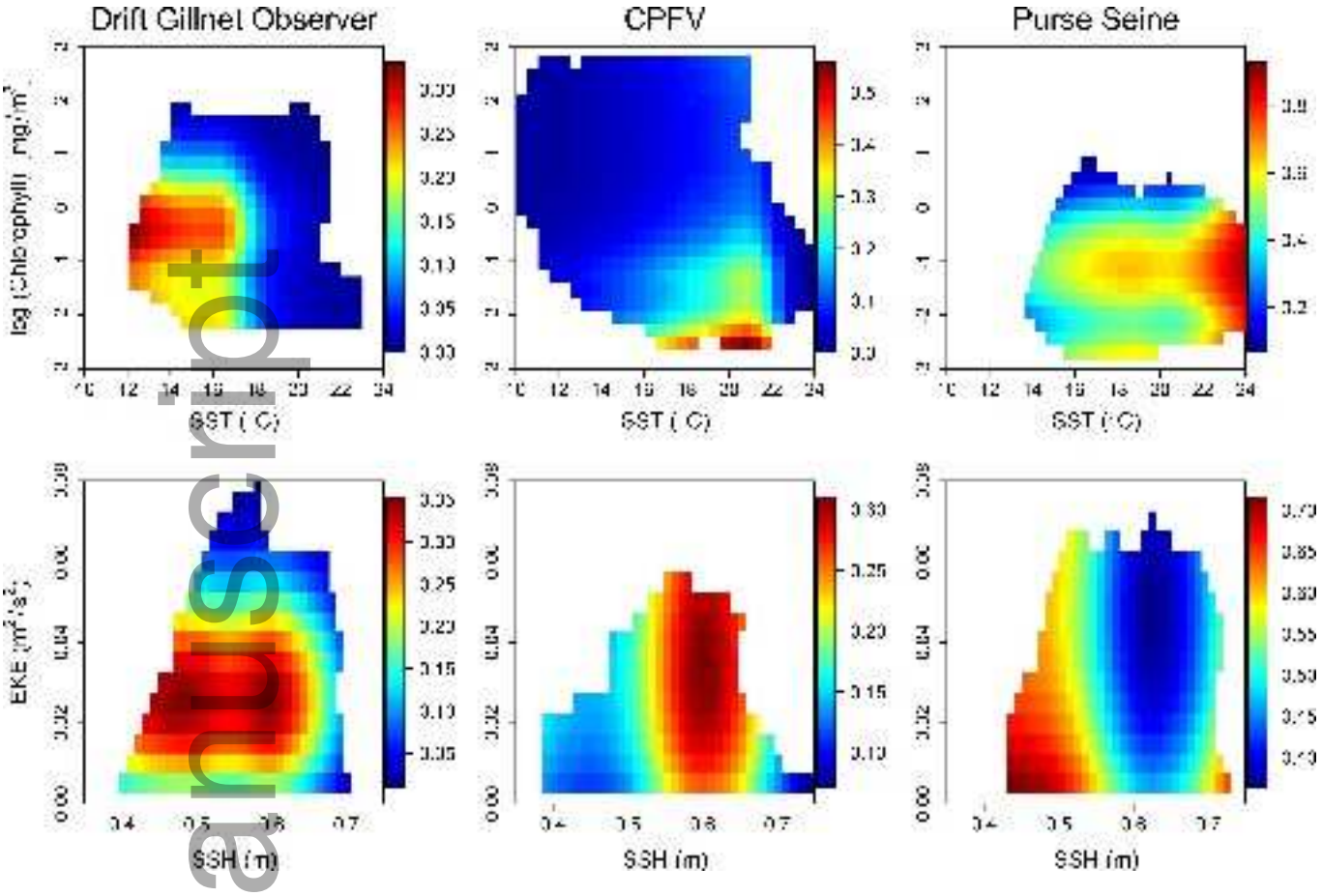

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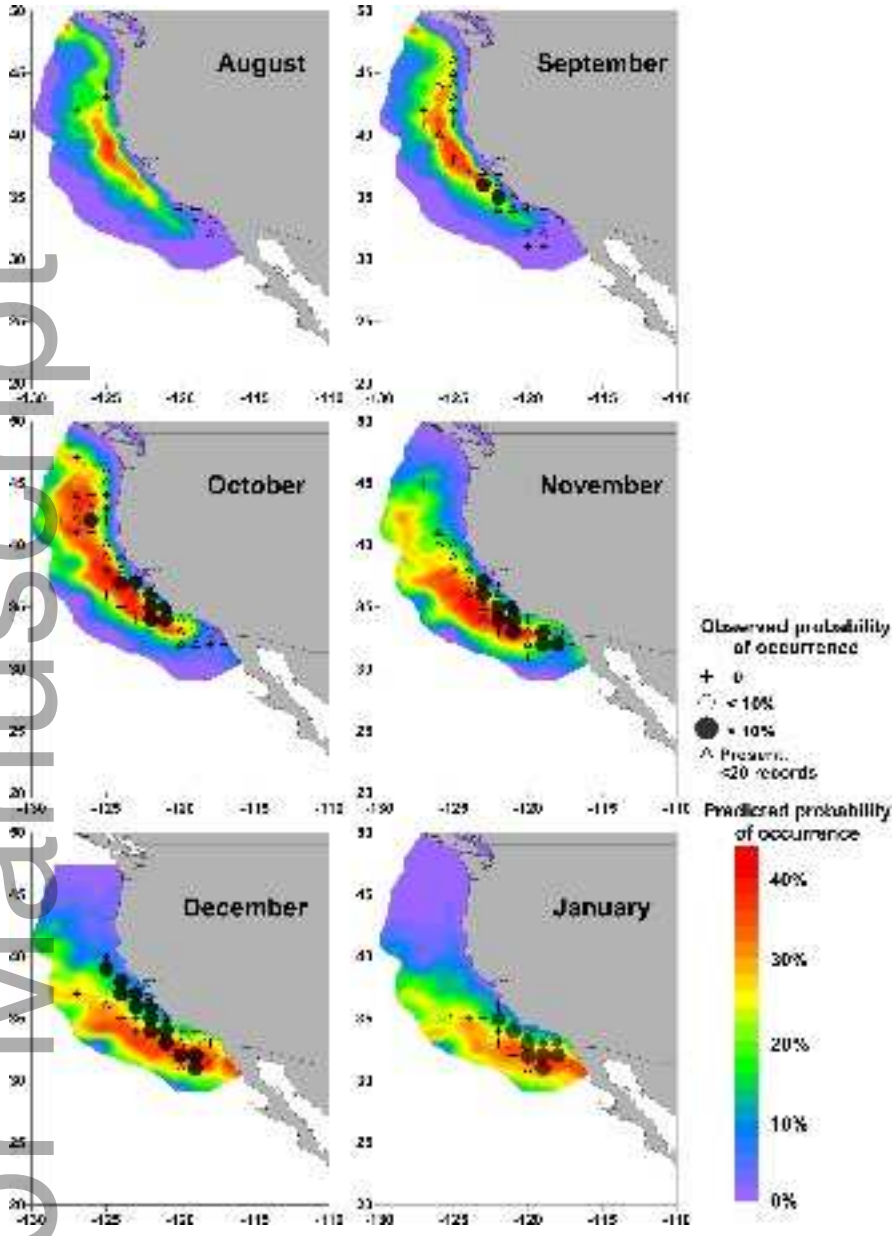

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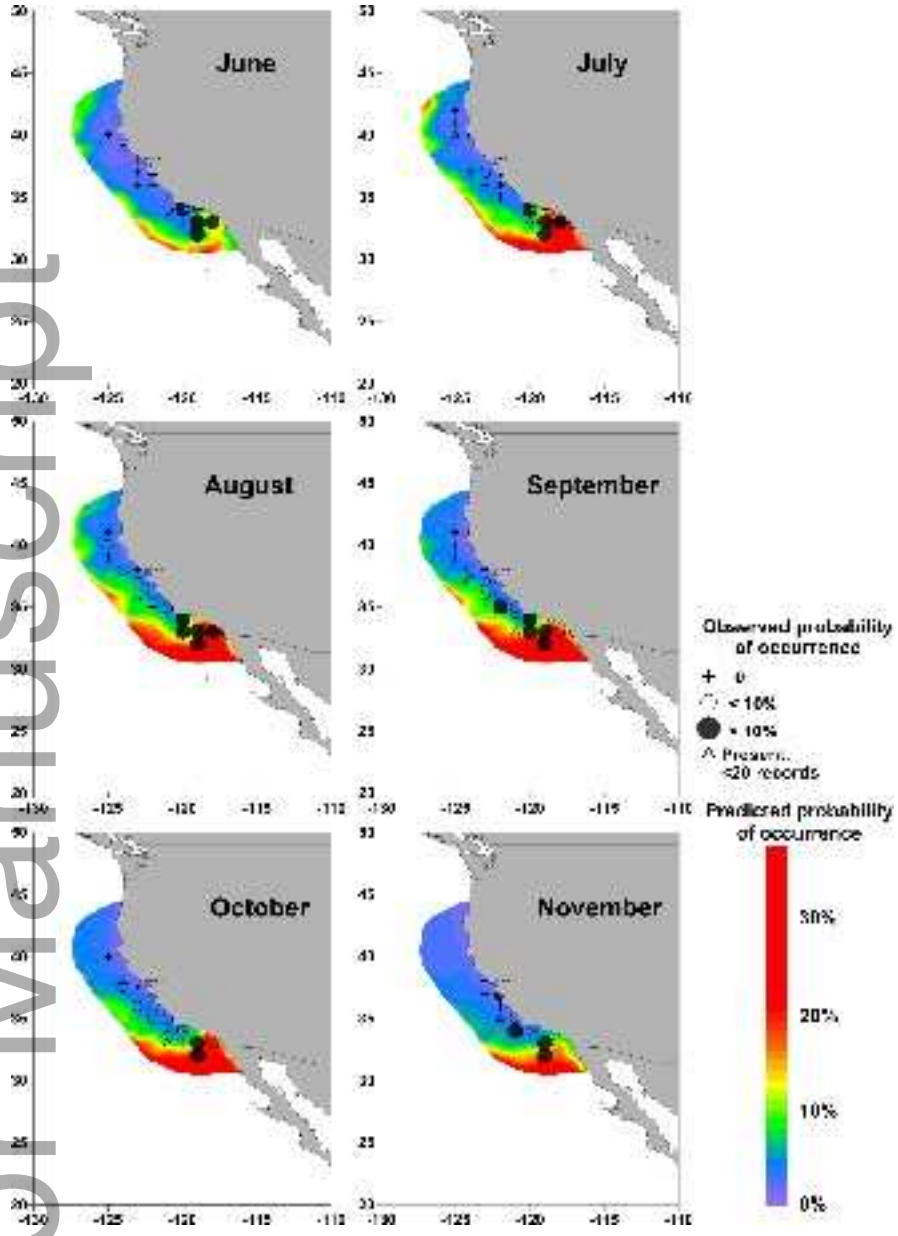

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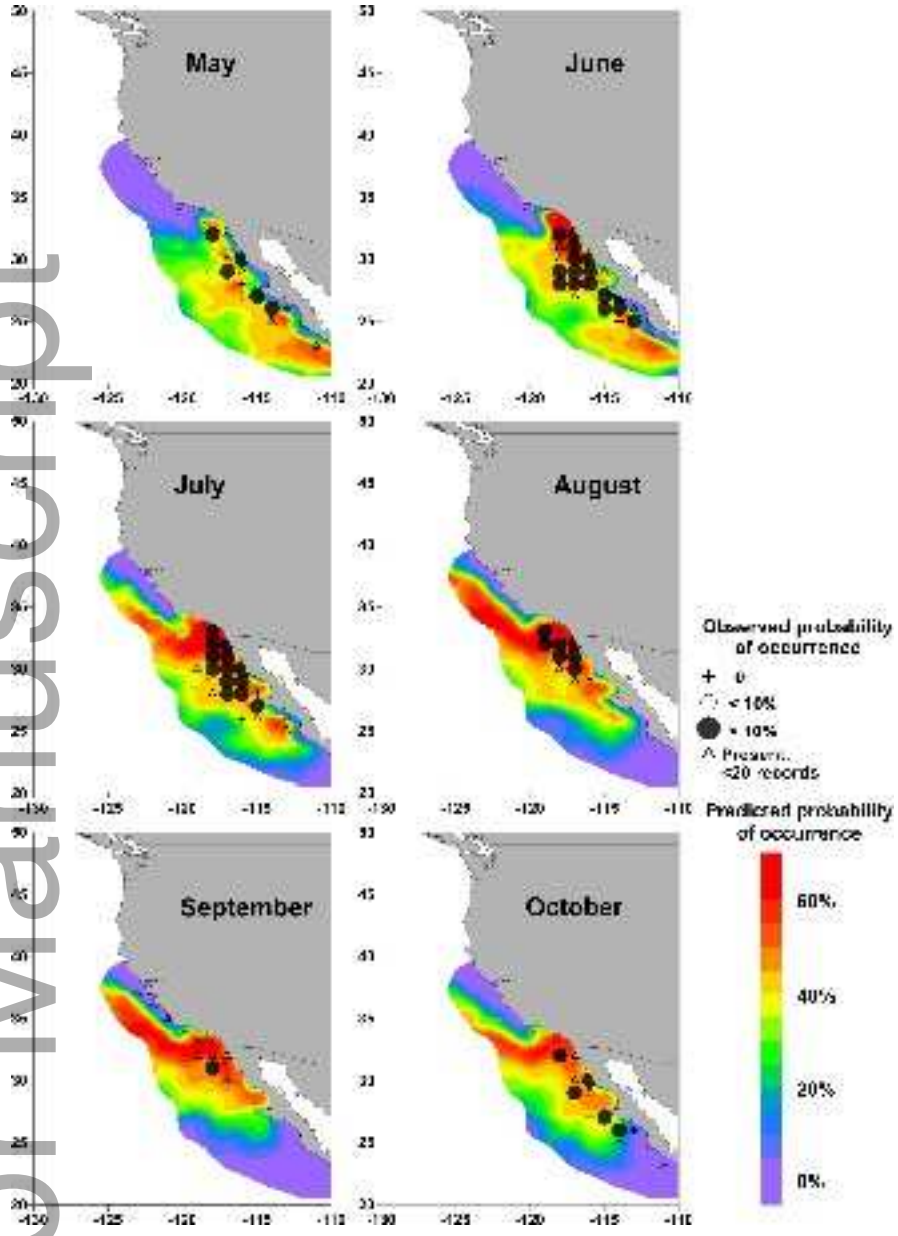

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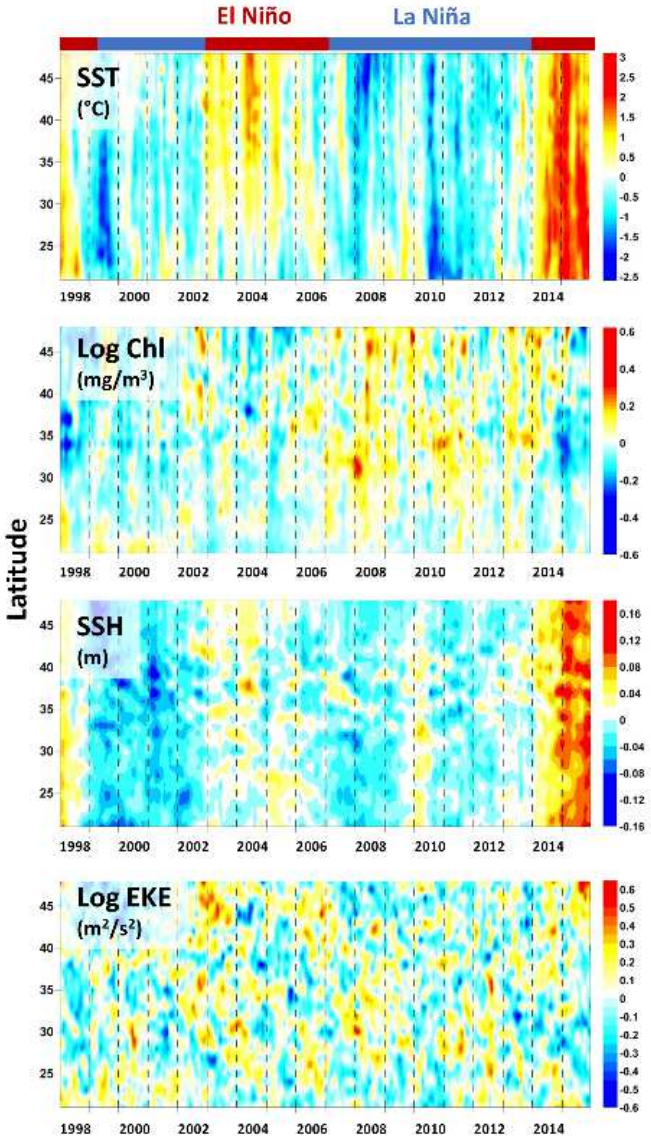

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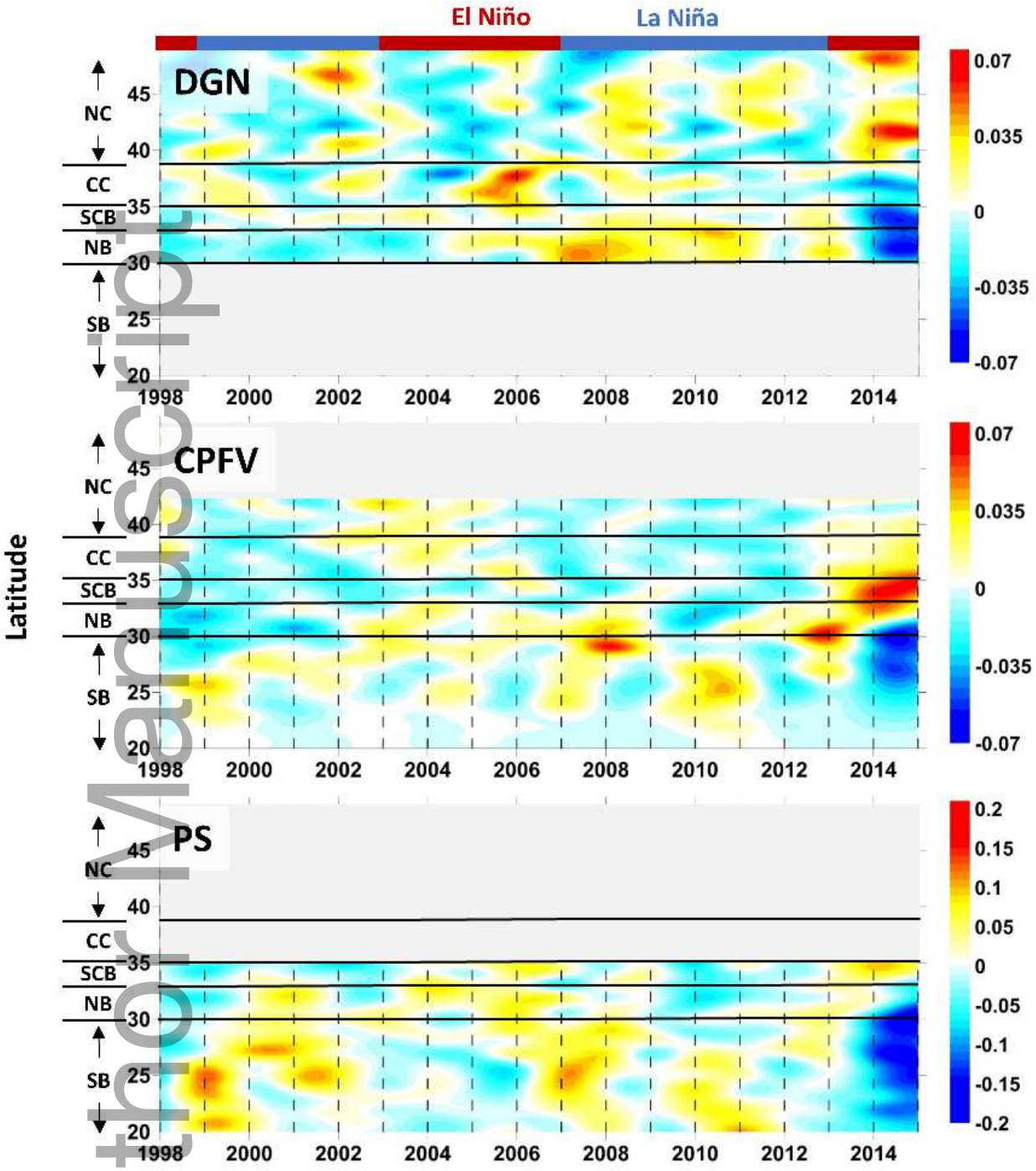

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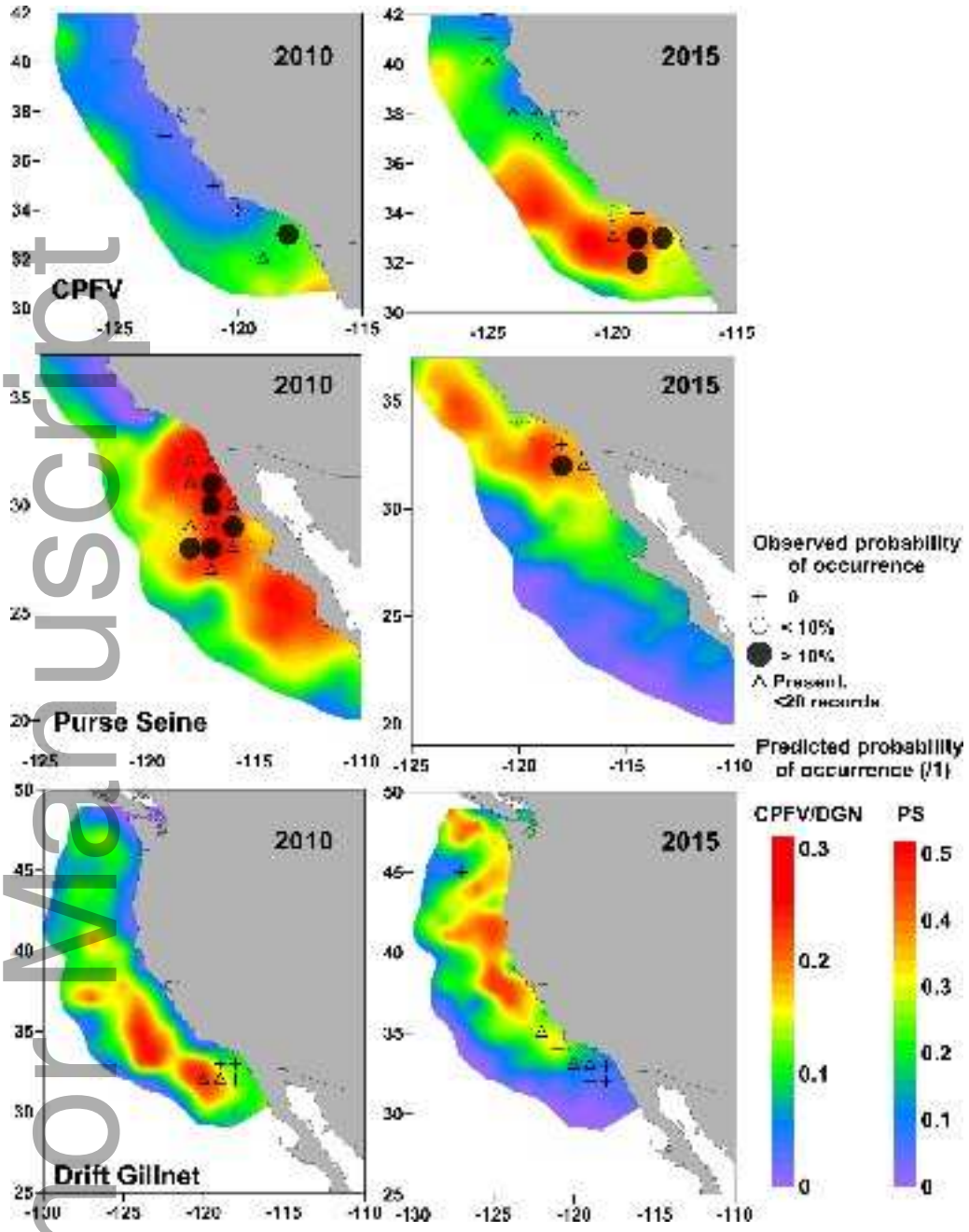

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