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Projections of climate-driven changes in tuna vertical habitat based on species-specific differences in blood oxygen affinity

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Abstract

Oxygen concentrations are hypothesized to decrease in many areas of the ocean as a result of anthropogenically driven climate change, resulting in habitat compression for pelagic animals. The oxygen partial pressure, pO_2, at which blood is 50% saturated (P_{50}) is a measure of blood oxygen affinity and a gauge of the tolerance of animals for low ambient oxygen. Tuna species display a wide range of blood oxygen affinities (i.e., P_{50} values) and therefore may be differentially impacted by habitat compression as they make extensive vertical movements to forage on subdaily time scales. To project the effects of end-of-the-century climate change on tuna habitat, we calculate tuna P_{50} depths (i.e., the vertical position in the water column at which ambient pO_2 is equal to species-specific blood P_{50} values) from 21st century Earth System Model (ESM) projections included in the fifth phase of the Climate Model Intercomparison Project (CMIP5). Overall, we project P_{50} depths to shoal, indicating likely habitat compression for tuna species due to climate change. Tunas that will be most impacted by shoaling are Pacific and southern bluefin tunas—habitat compression is projected for the entire geographic range of Pacific bluefin tuna and for the spawning region of southern bluefin tuna. Vertical shifts in P_{50} depths will potentially influence resource partitioning among Pacific bluefin, bigeye, yellowfin, and skipjack tunas in the northern subtropical and eastern tropical Pacific Ocean, the Arabian Sea, and the Bay of Bengal. By establishing linkages between tuna physiology and environmental conditions, we provide a mechanistic basis to project the effects of anthropogenic climate change on tuna habitats.

KEYWORDS
bigeye, bluefin, CMIP5, deoxygenation, hypoxia, skipjack, *Thunnus*, yellowfin

1 | INTRODUCTION

Many pelagic animal species cross steep temperature and oxygen gradients during their daily vertical migrations. Reduced ambient oxygen levels (i.e., hypoxia) at depth limit the vertical movements of tunas in some regions depending on species-specific hypoxia tolerance (e.g., Brill, 1994; Gilly, Beman, Litvin, & Robison, 2013; Koslow,

Goericke, Lara-Lopez, & Watson, 2011; Schaefer, Fuller, & Block, 2009; Stramma, Schmidtko, Levin, & Johnson, 2010; Stramma et al., 2011). Climate models project warmer temperatures and lower oxygen concentrations in the pelagic realms of the world's oceans by 2100 (Bopp et al., 2013; Ciais et al., 2014; Rhein et al., 2014); and these effects have been referred to as "habitat compression" (Prince & Goodyear, 2007; Prince et al., 2010). Habitat compression may

have pervasive effects on marine ecosystems by altering predator–prey and competitive interactions (e.g., Gallo & Levin, 2016; Gilly et al., 2013; Lehodey et al., 2011; Stramma et al., 2010).

Tunas are large predators that often make extensive vertical movements (e.g., Block et al., 2001, 2011; Brill et al., 1999; Holland, Brill, & Chang, 1990; Howell, Hawn, & Polovina, 2010; Musyl et al., 2003; Schaefer & Fuller, 2007, 2010; Schaefer, Fuller, & Block, 2011; Walli et al., 2009) to forage (Pusineri, Chancollon, Ringelstein, & Ridoux, 2008; Young et al., 2010). Tunas exhibit different behaviors when tracking prey vertically in the water column (Schaefer et al., 2009). The typical characteristic behavior for bigeye tuna is to remain in the surface water at night when the deep scattering layer organisms are at the surface and follow the deep scattering layer organisms to deeper depths just above the oxygen minimum layers during the day (Schaefer & Fuller, 2010; Schaefer et al., 2009). When at deeper depths, bigeye tuna repetitively return to shallower depths because they cannot remain in cold, hypoxic conditions for the entire day (Schaefer & Fuller, 2010; Schaefer et al., 2009). Yellowfin and skipjack tunas remain in the surface waters during both night and day (Schaefer & Fuller, 2007; Schaefer et al., 2011). They make forays to deeper depths during the day to forage in the deep scattering layer when there are no other sources of food at the surface (Schaefer & Fuller, 2007; Schaefer et al., 2011). However, they can only remain at deeper depths for brief periods because they are not hypoxia tolerant (Schaefer & Fuller, 2007; Schaefer et al., 2011). These foraging behaviors influence frequency of vertical habitat usage by different tunas.

Multiple tuna species are sympatric (Figure 1), but analyses of prey composition in the water column, tuna gut contents, and foraging depths indicate that the ability to tolerate temperature and oxygen levels at depth is critical for niche partitioning (Bernal,
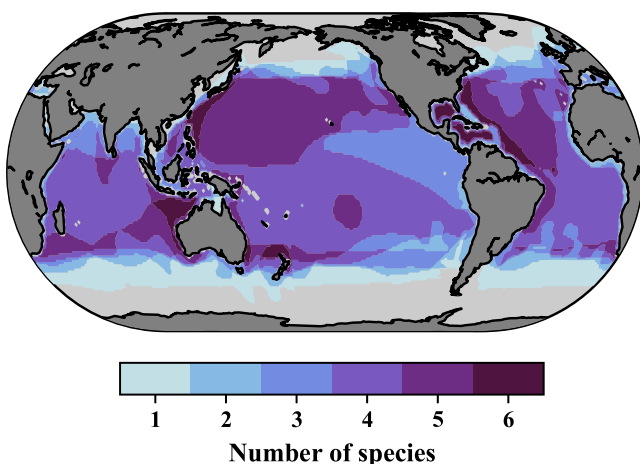

FIGURE 1 Tuna species richness in the global ocean (IUCN, 2011, 2014). The map includes skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), southern bluefin (*Thunnus maccoyii*), bigeye (*Thunnus obesus*), Pacific bluefin (*Thunnus orientalis*), Atlantic bluefin (*Thunnus thynnus*), albacore (*Thunnus alalunga*), blackfin (*Thunnus atlanticus*), and longtail (*Thunnus tonggol*) tunas. There are no tuna species present in grey colored areas of the ocean. Competitive interactions and/or niche partitioning are likely to occur in areas with multiple species present

Sepulveda, Musyl, & Brill, 2010; Bertrand, Bard, & Josse, 2002; Olson et al., 2016; Potier et al., 2004; Varghese, Somvanshi, & Dalvi, 2014; Young et al., 2010). Niche partitioning may be less critical for decreasing direct competition among tunas because they are fished throughout the global ocean (Pons et al., 2017). Prey abundances have increased as predation rates have decreased due to fishing, thereby decreasing competition among the highest trophic levels in marine food webs (Baum & Worm, 2009; Essington et al., 2002). Tuna populations are relatively robust to the effects of exploitation (Schindler, Essington, Kitchell, Boggs, & Hilborn, 2002). Therefore, if tunas are more sustainably fished in the future, then they may be in direct competition with each other unless there is niche partitioning so ecological interactions should be considered.

Blood oxygen affinity is one of the primary determinants of hypoxia tolerance of fish (Farrell & Richards, 2009; Mandic, Todgham, & Richards, 2009; Wells, 2009). It is generally quantified as P_{50}, which is the partial pressure of oxygen (pO_2) at which blood is 50% saturated. Blood with a high affinity for oxygen has a low P_{50}, and animals with blood with a low P_{50} are more hypoxia tolerant. A potential trade-off for an animal with high oxygen affinity blood is slow oxygen off-loading at tissues (Yang, Lai, Graham, & Somero, 1992). Highly active animals need fast off-loading of oxygen at muscles, for example, to maintain fast swimming speeds. Oxygen binding to hemoglobin may be either an exothermic or endothermic reaction (i.e., the heat of oxygenation may be either negative or positive, respectively) (Hochachka & Somero, 2002). In the former, higher temperatures reduce oxygen affinity (i.e., increase P_{50}) because heat is released when oxygen binds to the blood pigment. In the latter, higher temperatures increase oxygen affinity (i.e., reduce P_{50}) because heat is absorbed when oxygen binds to the blood pigment. For some tuna species, heat is neither absorbed nor released during blood oxygen binding (the apparent heat of oxygenation, $\Delta H' \approx 0$) due to the presence of multiple forms of hemoglobin—a characteristic which makes their blood oxygen affinity temperature independent (Rossi-Fanelli & Antonini, 1960; Wood, 1980). Tunas have species-specific blood oxygen affinities and $\Delta H'$ values; the former ranging from 2.1 to 5.8 kPa and the latter from −17 to 27 kJ mol (Brill & Bushnell, 1991, 2006; Clark, Seymour, Wells, & Frappell, 2008; Lilly, Bonaventura, Lipnick, & Block, 2015; Lowe, Brill, & Cousins, 2000). The data are from different studies, and the reported species-specific differences may result from differences in experimental protocols. Differences in P_{50} and $\Delta H'$ have, however, been found among very closely related species measured using the same experimental protocols in the same laboratory (e.g., Brill & Bushnell, 1991; Lowe et al., 2000; Mandic et al., 2009), we therefore posit that differences in the blood oxygen binding characteristics among the tunas result from species-specific physiological adaptations.

Mechanistic analysis helps reveal regional and temporal patterns in tunas' habitat and vertical movement (e.g., Horodysky, Cooke, & Brill, 2015; Horodysky, Cooke, Graves, & Brill, 2016; Lehodey et al., 2011). Physiological thresholds for blood oxygen binding have been mapped in the ocean as the P_{50} depth (Mislan, Dunne, & Sarmiento, 2015). The P_{50} depth is the shallowest depth at which pO_2 is equal to

species-specific blood P_{50}. We use P_{50} depth because P_{50} is a primary determinant of hypoxia tolerance (Mandic et al., 2009), and, therefore, P_{50} depth provides a mechanistic assessment of habitat suitability and zonation in hypoxic regions. Our objective is to project effects of climate change on the vertical habitat of tunas using P_{50} depth. Given the differences in oxygen affinity (i.e., blood P_{50}) and temperature sensitivity of blood oxygen affinity (i.e., $\Delta H'$), we test the hypothesis that tuna species are highly likely to display species-specific habitat compression due to changes in P_{50} depth under the effects of climate change which will, in turn, alter the dynamics of competition and resource partitioning among sympatric tuna species.

2 | MATERIALS AND METHODS

2.1 | Data sources

Oceanographic, physiological, and biogeographic data were used as part of this study. The oceanographic data (monthly temperature, oxygen concentration, and salinity on a $1°$ grid) were from the National Oceanographic and Atmospheric Administration (NOAA), National Centers for Environmental Information, World Ocean Atlas 2009 (WOA 2009) (Antonov et al., 2010; Garcia et al., 2010; Locarnini et al., 2009). The physiological data were from the published literature: skipjack tuna: $P_{50} = 3$ kPa, $\Delta H' = 1.5$ kJ mol^{-1} (Brill & Bushnell, 1991); yellowfin: $P_{50} = 2.7$ kPa, $\Delta H' = -0.81$ kJ mol^{-1} (Brill & Bushnell, 1991); southern bluefin tuna: $P_{50} = 2.1$ kPa, $\Delta H' = 27$ kJ mol^{-1} (Clark et al., 2008); bigeye tuna: $P_{50} = 2.1$ kPa, $\Delta H' = -17$ kJ mol^{-1} (Lowe et al., 2000); Pacific bluefin tuna: $P_{50} = 5.8$ kPa, $\Delta H' = 13$ kJ mol^{-1} (Lilly et al., 2015); Atlantic bluefin tuna: $P_{50} = 2.5$ kPa, $\Delta H' = 13$ kJ mol^{-1} (Brill & Bushnell, 2006). P_{50} was measured in blood collected from animals that were captured in the wild and brought to a laboratory facility where they were acclimated to particular temperatures. P_{50} measurements are sensitive to changes in blood chemistry (Hochachka & Somero, 2002), particularly when animals are stressed by activities such as capture from the wild. By using measurements from laboratory acclimated animals, we are able to make geographic assessments for baseline P_{50} of unstressed tunas. Table S1 includes information on acclimation temperatures, and the temperatures that were used to calculate the apparent heat of oxygenation using the Van't Hoff equation. Tuna biogeographic range data were obtained from the International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species (IUCN, 2011, 2014). Biogeographic range data were in vector shape files that were converted into raster NetCDF files with a $1°$ grid using the Geospatial Data Abstraction Library v. 1.11.5 (Warmerdam, 2016) and Generic Mapping Tools v. 5.4.1 for file format conversions (Wessel & Smith, 2015).

2.2 | Model results

Projections were made using temperature and oxygen concentration results from six Earth System Models (CESM1-BGC, GFDL-ESM2G, GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-LR, and MPI-ESM-LR)

obtained from the Coupled Model Intercomparison Project Phase 5 (CMIP5) archive (Aumont & Bopp, 2006; Collins et al., 2011; Dufresne et al., 2013; Dunne et al., 2012, 2013; Gent et al., 2011; Giorgetta et al., 2013; Ilyina et al., 2013; Jones et al., 2011; Lindsay et al., 2014; Palmer & Totterdell, 2001; Taylor, Stouffer, & Meehl, 2012). In contrast to climate models, Earth System Models include numerical representations of the biogeochemical cycling in the ocean in addition to numerical representations of the atmosphere, ocean, and land. The inclusion of biogeochemical cycling in the ocean allows them to project future changes in oxygen concentration. The climate scenario used for this study was Representative Concentration Pathway (RCP) 8.5 which simulates a positive radiative forcing perturbation of 8.5 W m^{-2} in 2100 (Riahi et al., 2011). RCP 8.5 was the most extreme scenario in CMIP5. The model results were bilinearly interpolated to the same grid as the monthly World Ocean Atlas 2009 data, a $1°$ grid with 24 depths ranging from 0 to 1500 m, using the Climate Data Operators v. 1.6.2 (Kornblueh, Mueller, & Schulzweida, 2013). The changes in temperature and oxygen concentration were calculated by subtracting the 30-year average of historical results from 1975 to 2005 from the 30-year average of the future projections from 2070 to 2100. Thirty-year averages were used to suppress the internal variability within the models. The calculated changes in temperature and oxygen concentration were then added to the average of the World Ocean Atlas 2009 data to generate projections for future conditions, thus eliminating the mean biases present in model simulations of the baseline climate.

2.3 | Analysis

Oxygen concentrations in the data and model results were converted into pO_2 (i.e., oxygen partial pressures) to take into account changes in O_2 solubility resulting from differences in temperature and salinity (Seibel, 2011). First, we converted oxygen concentration into percent oxygen saturation using the equations from García and Gordon (1992). The percent oxygen saturation was divided by 0.21 (the fractional atmospheric concentration of oxygen) to get pO_2 in atmospheres (atm); pO_2 was then corrected for the hydrostatic pressure at depth (Enns, Scholander, & Bradstreet, 1965). In the final step, the units for pO_2 were converted into kilopascals (kPa), the SI Units for pressure.

Blood P_{50} (from hereafter referred to as simply "P_{50}") shifts as tuna move vertically if $\Delta H' \neq 0$ because temperature in the water column generally changes with depth, and blood is at ambient temperature as it passes through the gills. We calculated blood P_{50} at all depths using the van't Hoff equation:

$$P_{50(x,y,z)} = 10^{\left(\log P_{50(x,y,10)} - \frac{\Delta H'(1/T_{(x,y,10)} - 1/T_{(x,y,z)})}{2.303R}\right)} \quad (1)$$

where (x,y,z) is (longitude, latitude, depth), $T_{(x,y,10)}$ is the temperature at 10 m, $P_{50(x,y,10)}$ is a measure of blood oxygen affinity at the fishes' acclimation temperature, $T_{(x,y,z)}$ is temperatures at depth intervals below 10 m in the water column, $\Delta H'$ is the apparent heat of oxygenation of whole blood (i.e., the change in blood P_{50} with

temperature in kJ mol^{-1}) measured under open-system conditions (Brill & Bushnell, 1991; Lowe et al., 2000; Wood, 1980), and R is the universal gas constant. We assumed temperature at 10 m depth to be the acclimation temperature (i.e., the temperature within the surface layer) and based the $P_{50(x,y,10)}$ on measurements found in the published literature.

We define the P_{50} depth as the shallowest depth in the ocean where $pO_2 = P_{50}$. P_{50} depths were determined using NOAA Ferret v. 7 (Manke & Smith, 2012) for all the tuna species, and mapped using Python v. 3.5.1 (van Rossum, 2015). Animals can alter their baseline P_{50} to acclimate to different environmental conditions over the course of several days by altering concentrations of guanosine triphosphate, GTP, and adenosine triphosphate, ATP, in the blood (Weber & Lykkeboe, 1978). We assume the animals are acclimated to surface conditions and forays to deeper depths are not long enough for acclimation to a new baseline P_{50} to occur. The projected changes in P_{50} depths from the six Earth System Models were averaged to assess the effect of climate change on tuna habitat thickness and vertical movement patterns. Ensembling of models allows one to take advantage of the cancelation of random (opposing) differences for an overall more robust solution among models of otherwise equivalent skill. We assessed habitat compression based on the changes in P_{50} depth over the current range of each species. Analyses of P_{50} depth in the CMIP5 results were conducted for both future pO_2 and future temperature, and future pO_2 and WOA 2009 temperature. We thus assess the relative impact of each variable on projected P_{50} depths. The overall changes in P_{50} depths for the current range of each species were summarized as boxplots using R v. 3.2.3 (The R Core Team, 2015). The code used for the analysis is archived in Zenodo (https://doi.org/10.5281/zenodo.808742).

3 | RESULTS

3.1 | P_{50} depths

Tunas encounter different temperature and oxygen conditions as they move vertically. Blood P_{50} therefore shifts as tunas with $\Delta H' \neq 0$ descend from the surface layer to depths below the thermocline (Fig. S1). The direction in P_{50} shift is species specific. Bigeye and southern bluefin tunas have the most exothermic ($\Delta H' = -17$ kJ mol^{-1}), and the most endothermic ($\Delta H' = 27$ kJ mol^{-1}), respectively, blood oxygen binding reactions of the tuna species. As such, the P_{50} of bigeye tuna (T. obesus) decreases with depth (Fig. S1a). This, and the low P_{50} of bigeye tuna blood, makes bigeye tuna more hypoxia tolerant than other tunas at depth, while the P_{50} of southern bluefin tuna (T. maccoyii) increases with depth (Fig. S1b), thus making southern bluefin tuna less tolerant of hypoxia than other tunas at depth. Yellowfin (T. albacares) and skipjack (Katsuwonus pelamis) tunas have temperature-independent blood oxygen binding reactions ($\Delta H' \approx 0$), so P_{50} does not shift as these tuna species move vertically in the water column. Therefore, the hypoxia tolerance of these species is the same at the surface and depth. Yellowfin, skipjack, bigeye, and southern bluefin have similar oxygen

affinity (P_{50} range 2.1 to 3) for the surface. However, if there is a steep thermocline, the blood oxygen affinity of bigeye tuna is much higher, and the blood oxygen affinity of southern bluefin is much lower, than blood oxygen affinities of yellowfin and skipjack tunas at deeper depths.

The geographic ranges of tuna species have varying degrees of overlap with their P_{50} depth areas (Figure 2). Almost the entire geographic range of Pacific bluefin tuna has a P_{50} depth restriction. Bigeye and skipjack tunas occupy geographic areas that include areas where vertical movements are restricted by P_{50} depth (Figure 2). The extent of the vertical movements of Atlantic bluefin tuna (T. thynnus) and southern bluefin tuna is not restricted by P_{50} depth over most of their geographic ranges (Fig. S2). P_{50} depths are shallowest in the tropics (Figure 2).

3.2 | P_{50} depth changes in the future

Climate change is projected to change P_{50} depths in many geographic areas and thus the depth ranges occupied by tunas (Figure 2). Figure 2 includes three tuna species, bigeye, skipjack, and Pacific bluefin tunas, with P_{50} depths in large proportions of their habitat areas. The P_{50} depths and habitat area of yellowfin tuna are similar to skipjack tuna (Fig. S2). Atlantic and southern bluefin tunas have little to no overlap between the area with P_{50} depths and the habitat area (Fig. S2). The greatest changes are projected to occur in the Northwest Pacific Ocean where P_{50} depths are likely to be >200 m shallower at the edges of the geographic ranges of bigeye, yellowfin, and skipjack tunas (Figures 2, S2). Shoaling of P_{50} depths should result in a compression of the vertical habitat. In contrast, P_{50} depths are projected to be deeper in the much of the tropics (30°S to 30°N), particularly in regions where P_{50} depths are currently the most shallow (Figure 2). Deeper P_{50} depths indicate an expansion of the vertical habitat. As we note in the discussion, a caveat to this finding of deeper P_{50} depths in the tropics in the future is that trends in modeled oxygen do not agree with observations from the eastern tropical Pacific.

Overall, the ESM's project more vertical compression than expansion of tuna habitats in the future (Figure 3). The greatest compression is projected for the habitats of tuna species with endothermic blood oxygen binding, particularly southern bluefin tuna (Figure 3). Although most of the habitat of southern bluefin tuna does not have a P_{50} depth (Fig. S2), changes in P_{50} depths are projected to occur in the spawning region (Figure 4). P_{50} depths of southern bluefin tuna are projected to be 80–600 m shallower, and the P_{50} depth area is projected to expand in size (Figure 4). The projected changes in P_{50} depths are due to either changes in temperature or oxygen in the water column. The median P_{50} depth of southern bluefin tuna is projected to be 410 m shallower in the future and 180 m of the projected shift is due to temperature changes in the water column. In contrast, temperature is projected to cause <10 m change in the median P_{50} depths of yellowfin, skipjack, bigeye, and Pacific bluefin tunas. The vertical separation between P_{50} depths of pairs of tuna species is projected to change in the Pacific Ocean, Arabian Sea, and
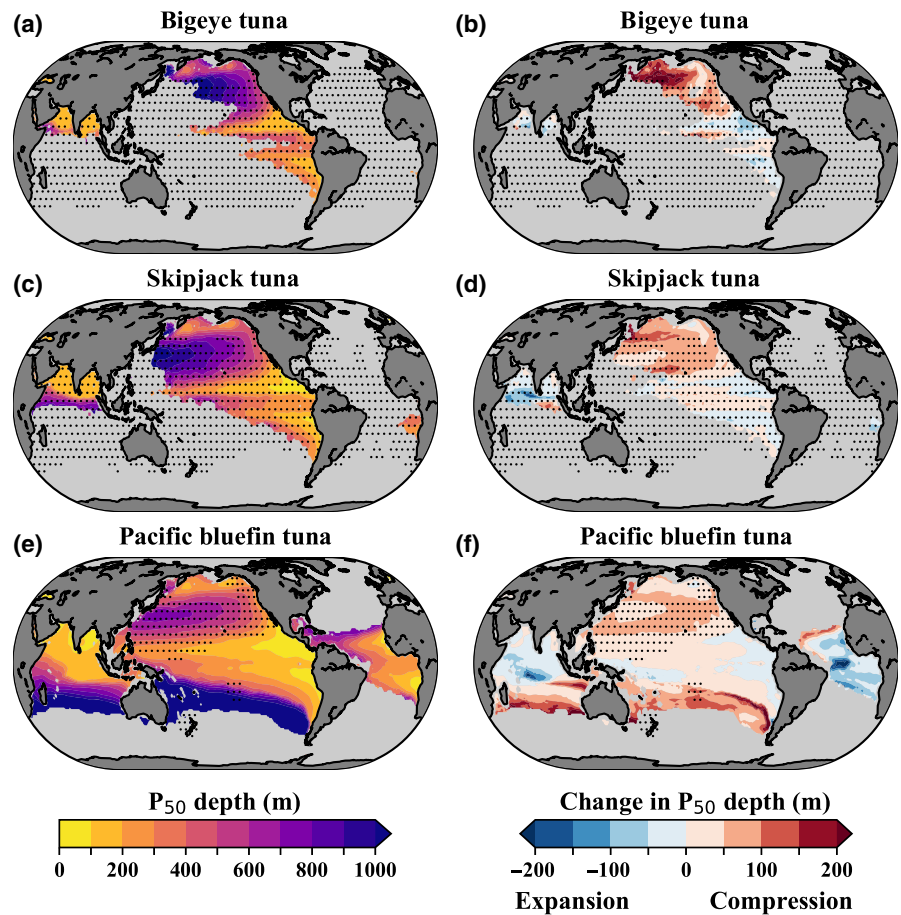
FIGURE 2 P$_{50}$ depths and the projected changes in P$_{50}$ depths due to climate change. Grey indicates locations where there are no P$_{50}$ depths. (a), (c), and (e) are the present-day P$_{50}$ depths of bigeye, skipjack, and Pacific bluefin tuna calculated using data from World Ocean Atlas 2009. (b), (d), and (f) are the average projected changes in P$_{50}$ depths for bigeye, skipjack, and Pacific bluefin tunas from the six Earth System Models included in the Climate Model Intercomparison Project 5. Expansion occurs in locations where P$_{50}$ depths are deeper in the future. Compression occurs in locations where P$_{50}$ depths are shallower in the future. The stippling indicates known habitat for each tuna species (IUCN, 2011, 2014)

Bay of Bengal (Figure 5). In the North Pacific Ocean and the Northern Tropical Pacific Ocean, the vertical separation between all pairs of tuna species is projected to decrease. There is only a very small area where the vertical separation between all pairs of tuna species is projected to expand. In general, vertical separation between pairs of tuna species is not projected to increase or decrease uniformly at the same geographic location (Figure 5).

4 | DISCUSSION

Our results suggest that climate change will impact the vertical environment of tunas because of species-specific differences in blood oxygen affinity (Figure 3). The P$_{50}$ depths of tunas with endothermic blood oxygen binding reactions, Pacific and southern bluefin tunas, are projected to be shallower in the future (Figure 3). The greatest decreases in oxygen concentrations are occurring in the North Pacific (Bopp et al., 2013), which is the habitat of Pacific bluefin tuna (*T. orientalis*), a species with endothermic blood oxygen binding. Tuna species with exothermic and temperature-independent blood oxygen affinity also have habitats in the North Pacific including bigeye, skipjack, and yellowfin tunas, but in low abundance relative to tropical regions. Interestingly, the greatest vertical compression is projected to be just outside the northern range of these three species (Figures 2, S3). Decreases in oxygen concentrations are also projected

for the Eastern Indian Ocean where southern bluefin tuna spawn (Bopp et al., 2013). The vertical habitat of southern bluefin tuna is projected to be >500 m shallower in some locations in this region (Figure 4). The underlying cause for changes in P$_{50}$ depth could be due to temperature increases shifting blood oxygen affinity (i.e., P$_{50}$). Warming in the surface ocean is projected to be faster than in the deeper ocean, increasing the temperature gradient with depth. P$_{50}$ increases as species with endothermic blood oxygen binding reactions swim from the warm surface layer to cold deep depths (Fig. S1b). Therefore, southern bluefin tuna, which has an endothermic blood oxygen binding reaction, is projected to reach P$_{50}$ at shallower depths in the future.

Multiple tuna species are sympatric in the North Pacific where the ESMs project the greatest changes in P$_{50}$ depths will occur (Figures 1 and 2). Tunas have species-specific vertical movement patterns (e.g., Bernal et al., 2010; Schaefer et al., 2009). Skipjack and yellowfin are most frequently in the upper thermocline (<100 m depth) during both day and night and make only occasional forays for brief periods down to deeper depths during the day (Schaefer & Fuller, 2007; Schaefer et al., 2009, 2011). Shallower and deeper P$_{50}$ depths in the future may decrease or increase, respectively, the frequency with which these species can forage at deeper depths (Figure 2). Skipjack and yellowfin tunas exhibit similar vertical habitat usage behaviors and also both have temperature-independent blood oxygen affinities. The degree to which behaviors and physiological
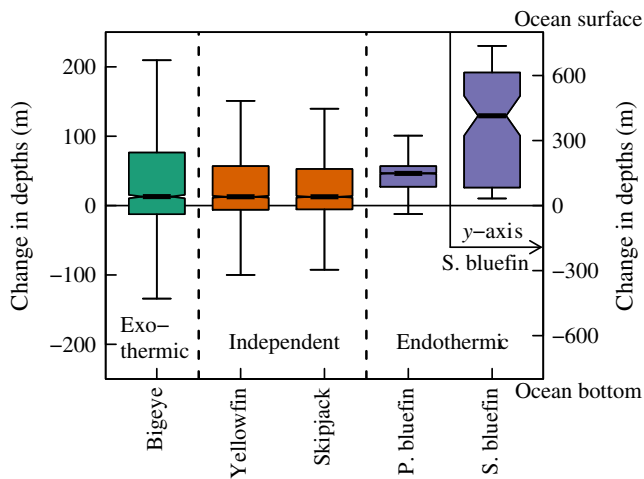
FIGURE 3 Compression of P_{50} depths in tuna habitats projected for the end of the century. P. bluefin and S. bluefin are Pacific and southern bluefin tunas, respectively. The right y-axis is for S. bluefin, which has much larger projected changes than the other species. Tuna species with blood oxygen binding reactions that are endothermic are projected to experience more compression than species with blood oxygen binding reactions that are exothermic or temperature independent. There are no boxes for Atlantic bluefin tuna because the geographic range of this species does not overlap with the geographic area where individuals would encounter a P_{50} depth during descents (Figs. S2, S3). Outliers that are greater than 1.5 times the interquartile range are not shown

FIGURE 5 Locations where the vertical separation in P_{50} depths of tuna species are projected to change by more than 10 m. The species include skipjack (*K. pelamis*), yellowfin (*T. albacares*) southern bluefin (*T. maccoyii*), bigeye (*T. obesus*), and Pacific bluefin (*T. orientalis*). Expansion: all pairwise vertical separations increase. Mixed: pairwise vertical separations increase and decrease. Compression: all pairwise vertical separations decrease. Competition is projected to increase in areas with compression and decrease in areas with expansion. For areas with mixed changes in vertical separation, competitive interactions are projected to increase for some pairs of species and decrease for other pairs of species

characteristics are linked will need to be investigated in a future study. Bigeye tuna are most frequently in the upper thermocline at night and frequently at depths deeper than 200 m during the day from which they make regular forays to the surface layer where oxygen concentrations are higher and temperatures are warmer (Schaefer & Fuller, 2010; Schaefer et al., 2009). A change in the P_{50} depth may either influence the daytime foraging depth or alter the frequency of trips to the surface layer during the day (Figure 2). Although these behaviors are considered characteristic, bigeye tuna occasionally dive to depths >1000 m to forage below the lower
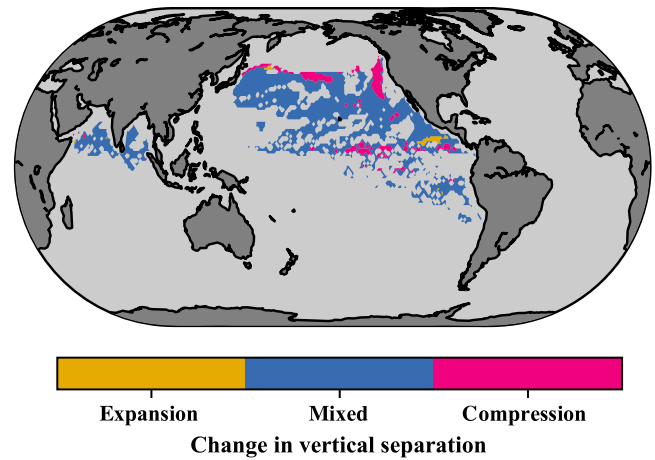
oxycline (Schaefer et al., 2009). Changes in P_{50} depths could alter the thickness of oxycline making it either easier or more difficult for bigeye tuna to access areas below the oxycline (Figure 2).

The changes in P_{50} depth separations between pairs of tuna species may lead to changes in the frequency of competitive interactions, especially in deeper foraging zones (Figure 5). Both increases and decreases in species-specific vertical movement patterns resulting from P_{50} depths are projected to occur at the same locations between different pairs of tuna species. As a result, competition is not projected to universally increase or decrease. The main exception is the North Pacific where projected decreases in the vertical
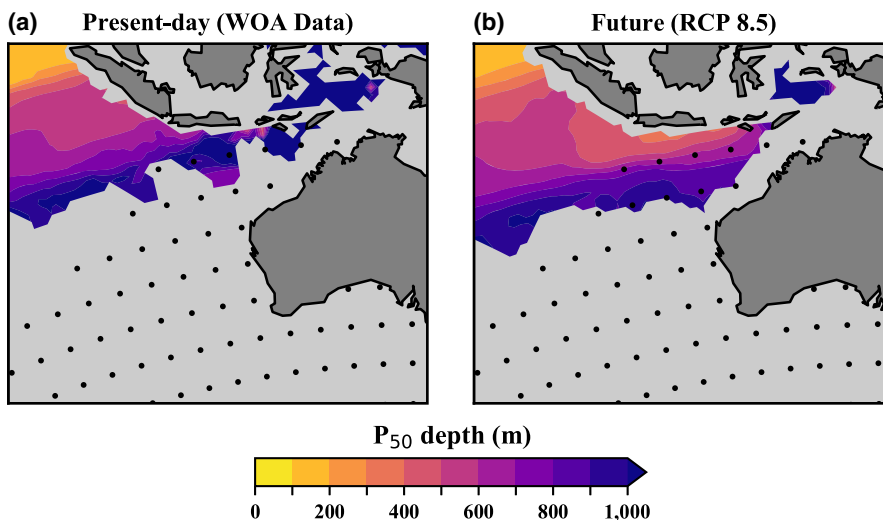

FIGURE 4 P_{50} depths in the spawning area of southern bluefin tuna. (a) Present-day P_{50} depths based on World Ocean Atlas (WOA) data. (b) Future projections of P_{50} depths based on greenhouse gas emissions scenario RCP 8.5. The stippling indicates known habitat (IUCN, 2011). In the future, the area with a P_{50} depth is projected to expand south, further into the spawning region of southern bluefin tuna. The P_{50} depths are also projected to be shallower

separation among all pairs of tuna species indicate a potential increase in the frequency of interactions (Figure 5). The effects of climate change on vertical movements and distribution of tuna prey species are also relevant for determining frequency of competitive interactions among tuna species (Polovina, 1996). If the vertical distributions of prey species shift similarly to that of tunas, there may be few changes in ecological interactions. Also, because fish track environmental variables and shift the geographic centers of their range to remain in optimal conditions (Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013), horizontal shifts in tunas' geographic ranges may preempt any effects of climate change on their vertical habitats. As fish species reorganize in a "musical chairs" of habitats, some habitats may be excluded due to geographic range incompatibility or increases in ecological interactions. Geographic ranges of tunas cover much of the global ocean, so there is limited potential for tunas to change geographic ranges without also increasing competitive interactions (Figure 1).

Factors in addition to hypoxia tolerance limit the vertical extent of tuna habitat. Atlantic bluefin tuna occupy a region where oxygen concentrations change only minimally with depth, which is exemplified by the lack of P_{50} depths throughout the range of this species (Fig. S2). However, Atlantic bluefin tuna have limitations on vertical movements (Walli et al., 2009). Tuna maintain tissues at optimal temperatures by spending time in warmer surface waters (Brill, Dewar, & Graham, 1994; Dewar, Graham, & Brill, 1994; Graham & Dickson, 2001; Malte, Larsen, Musyl, & Brill, 2007), which means that vertical movements are limited by the length of time tuna can remain at depth before needing to return to the warmer surface layer to get a "gulp of heat". Another factor that limits the depths to which tuna can descend is the effect of temperature on cardiac function. Because of circulatory anatomy, the heart remains at ambient environmental temperature which results in a decline in cardiac performance at colder deeper depths (Galli, Shiels, & Brill, 2009). Bigeye tuna, which spend the most time relative to other tuna species at deeper depths, has adaptations, including enhanced cardiac Ca^{2+} cycling and stimulation using adrenaline, to maintain cardiac performance in colder temperatures (Galli et al., 2009). While a combination of these factors limits the vertical extent of tuna habitats, the effects of climate change on oxygen concentration will have the greatest impact of tuna vertical habitat.

Our results also suggest that blood oxygen affinity is projected to change the spawning area for southern bluefin tuna, which is located in the Indian Ocean off the coast of northwestern Australia (Hobday et al., 2016). Adaptation tends to be more rapid when directly related to reproduction, therefore, tracking changes in P_{50} and $\Delta H'$ of southern bluefin tuna over time may provide a record of adaptation to climate change. A key step will be to connect physiological changes to gene expression and environmental changes. Tunas have physiological and morphological differences in addition to the differences in blood oxygen affinity (e.g., Bernal et al., 2010; Graham, 1975). For example, Atlantic bluefin, Pacific bluefin, and southern bluefin tunas (whose blood oxygen binding is endothermic) do not have central vascular counter current heat exchangers (i.e.,

those formed from branches of dorsal aorta and postcardinal vein contained within the hemal arch of the spinal column), and rely exclusively on lateral heat exchangers to supply blood to the red muscle fiber portions of the swimming muscles (Graham, 1975; Graham & Dickson, 2001).

We used oxygen and temperature results from Earth System Models to project changes in tuna physiology and ecology over the next century. Models have many uncertainties which can be reduced by combining results from multiple models, as we did. Even so, the temperature results were generally more robust than the oxygen results (Bopp et al., 2013). Robustness is determined by comparing model results to measurements over a historical period. Temperature mean state from the models is similar to observations throughout most of the global ocean (Bopp et al., 2013). Oxygen mean state is similar to observations in some regions of the ocean including the North Pacific where the greatest changes in blood oxygen binding and competitive interactions are projected to occur (Figures 2 and 5) (Bopp et al., 2013). The oxygen mean state is, however, much less robust in the Eastern Tropical Pacific Ocean where P_{50} depths are the shallowest (Figure 2). Recent observations show oxygen concentrations decreasing in the Eastern Tropical Pacific Ocean (Schmidtko, Stramma, & Visbeck, 2017; Stramma, Johnson, Sprintall, & Mohrholz, 2008), but there were no changes in oxygen concentrations in the model mean state for the region over the same period (Bopp et al., 2013). Cabré, Marinov, Bernardello, and Bianchi (2015) found that all the models overestimated the total volume of hypoxic water in the Eastern Tropical Pacific because of biases in ventilation. Blood oxygen affinity of tunas is not projected to change in the Eastern Tropical Pacific based on results from existing models, but this projection could change as improvements are made to the parameterizations for ventilation in new model versions. The measurements of blood oxygen affinity also have uncertainties; the measurements used here were made by different researchers, using different equipment and procedures over a 20-year period on a small number of animals. The limited numbers of measurements ignore potential intraspecies plasticity and geographic variation in the blood oxygen affinity of various tuna species. Furthermore, the effects of blood oxygen affinity on vertical movement behavior and metabolic rates of tuna still need to be determined. In summary, the projected effects of climate change on tuna habitats are uncertain and will be further improved by a combination of Earth System Model development and additional measurements of blood oxygen affinity, behavior, and metabolism.

Resource managers will benefit from information on the physiological mechanisms controlling habitat use when making decisions for tuna fisheries in a changing climate (e.g., Brill & Lutcavage, 2001; Horodysky et al., 2015, 2016; McKenzie et al., 2016). Ocean warming and changes in the depths of the oxycline could have dire consequences for the movements, distribution, and abilities of tunas to withstand various levels of fishing mortality if the frequency of competitive interactions increases or prey have refuges from predation. Our results imply that different tuna species will experience different degrees of habitat compression. We project that Pacific and southern bluefin tunas will experience the greatest habitat compression.

Fisheries management should account for physiological differences in the responses of tuna species to changes in the temperature and oxygen conditions of the upper water column resulting from climate change. As improvements to Earth System Models further decrease uncertainties, continued efforts to link model projections of environmental changes to physiological consequences will provide a more complete picture of pelagic habitat structure over the 21st century.

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SUPPORTING INFORMATION

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