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

Running head: Climate change projections for tuna habitats

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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 sub-daily 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

59 conditions, we provide a mechanistic basis to project the effects of anthropogenic climate change
60 on tuna habitats.

61

62 **Introduction**

63 Many pelagic animal species cross steep temperature and oxygen gradients during their daily
64 vertical migrations. Reduced ambient oxygen levels (i.e., hypoxia) at depth limit the vertical
65 movements of tunas in some regions depending on species-specific hypoxia tolerance (e.g., Brill,
66 1994; Schaefer *et al.*, 2009; Stramma *et al.*, 2010, 2011; Koslow *et al.*, 2011; Gilly *et al.*, 2013).
67 Climate models project warmer temperatures and lower oxygen concentrations in the pelagic
68 realms of the world's oceans by 2100 (Bopp *et al.*, 2013; Ciais *et al.*, 2014; Rhein *et al.*, 2014);
69 and these effects have been referred to as “habitat compression” (Prince & Goodyear, 2007;
70 Prince *et al.*, 2010). Habitat compression may have pervasive effects on marine ecosystems by
71 altering predator-prey and competitive interactions (e.g., Stramma *et al.*, 2010; Lehodey *et al.*,
72 2011; Gilly *et al.*, 2013; Gallo & Levin, 2016).

73 Tunas are large predators that often make extensive vertical movements (e.g., Holland *et al.*,
74 1990; Brill *et al.*, 1999; Block *et al.*, 2001, 2011; Musyl *et al.*, 2003; Schaefer & Fuller, 2007,
75 2010; Walli *et al.*, 2009; Howell *et al.*, 2010; Schaefer *et al.*, 2011) in order to forage (Pusineri *et al.*,
76 2008; Young *et al.*, 2010). Tunas exhibit different behaviors when tracking prey vertically in
77 the water column (Schaefer *et al.*, 2009). The typical characteristic behavior for bigeye tuna is to
78 remain in the surface water at night when the deep scattering layer organisms are at the surface
79 and follow the deep scattering layer organisms to deeper depths just above the oxygen minimum
80 layers during the day (Schaefer *et al.*, 2009; Schaefer & Fuller, 2010). When at deeper depths,
81 bigeye tuna repetitively return to shallower depths because they cannot remain in cold, hypoxic
82 conditions for the entire day (Schaefer *et al.*, 2009; Schaefer & Fuller, 2010). Yellowfin and
83 skipjack tunas remain in the surface waters during both night and day (Schaefer & Fuller, 2007;
84 Schaefer *et al.*, 2011). They make forays to deeper depths during the day to forage in the deep
85 scattering layer when there are no other sources of food at the surface (Schaefer & Fuller, 2007;
86 Schaefer *et al.*, 2011). However, they can only remain at deeper depths for brief periods because
87 they are not hypoxia tolerant (Schaefer & Fuller, 2007; Schaefer *et al.*, 2011). These foraging
88 behaviors influence frequency of vertical habitat usage by different tunas.

89 Multiple tuna species are sympatric (Fig. 1), but analyses of prey composition in the water
90 column, tuna gut contents, and foraging depths indicate that the ability to tolerate temperature
91 and oxygen levels at depth is critical for niche partitioning (Bertrand *et al.*, 2002; Potier *et al.*,
92 2004; Bernal *et al.*, 2010; Young *et al.*, 2010; Varghese *et al.*, 2014; Olson *et al.*, 2016). Niche
93 partitioning may be less critical for decreasing direct competition among tunas because they are
94 fished throughout the global ocean (Pons *et al.*, 2017). Prey abundances have increased as
95 predation rates have decreased due to fishing, thereby decreasing competition among the highest
96 trophic levels in marine food webs (Essington *et al.*, 2002; Baum & Worm, 2009). Tuna
97 populations are relatively robust to the effects of exploitation (Schindler *et al.*, 2002). Therefore,
98 if tunas are more sustainably fished in the future, then they may be in direct competition with
99 each other unless there is niche partitioning so ecological interactions should be considered.

100 Blood-oxygen affinity is one of the primary determinants of hypoxia tolerance of fish (Farrell
101 & Richards, 2009; Mandic *et al.*, 2009; Wells, 2009). It is generally quantified as P_{50} , which is
102 the partial pressure of oxygen (pO_2) at which blood is 50% saturated. Blood with a high affinity
103 for oxygen has a low P_{50} , and animals with blood with a low P_{50} are more hypoxia tolerant. A
104 potential trade-off for an animal with high oxygen affinity blood is slow oxygen off-loading at
105 tissues (Yang *et al.*, 1992). Highly active animals need fast off-loading of oxygen at muscles, for
106 example, to maintain fast swimming speeds. Oxygen binding to hemoglobin may be either an
107 exothermic or endothermic reaction (i.e., the heat of oxygenation may be either negative or
108 positive, respectively) (Hochachka & Somero, 2002). In the former, higher temperatures reduce
109 oxygen affinity (i.e., increase P_{50}) because heat is released when oxygen binds to the blood
110 pigment. In the latter, higher temperatures increase oxygen affinity (i.e., reduce P_{50}) because heat
111 is absorbed when oxygen binds to the blood pigment. For some tuna species, heat is neither
112 absorbed or released during blood oxygen binding (the apparent heat of oxygenation, $\Delta H' \approx 0$)
113 due to the presence of multiple forms of hemoglobin - a characteristic which makes their blood
114 oxygen affinity temperature-independent (Rossi-Fanelli & Antonini, 1960; Wood, 1980). Tunas
115 have species-specific blood oxygen affinities and $\Delta H'$ values; the former ranging from 2.1 to 5.8
116 kPa and the latter from -17 to 27 kJ mol (Brill & Bushnell, 1991, 2006; Lowe *et al.*, 2000; Clark
117 *et al.*, 2008; Lilly *et al.*, 2015). The data are from different studies, and the reported species-
118 specific differences may result from differences in experimental protocols. Differences in P_{50} and
119 $\Delta H'$ have, however, been found among very closely related species measured using the same

120 experimental protocols in the same laboratory (e.g., Brill & Bushnell, 1991; Lowe *et al.*, 2000;
121 Mandic *et al.*, 2009), we therefore posit that differences in the blood oxygen binding
122 characteristics among the tunas result from species-specific physiological adaptations.

123 Mechanistic analysis helps reveal regional and temporal patterns in tunas' habitat and vertical
124 movement (e.g., Lehodey *et al.*, 2011; Horodysky *et al.*, 2015, 2016). Physiological thresholds
125 for blood-oxygen binding have been mapped in the ocean as the P_{50} depth (Mislán *et al.*, 2015).
126 The P_{50} depth is the shallowest depth at which pO_2 is equal to species-specific blood P_{50} . We use
127 P_{50} depth because P_{50} is a primary determinant of hypoxia tolerance (Mandic *et al.*, 2009), and,
128 therefore, P_{50} depth provides a mechanistic assessment of habitat suitability and zonation in
129 hypoxic regions. Our objective is to project effects of climate change on the vertical habitat of
130 tunas using P_{50} depth. Given the differences in oxygen affinity (i.e., blood P_{50}) and temperature
131 sensitivity of blood oxygen affinity (i.e., $\Delta H'$), we test the hypothesis that tuna species are highly
132 likely to display species-specific habitat compression due to changes in P_{50} depth under the
133 effects of climate change which will, in turn, alter the dynamics of competition and resource
134 partitioning among sympatric tuna species.

135 **Materials and Methods**

136 *Data sources*

137 Oceanographic, physiological, and biogeographic data were used as part of this study. The
138 oceanographic data (monthly temperature, oxygen concentration, and salinity on a 1° grid) were
139 from the National Oceanographic and Atmospheric Administration (NOAA), National Centers
140 for Environmental Information, World Ocean Atlas 2009 (WOA 2009) (Locarnini *et al.*, 2009;
141 Antonov *et al.*, 2010; Garcia *et al.*, 2010). The physiological data were from the published
142 literature: skipjack tuna: $P_{50} = 3$ kPa, $\Delta H' = 1.5$ kJ mol⁻¹ (Brill & Bushnell, 1991); yellowfin: P_{50}
143 $= 2.7$ kPa, $\Delta H' = -0.81$ kJ mol⁻¹ (Brill & Bushnell, 1991); southern bluefin tuna: $P_{50} = 2.1$ kPa,
144 $\Delta H' = 27$ kJ mol⁻¹ (Clark *et al.*, 2008); bigeye tuna: $P_{50} = 2.1$ kPa, $\Delta H' = -17$ kJ mol⁻¹ (Lowe *et al.*
145 *et al.*, 2000); Pacific bluefin tuna: $P_{50} = 5.8$ kPa, $\Delta H' = 13$ kJ mol⁻¹ (Lilly *et al.*, 2015); Atlantic
146 bluefin tuna: $P_{50} = 2.5$ kPa, $\Delta H' = 13$ kJ mol⁻¹ (Brill & Bushnell, 2006). P_{50} were measured in
147 blood collected from animals that were captured in the wild and brought to a laboratory facility
148 where they were acclimated to particular temperatures. P_{50} measurements are sensitive to
149 changes in blood chemistry (Hochachka & Somero, 2002), particularly when animals are stressed
150 by activities such as capture from the wild. By using measurements from laboratory acclimated

151 animals, we are able to make geographic assessments for baseline P_{50} of unstressed tunas. Table
152 S1 includes information on acclimation temperatures, and the temperatures that were used to
153 calculate the apparent heat of oxygenation using the Van't Hoff equation. Tuna biogeographic
154 range data were obtained from the International Union for Conservation of Nature and Natural
155 Resources (IUCN) Red List of Threatened Species (IUCN, 2011, 2014). Biogeographic range
156 data were in vector shape files that were converted to raster NetCDF files with a 1° grid using the
157 Geospatial Data Abstraction Library v. 1.11.5 (Warmerdam, 2016) and Generic Mapping Tools
158 v. 5.4.1 for file format conversions (Wessel & Smith, 2015).

159 *Model results*

160 Projections were made using temperature and oxygen concentration results from six Earth
161 System Models (CESM1-BGC, GFDL-ESM2G, GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-
162 LR, MPI-ESM-LR) obtained from the Coupled Model Intercomparison Project Phase 5 (CMIP5)
163 archive (Palmer & Totterdell, 2001; Aumont & Bopp, 2006; Collins *et al.*, 2011; Gent *et al.*,
164 2011; Jones *et al.*, 2011; Dunne *et al.*, 2012, 2013; Taylor *et al.*, 2012; Dufresne *et al.*, 2013;
165 Giorgetta *et al.*, 2013; Ilyina *et al.*, 2013; Lindsay *et al.*, 2014). In contrast to climate models,
166 Earth System Models include numerical representations of the biogeochemical cycling in the
167 ocean in addition to numerical representations of the atmosphere, ocean, and land. The inclusion
168 of biogeochemical cycling in the ocean allows them to project future changes in oxygen
169 concentration. The climate scenario used for this study was Representative Concentration
170 Pathway (RCP) 8.5 which simulates a positive radiative forcing perturbation of 8.5 W m^{-2} in
171 2100 (Riahi *et al.*, 2011). RCP 8.5 was the most extreme scenario in CMIP5. The model results
172 were bilinearly interpolated to the same grid as the monthly World Ocean Atlas 2009 data, a 1°
173 grid with 24 depths ranging from 0 to 1500 m, using the Climate Data Operators v. 1.6.2
174 (Kornbluh *et al.*, 2013). The changes in temperature and oxygen concentration were calculated
175 by subtracting the 30 year average of historical results from 1975 to 2005 from the 30 year
176 average of the future projections from 2070 to 2100. Thirty-year averages were used to suppress
177 the internal variability within the models. The calculated changes in temperature and oxygen
178 concentration were then added to the average of the World Ocean Atlas 2009 data to generate
179 projections for future conditions, thus eliminating the mean biases present in model simulations
180 of the baseline climate.

181 *Analysis*

182 Oxygen concentrations in the data and model results were converted to pO₂ (i.e., oxygen
183 partial pressures) to take into account changes in O₂ solubility resulting from differences in
184 temperature and salinity (Seibel, 2011). First, we converted oxygen concentration to percent
185 oxygen saturation using the equations from Garcia and Gordon (1992). The percent oxygen
186 saturation was divided by 0.21 (the fractional atmospheric concentration of oxygen) to get pO₂ in
187 atmospheres (atm); pO₂ was then corrected for the hydrostatic pressure at depth (Enns *et al.*,
188 1965). In the final step, the units for pO₂ were converted to kilopascals (kPa), the SI Units for
189 pressure.

190 Blood P₅₀ (from hereafter referred to as simply as “P₅₀”) shifts as tuna move vertically if
191 $\Delta H' \neq 0$ because temperature in the water column generally changes with depth, and blood is at
192 ambient temperature as it passes through the gills. We calculated blood P₅₀ at all depths using the
193 van't Hoff equation:

$$194 \quad P_{50(x,y,z)} = 10^{\left(\log P_{50(x,y,10)} - \frac{\Delta H' (1/T_{(x,y,10)} - 1/T_{(x,y,z)})}{2.303R} \right)} \quad (1)$$

195 where (x,y,z) are (longitude, latitude, depth), T_(x,y,10) is the temperature at 10 m, P_{50(x,y,10)} is a
196 measure of blood oxygen affinity at the fishes' acclimation temperature, T_(x,y,z) are temperatures
197 at depth intervals below 10 m in the water column, $\Delta H'$ is the apparent heat of oxygenation of
198 whole blood (i.e., the change in blood P₅₀ with temperature in kJ mol⁻¹) measured under open-
199 system conditions (Wood, 1980; Brill & Bushnell, 1991; Lowe *et al.*, 2000), and R is the
200 universal gas constant. We assumed temperature at 10 m depth to be the acclimation temperature
201 (i.e., the temperature within the surface layer) and based the P_{50(x,y,10)} on measurements found in
202 the published literature.

203 We define the P₅₀ depth as the shallowest depth in the ocean where pO₂ = P₅₀. P₅₀ depths
204 were determined using NOAA Ferret v. 7 (Manke & Smith, 2012) for all the tuna species, and
205 mapped using Python v. 3.5.1 (van Rossum, 2015). Animals can alter their baseline P₅₀ to
206 acclimate to different environmental conditions over the course of several days by altering
207 concentrations of guanosine triphosphate, GTP, and adenosine triphosphate, ATP, in the blood
208 (Weber & Lykkeboe, 1978). We assume the animals are acclimated to surface conditions and
209 forays to deeper depths are not long enough for acclimation to a new baseline P₅₀ to occur. The
210 projected changes in P₅₀ depths from the six Earth System Models were averaged to assess the
211 effect of climate change on tuna habitat thickness and vertical movement patterns. Ensembling of

212 models allows one to take advantage of the cancelation of random (opposing) differences for an
213 overall more robust solution among models of otherwise equivalent skill. We assessed habitat
214 compression based on the changes in P_{50} depth over the current range of each species. Analyses
215 of P_{50} depth in the CMIP5 results were conducted for both future pO_2 and future temperature,
216 and future pO_2 and WOA 2009 temperature. We thus assess the relative impact of each variable
217 on projected P_{50} depths. The overall changes in P_{50} depths for the current range of each species
218 were summarized as boxplots using R v. 3.2.3 (The R Core Team, 2015). The code used for the
219 analysis is archived in Zenodo (<https://doi.org/10.5281/zenodo.808742>).

220

221 **Results**

222 *P₅₀ depths*

223 Tunas encounter different temperature and oxygen conditions as they move vertically. Blood
224 P_{50} therefore shifts as tunas with $\Delta H \neq 0$ descend from the surface layer to depths below the
225 thermocline (Fig. S1). The direction in P_{50} shift is species-specific. Bigeye and southern bluefin
226 tunas have the most exothermic ($\Delta H = -17 \text{ kJ mol}^{-1}$), and the most endothermic ($\Delta H = 27 \text{ kJ}$
227 mol^{-1}), respectively, blood-oxygen binding reactions of the tuna species. As such, the P_{50} of
228 bigeye tuna (*T. obesus*) decreases with depth (Fig. S1a). This, and the low P_{50} of bigeye tuna
229 blood, makes bigeye tuna more hypoxia tolerant than other tunas at depth, while the P_{50} of
230 southern bluefin tuna (*T. maccoyii*) increases with depth (Fig. S1b) thus making southern bluefin
231 tuna less tolerant of hypoxia than other tunas at depth. Yellowfin (*T. albacares*) and skipjack
232 (*Katsuwonus pelamis*) tunas have temperature-independent blood-oxygen binding reactions (ΔH
233 ≈ 0) so P_{50} does not shift as these tuna species move vertically in the water column. Therefore the
234 hypoxia tolerance of these species is the same at the surface and depth. Yellowfin, skipjack,
235 bigeye, and southern bluefin have similar oxygen affinity (P_{50} range 2.1 to 3) for the surface.
236 However, if there is a steep thermocline, the blood oxygen affinity of bigeye tuna is much higher,
237 and the blood oxygen affinity of southern bluefin is much lower, than blood oxygen affinities of
238 yellowfin and skipjack tunas at deeper depths.

239 The geographic ranges of tuna species have varying degrees of overlap with their P_{50} depth
240 areas (Fig. 2). Almost the entire geographic range of Pacific bluefin tuna has a P_{50} depth
241 restriction. Bigeye and skipjack tunas occupy geographic areas that include areas where vertical
242 movements are restricted by P_{50} depth (Fig. 2). The extent of the vertical movements of Atlantic

243 bluefin tuna (*T. thynnus*) and southern bluefin tuna are not restricted by P_{50} depth over most of
244 their geographic ranges (Fig. S2). P_{50} depths are shallowest in the tropics (Fig. 2).

245 *P₅₀ depth changes in the future*

246 Climate change is projected to change P_{50} depths in many geographic areas and thus the
247 depth ranges occupied by tunas (Fig. 2). Fig. 2 includes three tuna species, bigeye, skipjack, and
248 Pacific bluefin tunas, with P_{50} depths in large proportions of their habitat areas. The P_{50} depths
249 and habitat area of yellowfin tuna are similar to skipjack tuna (Fig. S2). Atlantic and southern
250 bluefin tunas have little to no overlap between the area with P_{50} depths and the habitat area (Fig.
251 S2). The greatest changes are projected to occur in the Northwest Pacific Ocean where P_{50} depths
252 are likely to be >200 m shallower at the edges of the geographic ranges of bigeye, yellowfin, and
253 skipjack tunas (Fig. 2, S2). Shoaling of P_{50} depths should result in a compression of the vertical
254 habitat. In contrast, P_{50} depths are projected to be deeper in the much of the tropics (30°S to
255 30°N), particularly in regions where P_{50} depths are currently the most shallow (Fig. 2). Deeper
256 P_{50} depths indicate an expansion of the vertical habitat. As we note in the discussion, a caveat to
257 this finding of deeper P_{50} depths in the tropics in the future is that trends in modeled oxygen do
258 not agree with observations from the eastern tropical Pacific.

259 Overall, the ESM's project more vertical compression than expansion of tuna habitats in the
260 future (Fig. 3). The greatest compression is projected for the habitats of tuna species with
261 endothermic blood-oxygen binding, particularly southern bluefin tuna (Fig. 3). Although most of
262 the habitat of southern bluefin tuna does not have a P_{50} depth (Fig. S2), changes in P_{50} depths are
263 projected to occur in the spawning region (Fig. 4). P_{50} depths of southern bluefin tuna are
264 projected to be 80 to 600 m shallower, and the P_{50} depth area is projected to expand in size (Fig.
265 4). The projected changes in P_{50} depths are due to either changes in temperature or oxygen in the
266 water column. The median P_{50} depth of southern bluefin tuna is projected to be 410 m shallower
267 in the future and 180 m of the projected shift is due to temperature changes in the water column.
268 In contrast, temperature is projected to cause < 10 m change in the median P_{50} depths of
269 yellowfin, skipjack, bigeye, and Pacific bluefin tunas. The vertical separation between P_{50} depths
270 of pairs of tuna species is projected to change in the Pacific Ocean, Arabian Sea, and Bay of
271 Bengal (Fig. 5). In the North Pacific Ocean and the Northern Tropical Pacific Ocean, the vertical
272 separation between all pairs of tuna species is projected to decrease. There is only a very small
273 area where the vertical separation between all pairs of tuna species is projected to expand. In

274 general, vertical separation between pairs of tuna species is not projected to increase or decrease
275 uniformly at the same geographic location (Fig. 5).

276

277 **Discussion**

278 Our results suggest that climate change will impact the vertical environment of tunas because
279 of species-specific differences in blood oxygen affinity (Fig. 3). The P_{50} depths of tunas with
280 endothermic blood-oxygen binding reactions, Pacific and southern bluefin tunas, are projected to
281 be shallower in the future (Fig. 3). The greatest decreases in oxygen concentrations are occurring
282 in the North Pacific (Bopp *et al.*, 2013), which is the habitat of Pacific bluefin tuna (*T.*
283 *orientalis*), a species with endothermic blood-oxygen binding. Tuna species with exothermic and
284 temperature-independent blood oxygen affinity also have habitats in the North Pacific including
285 bigeye, skipjack, and yellowfin tunas, but in low abundance relative to tropical regions.
286 Interestingly, the greatest vertical compression is projected to be just outside the northern range
287 of these three species (Fig. 2, S3). Decreases in oxygen concentrations are also projected for the
288 Eastern Indian Ocean where southern bluefin tuna spawn (Bopp *et al.*, 2013). The vertical habitat
289 of southern bluefin tuna is projected to be >500 m shallower in some locations in this region (Fig.
290 4). The underlying cause for changes in P_{50} depth could be due to temperature increases shifting
291 blood oxygen affinity (i.e., P_{50}). Warming in the surface ocean is projected to be faster than in
292 the deeper ocean, increasing the temperature gradient with depth. P_{50} increases as species with
293 endothermic blood-oxygen binding reactions swim from the warm surface layer to cold deep
294 depths (Fig. S1b). Therefore, southern bluefin tuna, which has an endothermic blood-oxygen
295 binding reaction, is projected to reach P_{50} at shallower depths in the future.

296 Multiple tuna species are sympatric in the North Pacific where the ESMs project the greatest
297 changes in P_{50} depths will occur (Fig. 1, 2). Tunas have species-specific vertical movement
298 patterns (e.g., Schaefer *et al.*, 2009; Bernal *et al.*, 2010). Skipjack and yellowfin are most
299 frequently in the upper thermocline (<100 m depth) during both day and night and make only
300 occasional forays for brief periods down to deeper depths during the day (Schaefer & Fuller,
301 2007; Schaefer *et al.*, 2009, 2011). Shallower and deeper P_{50} depths in the future may decrease or
302 increase, respectively, the frequency with which these species can forage at deeper depths (Fig.
303 2). Skipjack and yellowfin tunas exhibit similar vertical habitat usage behaviors and also both
304 have temperature-independent blood oxygen affinities. The degree to which behaviors and

305 physiological characteristics are linked will need to be investigated in a future study. Bigeye tuna
306 are most frequently in the upper thermocline at night and frequently at depths deeper than 200 m
307 during the day from which they make regular forays to the surface layer where oxygen
308 concentrations are higher and temperatures are warmer (Schaefer *et al.*, 2009; Schaefer & Fuller,
309 2010). A change in the P₅₀ depth may either influence the daytime foraging depth or alter the
310 frequency of trips to the surface layer during the day (Fig. 2). Although these behaviors are
311 considered characteristic, bigeye tuna occasionally dive to depths > 1000 m to forage below the
312 lower oxycline (Schaefer *et al.*, 2009). Changes in P₅₀ depths could alter the thickness of
313 oxycline making it either easier or more difficult for bigeye tuna to access areas below the
314 oxycline (Fig. 2).

315 The changes in P₅₀ depth separations between pairs of tuna species may lead to changes in
316 the frequency of competitive interactions, especially in deeper foraging zones (Fig. 5). Both
317 increases and decreases in species-specific vertical movement patterns resulting from P₅₀ depths
318 are projected to occur at the same locations between different pairs of tuna species. As a result,
319 competition is not projected to universally increase or decrease. The main exception is the North
320 Pacific where projected decreases in the vertical separation among all pairs of tuna species
321 indicate a potential increase in the frequency of interactions (Fig. 5). The effects of climate
322 change on vertical movements and distribution of tuna prey species are also relevant for
323 determining frequency of competitive interactions among tuna species (Polovina, 1996). If the
324 vertical distributions of prey species shift similarly to that of tunas, there may be few changes in
325 ecological interactions. Also, because fish track environmental variables and shift the geographic
326 centers of their range to remain in optimal conditions (Pinsky *et al.*, 2013), horizontal shifts in
327 tunas' geographic ranges may preempt any effects of climate change on their vertical habitats. As
328 fish species reorganize in a "musical chairs" of habitats, some habitats may be excluded due to
329 geographic range incompatibility or increases in ecological interactions. Geographic ranges of
330 tunas cover much of the global ocean, so there is limited potential for tunas to change geographic
331 ranges without also increasing competitive interactions (Fig. 1).

332 Factors in addition to hypoxia tolerance limit the vertical extent of tuna habitat. Atlantic
333 bluefin tuna occupy a region where oxygen concentrations change only minimally with depth,
334 which is exemplified by the lack of P₅₀ depths throughout the range of this species (Fig. S2).
335 However, Atlantic bluefin tuna have limitations on vertical movements (Walli *et al.*, 2009). Tuna

336 maintain tissues at optimal temperatures by spending time in warmer surface waters (Brill *et al.*,
337 1994; Dewar *et al.*, 1994; Graham & Dickson, 2001; Malte *et al.*, 2007), which means that
338 vertical movements are limited by the length of time tuna can remain at depth before needing to
339 return to the warmer surface layer get a "gulp of heat". Another factor that limits the depths to
340 which tuna can descend is the effect of temperature on cardiac function. Because of circulatory
341 anatomy, the heart remains at ambient environmental temperature which results in a decline in
342 cardiac performance at colder deeper depths (Galli *et al.*, 2009). Bigeye tuna, which spend the
343 most time relative to other tuna species at deeper depths, has adaptations, including enhanced
344 cardiac Ca^{2+} cycling and stimulation using adrenaline, to maintain cardiac performance in colder
345 temperatures (Galli *et al.*, 2009). While a combination of these factors limits the vertical extent of
346 tuna habitats, the effects of climate change on oxygen concentration will have the greatest impact
347 of tuna vertical habitat.

348 Our results also suggest that blood oxygen affinity is projected to change the spawning area
349 for southern bluefin tuna, which is located in the Indian Ocean off the coast of northwestern
350 Australia (Hobday *et al.*, 2016). Adaptation tends to be more rapid when directly related to
351 reproduction, therefore tracking changes in P_{50} and $\Delta H'$ of southern bluefin tuna over time may
352 provide a record of adaptation to climate change. A key step will be to connect physiological
353 changes to gene expression and environmental changes. Tunas have physiological and
354 morphological differences in addition to the differences in blood-oxygen affinity (e.g., Graham,
355 1975; Bernal *et al.*, 2010). For example, Atlantic bluefin, Pacific bluefin, and southern bluefin
356 tunas (whose blood-oxygen binding is endothermic) do not have central vascular counter current
357 heat exchangers (i.e., those formed from branches of dorsal aorta and postcardinal vein contained
358 within the hemal arch of the spinal column), and rely exclusively on lateral heat exchangers to
359 supply blood to the red muscle fiber portions of the swimming muscles (Graham, 1975; Graham
360 & Dickson, 2001).

361 We used oxygen and temperature results from Earth System Models to project changes in
362 tuna physiology and ecology over the next century. Models have many uncertainties which can
363 be reduced by combining results from multiple models, as we did. Even so, the temperature
364 results were generally more robust than the oxygen results (Bopp *et al.*, 2013). Robustness is
365 determined by comparing model results to measurements over a historical period. Temperature
366 mean state from the models is similar to observations throughout most of the global ocean (Bopp

367 *et al.*, 2013). Oxygen mean state is similar to observations in some regions of the ocean including
368 the North Pacific where the greatest changes in blood-oxygen binding and competitive
369 interactions are projected to occur (Fig. 2, 5) (Bopp *et al.*, 2013). The oxygen mean state is,
370 however, much less robust in the Eastern Tropical Pacific Ocean where P₅₀ depths are the
371 shallowest (Fig. 2). Recent observations show oxygen concentrations decreasing in the Eastern
372 Tropical Pacific Ocean (Stramma *et al.*, 2008; Schmidtko *et al.*, 2017), but there were no changes
373 in oxygen concentrations in the model mean state for the region over the same period (Bopp *et*
374 *al.*, 2013). Cabré *et al.* (2015) found that all the models overestimated the total volume of
375 hypoxic water in the Eastern Tropical Pacific because of biases in ventilation. Blood-oxygen
376 affinity of tunas is not projected to change in the Eastern Tropical Pacific based on results from
377 existing models, but this projection could change as improvements are made to the
378 parameterizations for ventilation in new model versions. The measurements of blood oxygen
379 affinity also have uncertainties; the measurements used here were made by different researchers,
380 using different equipment and procedures over a 20 year period on a small number of animals.
381 The limited numbers of measurements ignore potential intraspecies plasticity and geographic
382 variation in the blood oxygen affinity of various tuna species. Furthermore, the effects of blood
383 oxygen affinity on vertical movement behavior and metabolic rates of tuna still need to be
384 determined. In summary, the projected effects of climate change on tuna habitats are uncertain
385 and will be further improved by a combination of Earth System Model development and
386 additional measurements of blood oxygen affinity, behavior, and metabolism.

387 Resource managers will benefit from information on the physiological mechanisms
388 controlling habitat use when making decisions for tuna fisheries in a changing climate (e.g., Brill
389 & Lutcavage, 2001; Horodysky *et al.*, 2015, 2016; McKenzie *et al.*, 2016). Ocean warming and
390 changes in the depths of the oxycline could have dire consequences for the movements,
391 distribution, and abilities of tunas to withstand various levels of fishing mortality if the frequency
392 of competitive interactions increase or prey have refuges from predation. Our results imply that
393 different tuna species will experience different degrees of habitat compression. We project that
394 Pacific and southern bluefin tunas will experience the greatest habitat compression. Fisheries
395 management should account for physiological differences in the responses of tuna species to
396 changes in the temperature and oxygen conditions of the upper water column resulting from
397 climate change. As improvements to Earth System Models further decrease uncertainties,

398 continued efforts to link model projections of environmental changes to physiological
399 consequences will provide a more complete picture of pelagic habitat structure over the 21st
400 century.

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651

652 **Supporting Information:**

653 **Code Release:** <https://doi.org/10.5281/zenodo.808742>

654 **gcb161708-sup-0001-Supinfo.docx:**

655 **Table S1:** Physiological characteristics of tuna species used for the P₅₀ depth analysis including
656 temperatures used to calculate $\Delta H'$.

657 **Figure S1:** Comparison of P₅₀ shifts with depth between bigeye and southern bluefin tunas along
658 152°W in the Pacific Ocean.

659 **Figure S2:** Comparison of P₅₀ depths for six tuna species.

660 **Figure S3:** Comparison projected changes in P₅₀ depths due to climate change for six tuna
661 species.

662

663

664 **Figure captions:**

665 **Figure 1:** Tuna species richness in the global ocean (IUCN, 2011, 2014). The map includes
666 skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), southern bluefin (*Thunnus*
667 *maccoyii*), bigeye (*Thunnus obesus*), Pacific bluefin (*Thunnus orientalis*), Atlantic bluefin
668 (*Thunnus thynnus*), albacore (*Thunnus alalunga*), blackfin (*Thunnus atlanticus*), and longtail
669 (*Thunnus tonggol*) tunas. There are no tuna species present in grey colored areas of the ocean.

670 Competitive interactions and/or niche partitioning are likely to occur in areas with multiple
671 species present.

672 **Figure 2:** P_{50} depths and the projected changes in P_{50} depths due to climate change. Grey
673 indicates locations where there are no P_{50} depths. (a), (c), and (e) are the present-day P_{50} depths
674 of bigeye, skipjack, and Pacific bluefin tuna calculated using data from World Ocean Atlas 2009.
675 (b), (d), and (f) are the average projected changes in P_{50} depths for bigeye, skipjack, and Pacific
676 bluefin tunas from the six Earth System Models included in the Climate Model Intercomparison
677 Project 5. Expansion occurs in locations where P_{50} depths are deeper in the future. Compression
678 occurs in locations where P_{50} depths are shallower in the future. The stippling indicates known
679 habitat for each tuna species (IUCN, 2011, 2014).

680 **Figure 3:** Compression of P_{50} depths in tuna habitats projected for the end of the century. P.
681 bluefin and S. bluefin are Pacific and southern bluefin tunas respectively. The right y-axis is for
682 S. bluefin, which has much larger projected changes than the other species. Tuna species with
683 blood-oxygen binding reactions that are endothermic are projected to experience more
684 compression than species with blood-oxygen binding reactions that are exothermic or
685 temperature independent. There are no boxes for Atlantic bluefin tuna because the geographic
686 range of this species does not overlap with the geographic area where individuals would
687 encounter a P_{50} depth during descents (Figs. S2, S3). Outliers that are greater than 1.5 times the
688 interquartile range are not shown.

689 **Figure 4:** P_{50} depths in the spawning area of southern bluefin tuna. (a) Present-day P_{50} depths
690 based on World Ocean Atlas (WOA) data. (b) Future projections of P_{50} depths based on
691 greenhouse gas emissions scenario RCP 8.5. The stippling indicates known habitat (IUCN,
692 2011). In the future, the area with a P_{50} depth is projected to expand south, further into the
693 spawning region of southern bluefin tuna. The P_{50} depths are also projected to be shallower.

694 **Figure 5:** Locations where the vertical separation in P_{50} depths of tuna species are projected to
695 change by more than 10 m. The species include skipjack (*Katsuwonus pelamis*), yellowfin
696 (*Thunnus albacares*) southern bluefin (*Thunnus maccoyii*), bigeye (*Thunnus obesus*), and Pacific
697 bluefin (*Thunnus orientalis*), Expansion: all pairwise vertical separations increase. Mixed:
698 pairwise vertical separations increase and decrease. Compression: all pairwise vertical
699 separations decrease. Competition is projected to increase in areas with compression and

700 decrease in areas with expansion. For areas with mixed changes in vertical separation,
701 competitive interactions are projected to increase for some pairs of species and decrease for other
702 pairs of species.

703

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Figure 1:

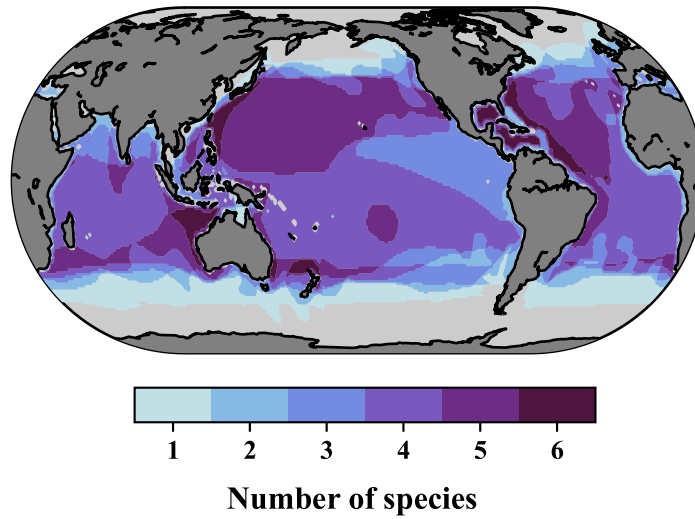


Figure 2:

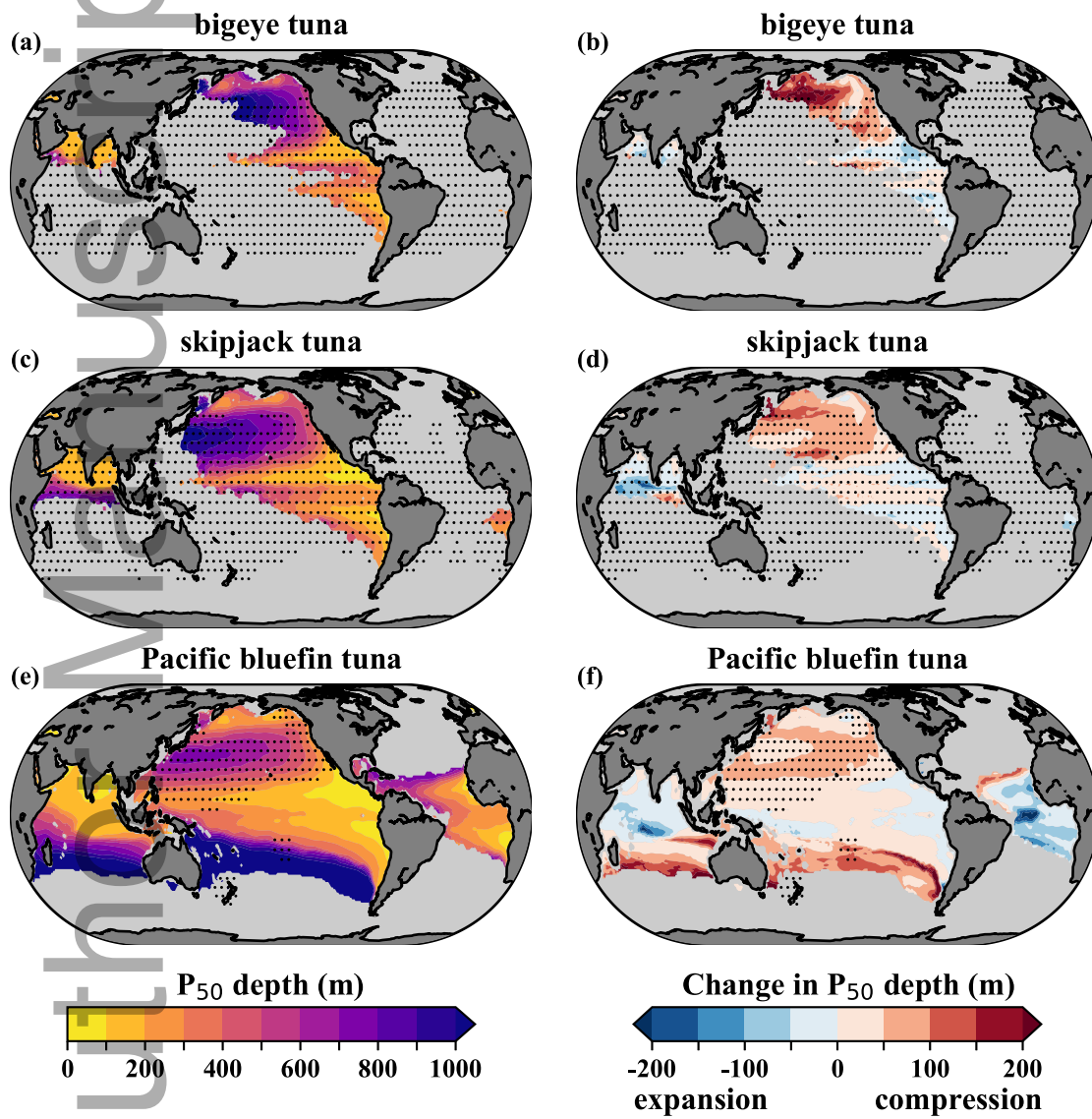


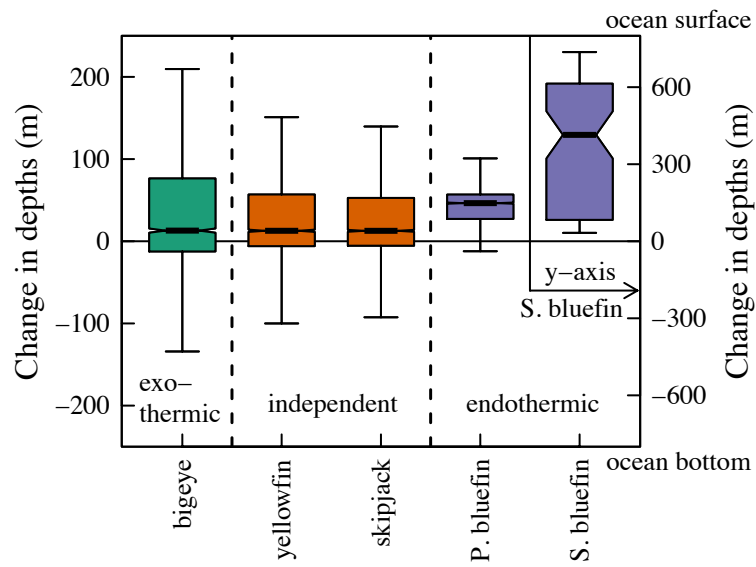
Figure 3:

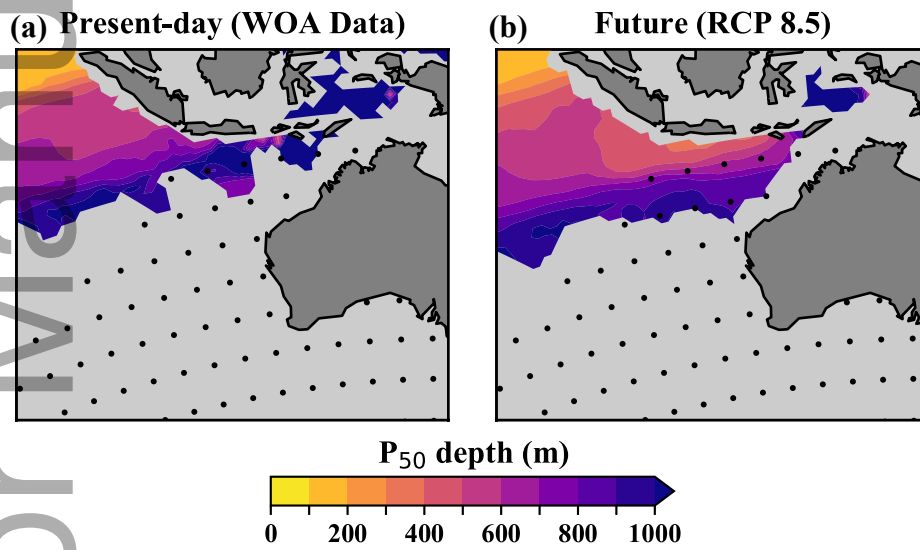
Figure 4:

Figure 5:

