



Original Article

Projections of future habitat use by Atlantic bluefin tuna: mechanistic vs. correlative distribution models

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Climate change is likely to drive complex shifts in the distribution and ecology of marine species. Projections of future changes may vary, however, depending on the biological impact model used. In this study, we compared a correlative species distribution model and a simple mechanistic oxygen balance model for Atlantic bluefin tuna (*Thunnus thynnus*: ABFT) in the North Atlantic Ocean. Both models gave similar results for the recent historical time period, and suggested that ABFT generally occupy favourable metabolic habitats. Projections from an earth system model showed largely temperature-induced reductions in ABFT habitat in the tropical and sub-tropical Atlantic by 2100. However, the oxygen balance model showed more optimistic results in parts of the subpolar North Atlantic. This was partially due to an inherent ability to extrapolate beyond conditions currently encountered by pelagic longline fishing fleets. Projections included considerable uncertainty due to the simplicity of the biological models, and the coarse spatiotemporal resolution of the analyses. Despite these limitations, our results suggest that climate change is likely to increase metabolic stress on ABFT in sub-tropical habitats, but may improve habitat suitability in subpolar habitats, with implications for spawning and migratory behaviours, and availability to fishing fleets.

Keywords: Atlantic bluefin tuna, climate change, North Atlantic, species distribution models.

Introduction

Anthropogenic climate change has the potential to change the face of modern fisheries management in the coming decades. Most stock assessment models and fishery management plans assume constant stock–recruitment relationships, environmentally invariant stock productivity, and relatively static species distribution ranges (McIlgorm, 2010; Punt *et al.*, 2013). These assumptions are likely to prove increasingly impractical as changes in ocean temperature, productivity, acidity, and biogeochemistry

result in complex, ecosystem-level impacts to managed fish populations (Kirby *et al.*, 2009; Poloczanska *et al.*, 2013; Pörtner *et al.*, 2014; Breitbart *et al.*, 2015).

This realization has led to multiple studies attempting to project the potential impacts of directional climate change on the distribution, recruitment potential, phenology, and productivity of marine species (Cheung *et al.*, 2010; Hobday, 2010; Bell *et al.*, 2013; Hollowed *et al.*, 2013; Lehodey *et al.*, 2013). Methods range from the relatively simple to the extremely complex, and may

include considerations of distribution, physiology and phenology across multiple life stages (Koenigstein *et al.*, 2016; Peck *et al.*, 2016). One of the more common approaches is to use statistical methods to relate present-day distributions of species to their environment, and to then apply these to future projections from general circulation models (GCMs) (Hartog *et al.*, 2011; Stock *et al.*, 2011; Hazen *et al.*, 2013; Muhling *et al.*, 2015; Coro *et al.*, 2016; Peck *et al.*, 2016). These methods are usually non-parametric, multivariate, and can cope with interactions among predictor variables, either explicitly or implicitly (Guisan and Zimmermann, 2000).

The main advantages of using correlative species distributions models (SDMs) for projecting climate change impacts on living marine resources are that they are conceptually simple, and usually require relatively few input variables. They require no explicit parameterization of physiology, behaviour, recruitment, or food web dynamics (Dormann *et al.*, 2012; Peck *et al.*, 2016). However, these characteristics also constitute their main disadvantages, as key processes driving climate impacts on the physiology and phenology of a species may be missed. These models also assume that statistical relationships observed between fish and their environment in the recent past will continue to apply into the future. This may not always be a valid assumption, particularly for correlations that have no obvious mechanistic basis (Dormann *et al.*, 2012; Horodysky *et al.*, 2015, 2016; Peck *et al.*, 2016). In addition, the assumption that observed species distributions correspond to ecological niches is often overly simplistic (Martinez-Meyer, 2005; Robinson *et al.*, 2011), particularly for highly migratory pelagic species with broad environmental tolerances, such as Atlantic bluefin tuna (*Thunnus thynnus*: ABFT).

Adult ABFT range throughout the northern Atlantic Ocean, and are capable of trans-basin migrations in as little as a few months (Mather *et al.*, 1995; Block *et al.*, 2005). They can tolerate near-freezing conditions on northern foraging grounds (Block *et al.*, 2005; Walli *et al.*, 2009; Teo and Boustany, 2016), and temperatures approaching 30 °C on their Gulf of Mexico spawning grounds (Teo *et al.*, 2007). Adult ABFT can also experience ambient temperature changes of >20 °C when descending to several hundred metres depth to feed (Block *et al.*, 2001; Teo and Boustany, 2016). However, they have several characteristics that may cause them to be highly vulnerable to climate change. First, both the eastern and western Atlantic stocks are currently recovering from historically low spawning stock biomasses caused by overfishing (ICCAT, 2014; Porch and Laretta, 2016). Over-exploited populations may show reduced genetic diversity, and compromised resilience to environmental change (Conover and Munch, 2002; Berkeley *et al.*, 2004; Ward *et al.*, 2016). Second, ABFT target specific environmental conditions for spawning, which constitute a small proportion of their overall range in both space and time (Muhling *et al.*, 2013; Reglero *et al.*, 2014). Larval collections suggest that the majority of spawning is concentrated in the Gulf of Mexico (western stock) and the Mediterranean Sea (eastern stock), although additional spawning areas have recently been confirmed (Muhling *et al.*, 2011; Lamkin *et al.*, 2015; Richardson *et al.*, 2016). Significant environmental changes to current spawning areas would therefore require either adaptation of both adults and larvae to new conditions on existing spawning grounds, or changes in migration behaviour to exploit new spawning grounds. The reproductive strategy of ABFT (long migrations to spatiotemporally restricted spawning grounds with specific environmental conditions) may prove to be a significant

bottleneck as the effects of directional climate change continue to accumulate.

The unique anatomy and physiology of ABFT may also render them vulnerable to climate change. Similar to the two other bluefin tuna species (Pacific: *T. orientalis*, and Southern: *T. maccoyii*), ABFT have a well-developed vascular counter-current heat exchange system that allows them to maintain internal temperature up to 20 °C above ambient. Along with other adaptations, this has allowed ABFT to exploit food resources in the cold, highly productive north Atlantic (Carey and Teal, 1966, 1969; Block *et al.*, 2001; Logan *et al.*, 2015). However, it has been speculated that these physiological adaptations for cold waters may be a hindrance on subtropical spawning grounds (Block *et al.*, 2005; Teo *et al.*, 2007). ABFT have proportionally higher oxygen demands than warm-water *Thunnus* species (e.g. yellowfin tuna, Blank *et al.*, 2007a), and very warm temperatures may induce metabolic stress more quickly in bluefin tunas than in other tunas (Blank *et al.*, 2004; Block *et al.*, 2005; Kitagawa *et al.*, 2006). Several authors have suggested that metabolic constraints may be major determinants of the spatial distribution of marine species (Brill, 1994; Pörtner and Knust, 2007; Farrell, 2009; Prince *et al.*, 2010; Deutsch *et al.*, 2015; Farrell, 2016) although the relationships between metabolic rates and ambient temperature/oxygen may not follow a universal form for all species and life stages (Clark *et al.*, 2013a). Future shifts in species ranges could therefore be partially driven by temperature-mediated oxygen availability.

In this study, we used two different approaches to project future distribution of suitable habitat for ABFT in the North Atlantic resulting from the effects of directional climate change. We first assessed the ability of a correlative SDM and a mechanistic metabolic oxygen balance model to reproduce present-day distributions of ABFT. We then projected both models forward in time using output from an earth system model, and compared the projections from both approaches between the late 20th century (1971–2000), and the late 21st century (2071–2100).

Methods

Metabolic oxygen balance model

Although similar in concept, our metabolic model does not rely on the traditional calculation of metabolic scope (e.g. maximum metabolic rate vs. standard metabolic rate: Del Raye and Weng, 2015; Farrell, 2016). We therefore named it an “oxygen balance model” to avoid confusion. The model was comprised of three sub-components: an oxygen demand model, an oxygen supply model, and a cardiac transport model (Figure 1). All three were parameterized using published results of experiments on captive tunas. Few studies have been published using ABFT, and so studies on Pacific bluefin tuna and yellowfin tuna (YFT) were adapted as required.

Due to difficulties inherent in keeping captive tunas, most studies to date have used juvenile fish: usually <3 kg for YFT, and ~10 kg for bluefin tunas (Bushnell and Brill, 1991; Blank *et al.*, 2007a, b; Clark *et al.*, 2013b). How applicable these are to adult ABFT is largely unknown. Metabolic rates scale with body size, as do gill ventilation volumes and heat conservation characteristics (Carey and Teal, 1969; Clarke and Johnston, 1999; Whitlock *et al.*, 2015). While juvenile tuna are also capable of endothermy, larger tuna may warm more extensive regions of the body, and show higher thermal inertia (Graham and Dickson, 2001). In terms of lower temperature limits, juvenile bluefin tunas forage in waters nearly as cold as those tolerated by adults, but dive to

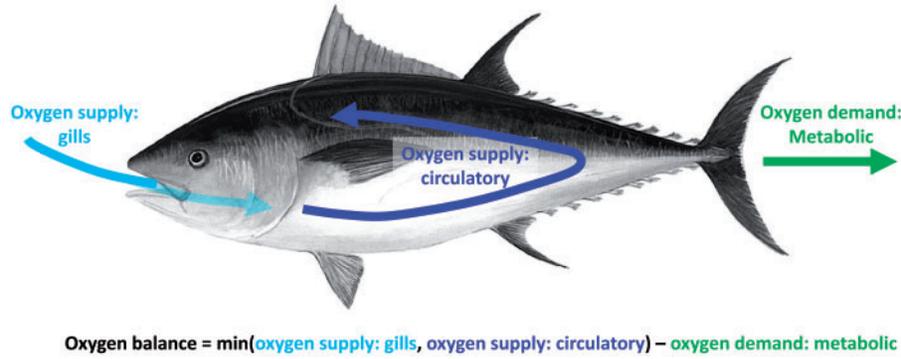


Figure 1. Schematic diagram of the metabolic oxygen balance model. (Tuna image: NOAA).

shallower depths, and may have a more restricted latitudinal range (Mather *et al.*, 1995; Gunn and Young, 1999; Brill *et al.*, 2002; Bestley *et al.*, 2009; Galuardi and Lutcavage, 2012). Predictions of suitable metabolic habitat from the oxygen balance model developed here are thus unlikely to be substantially different from those for larger adults, but will probably be more conservative at extreme low temperatures.

The oxygen demand model was built using experimental results on Pacific bluefin tuna from Blank *et al.* (2007a, b) and Clark *et al.* (2013b). These studies highlighted non-linear relationships between metabolic rates ($\text{mg O}_2/\text{kg/h}$) and water temperature, with minimum values at 10–20 °C, and higher values at <10 °C and >20 °C. Metabolic rates also increased non-linearly with swimming speed, but the scale of the response depended on water temperature (Blank *et al.*, 2007a). Observed measurements of metabolic rate were extracted directly from figures in Blank *et al.*, (2007a, b) and Clark *et al.* (2013b), and used to construct a Generalized Additive Model (GAM) with a Gaussian error distribution using the mgcv package in R 3.2.1 (Wood, 2006; R Core Team, 2015). The GAM predicted metabolic rate (MO_2) based on swimming speed (U) in BL/s and water temperature (T). A smoothing spline was applied to each predictor variable, and a linear interaction term was also included, such that:

$$\text{MO}_2 = f_1(U) + f_2(T) + f_3(U, T) \quad (1)$$

The oxygen supply model was adapted from equations developed for YFT (Bushnell and Brill, 1991). Ventilation volume (V_g : the volume of water passing through the gills) depended on swimming speed and mouth gape (assumed to be 1 at normoxia), which were in turn dependent on ambient oxygen concentrations. The first issue was the need to scale the equations in Bushnell and Brill (1991) from a 1.4 kg YFT to a ~10 kg ABFT. A 10 kg ABFT is 7.14 times the weight of a 1.4 kg YFT, but only about two times the length, with approximately three times as much gill area, and five times as much gill weight (Muir and Hughes, 1969; Pauly, 1979; Fromentin, 2006). It is not clear which of these metrics is the best scalar for V_g , and so we chose to assume that the V_g under normoxia for a 10 kg ABFT would be three times as much as a 1.4 kg YFT (an intermediate value among the scalars listed above). The equation to calculate base V_g under normoxia thus becomes

$$V_{gb} = 9.36 U \quad (2)$$

Where V_{gb} is ventilation volume (L/min; note conversion from

Bushnell and Brill, 1991, who used L/s) and U is swimming speed in body lengths per second (BL/s). Bushnell and Brill (1991) also found that V_g in YFT increases under hypoxic conditions. We used the same response for the ABFT model, but adjusted for the greater V_g of the larger fish. This was achieved by calculating a V_g multiplier (V_{gm}) such that when ambient oxygen concentrations are <7.0 mg/m^3

$$V_{gm} = -0.30 O_2 + 2.92 \quad (3)$$

And, when ambient oxygen is >7.0 mg/m^3

$$V_{gm} = 1 \quad (4)$$

where O_2 is ambient oxygen concentration (mg/m^3). Actual V_g is then simply

$$V_g = V_{gb} V_{gm} \quad (5)$$

The last parameter required was utilization of the available oxygen coming in through the gills (% U). This value varies inversely with V_g (Bushnell and Brill, 1991). We assumed that the drop in % U with V_g was proportionally the same for ABFT as observed in YFT, and that we could use Equation (9) presented in Bushnell and Brill (1991) (using normoxic $\text{PiO}_2 = 154 \text{ mmHg}$). We adjusted the V_g to be three times higher in ABFT (due to their larger size: see above), and took the same slope for % U versus V_g as for YFT in Bushnell and Brill (1991). After adjusting the equation to use V_g in L/min, % U for ABFT can be calculated as:

$$\%U = -0.007 V_g + 0.83 \quad (6)$$

Oxygen delivery via the gills (O_{2g}) was thus calculated as

$$\text{O}_{2g} = V_g \%U O_2 \quad (7)$$

The last element of the oxygen balance model was the cardiac transport sub-model, which depended on cardiac output (Q) and the difference in oxygen content of arterial and venous blood (O_{2a-v}) (i.e. the Fick equation; Brill and Bushnell, 2001). Q in tunas is primarily determined by heart rate (HR), with stroke volume staying relatively constant (Korsmeyer *et al.*, 1997a; Blank *et al.*, 2004). Pacific bluefin tuna heart rates have been shown to increase approximately logarithmically with water temperature (Blank *et al.*, 2004; Clark *et al.*, 2013b). Comparison of heart rates

from spinally blocked (Blank *et al.*, 2002) and free-swimming (Korsmeyer *et al.*, 1997a) YFT suggested that results from blocked fish under “maximal” conditions were roughly analogous to free swimming fish traveling at ~ 2.5 BL/s. However, the effect of swimming speed on heart rate was relatively minor compared to that of water temperature. We used observations of heart rate from spinally blocked Pacific bluefin tuna with temperature from Blank *et al.* (2004), assuming these were equivalent to a swimming speed of 2.5 BL/s, and from swimming Pacific bluefin tuna (average swimming speed of ~ 1.1 BL/s; Clark *et al.*, 2013b). A multivariate exponential relationship between heart rate, water temperature, and swimming speed was then estimated using non-linear least squares (nls) in R 3.2.1 (R Core Team 2015). The equation derived explained 92% of the variability in observations, and was defined by

$$\text{HR} = (11.91 + 2.88 U) e^{0.07 T} \quad (8)$$

where U is swimming speed (BL/s) and T is water temperature.

Experiments on spinally blocked fish suggest that tuna can maintain reasonably constant O_{2a-v} , even under hypoxic conditions (Bushnell and Brill, 1992). Korsmeyer *et al.* (1997b) showed that YFT O_{2a-v} was ~ 0.06 ml O_2 /ml at slow swimming speeds (1 BL/s), and Brill and Bushnell (2001) estimated a maximum value of ~ 0.16 ml O_2 /ml. However, bluefin tuna blood has a higher oxygen affinity than YFT blood. This means that bluefin tuna blood reaches half saturation at a lower oxygen partial pressure (i.e. ABFT will have a lower P_{50} than YFT). In addition, bluefin tuna blood shows a reverse temperature effect, meaning that blood oxygen affinity increases (i.e. P_{50} decreases) at cooler temperatures (Clark *et al.*, 2008: Southern bluefin tuna; Brill and Bushnell, 2006: ABFT). As the relationships between temperature, ambient oxygen concentrations, swimming speed and O_{2a-v} remain uncertain in ABFT, we assumed that O_{2a-v} would be 0.06 ml O_2 /ml at slow (1 BL/s) swimming speeds, and 0.11 ml O_2 /ml at moderate (2 BL/s) swimming speeds, with O_{2a-v} at other swimming speeds calculated using a simple linear regression. However, we note that this part of the model lacks direct experimental confirmation, and should be refined as data on O_{2a-v} in swimming ABFT are obtained. Cardiac oxygen delivery (O_{2c}) was thus defined as

$$O_{2c} = 60 \frac{\text{HR SV } O_{2a-v}}{0.7} \quad (9)$$

where HR is heart rate and SV is stroke volume (held constant at 1.2 ml/beats/kg). Dividing by 0.7 and then multiplying by 60 gives oxygen delivery in mg O_2 /kg/h.

Oxygen balance (i.e. surplus or deficit) was determined by subtracting metabolic demand from the lesser of O_{2g} and O_{2c} . Results were visualized by applying oxygen balances from the model to mean upper 50 m temperature (1995–2014 mean) and oxygen (long-term climatology) from the World Ocean Atlas (WOA: Garcia *et al.*, 2014; Locarnini *et al.*, 2013). ABFT can descend to several hundred metres to feed, and their vertical movement behaviour changes by geographic region (Teo *et al.*, 2007; Walli *et al.*, 2009; Abascal *et al.*, 2016). However, they usually return to the upper mixed layer between descents, and so we defined the upper 50 m of the water column as their core habitat, where oxygen debts incurred during deep descents could be repaid. Mean $5^\circ \times 5^\circ$ catch rate data (fish/1000 hooks) from the

International Commission for the Conservation of Atlantic Tunas (ICCAT) Task II database (1997–2014) were overlaid on model predictions (interpolated using kriging in Surfer 9: Golden Software), to assess relationships between favourable metabolic habitat, and observed ABFT distributions in the North Atlantic. Catch rates are strongly influenced by fishing methods, gear configurations, reporting accuracy and other confounding factors, which makes detailed spatial comparisons unwise. Catch rate data were therefore presented only as “absent” (no ABFT recorded), “low” (< 0.2 fish/1000 hooks), or “high” (> 0.2 fish/1000 hooks). Locations with > 0 ABFT recorded, but low overall fishing effort ($< 10,000$ total hooks set over the entire period), were categorized as “present (low effort)”.

Correlative species distribution model

Adult ABFT presence/absence data were sourced from the NOAA National Marine Fisheries Service (NMFS) pelagic longline fishery logbook program (Beerkircher *et al.*, 2002). Each set in the database has information on catch composition, gear configuration, fishing date, and longitude and latitude. Three available and potentially useful environmental habitat predictors were identified based on a literature search: temperature, chlorophyll α (chlorophyll hereafter), and dissolved oxygen. We used sea surface temperature, since these synoptic observations are widely available from satellite sensors, and temperature at 100 m depth, which can be used to distinguish among shallow water masses in sub-tropical regions, and has implications for vertical movement behaviour and thermoregulation (Teo *et al.*, 2007; Walli *et al.*, 2009; Muhling *et al.*, 2010; Teo and Boustany, 2016). Chlorophyll is available as sea surface chlorophyll from satellite sensors, which we employed as a proxy for upper ocean primary productivity. Dissolved oxygen limits vertical tuna distributions, particularly near hypoxic zones (Barkley *et al.*, 1978; Brill, 1994; Humpston *et al.*, 2000; Lowe *et al.*, 2000; Stramma *et al.*, 2012), so oxygen at 100 m depth was also included. Catchability of some target species on longline gear varies with moon phase (Bigelow *et al.*, 1999), and so the fraction of the moon illuminated was included for each set date from the U.S. Naval Observatory (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>).

Environmental conditions at each longline set location were obtained from a number of different sources, using the MGET toolbox in ArcGIS 10.0 (Roberts *et al.*, 2010). Surface temperatures were derived from the 8 day NOAA Pathfinder 5.1 and MODIS Aqua satellite datasets. If no satellite data were available due to clouds, we used results from the HYCOM + NCODA GLBu0.08 daily reanalysis. Surface chlorophyll concentration was extracted from the SeaWiFS and MODIS Aqua 8 day satellite datasets, with a mean taken if both were available. Water temperatures at 100 m were extracted from HYCOM GLBu0.08, and oxygen levels at 100 m were extracted from the WOA long-term climatology (Garcia *et al.*, 2014). A total of 62 115 longline sets from between September 1997 and August 2010, with all four environmental variables available for the time and location of the set, were selected for use in SDM training and testing.

One issue with use of the logbook data was that the lower temperature limit for ABFT remained undefined. ABFT were recorded at surface temperatures as low as $10\text{--}12^\circ\text{C}$, and there was no recorded fishing activity in waters cooler than this. To address this problem, we included eight “dummy” negative stations in the Davis Strait (between Canada and Greenland) at $55\text{--}60^\circ\text{N}$. ABFT

have not previously been recorded in this area, which is characterized by very cold waters ($<10^{\circ}\text{C}$ at the surface throughout the year) (Mather *et al.*, 1995; Block *et al.*, 2005; Boustany *et al.*, 2008; Walli *et al.*, 2009; Orbesen *et al.*, unpublished data). Each station was repeated 70 times in the training dataset, to give them sufficient weight in the SDM training process. This forced a lower temperature limit in the habitat model but, as discussed later, is a source of considerable uncertainty.

The predictive SDM was built as a presence/absence boosted regression tree model using the *gbm* (generalized boosted regression models) package in R 3.2.1 (Elith *et al.*, 2008), with a Bernoulli error distribution. Pearson correlations among the five predictor variables did not exceed 0.65, and so all were retained in the model. The best learning rate and tree complexity were determined using the optimization routines described in Elith *et al.* (2008), with half of the dataset used for training the model, and the other half retained for skill testing. Importance of predictor variables was defined based on the number of times each variable was used for tree splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees (Friedman and Meulman 2003; Elith *et al.*, 2008). Results were visualized by applying the model to climatological surface and 100 m temperature (1995–2014), and 100 m oxygen (long-term climatology) from WOA, and climatological surface chlorophyll from SeaWiFS (1997–2014) from the broader North Atlantic, and kriging these in Surfer 9. Moon illumination assumed a climatological value of 1. ICCAT catch rate data were again overlaid, and compared to predictions of favourable habitat from the SDM.

Earth system model

A GCM with biogeochemical components (dissolved oxygen, surface chlorophyll) was required to project both the oxygen balance model and SDM forward in time. However, available GCMs from the latest Coupled Model Intercomparison Project Phase 5 (CMIP5) often give markedly different values for biogeochemical tracers in both historical runs and future projections (Bopp *et al.*, 2013). Assessment of four commonly used models that spanned a range of potential futures (GFDL-ESM2M, IPSL-CM5A-LR, CESM1-BGC, and MPI-ESM-LR; Bopp *et al.*, 2013; Flato *et al.*, 2013) showed that historical runs of the GFDL model reproduced spatial patterns of surface chlorophyll in the North Atlantic Ocean much more realistically than the other models, or a mean ensemble of all four models (results not shown). As there is reasonably close agreement in projected future changes in surface chlorophyll from these models (Bopp *et al.*, 2013), we chose to use only the GFDL-ESM2M model for our study (Dunne *et al.*, 2013). Sea surface temperature, 100 m temperature, 100 m oxygen and surface chlorophyll were obtained at monthly resolution from the Earth System Grid Federation portal at the Lawrence Livermore National Laboratory (<https://pcmdi.llnl.gov/projects/esgf-llnl/>). Oxygen fields were only available from ESM2M at an annual time step. We therefore applied the mean seasonal signal observed from the WOA oxygen climatology at interpolated (kriging) $1^{\circ} \times 1^{\circ}$ resolution to the annual 100 m oxygen fields from ESM2M, to estimate the seasonal cycle. Results were compared between a historical run of the model (1971–2000 mean), and a late 21st century projection (2071–2100) under Representative Concentration Pathway (RCP) 8.5.

We used a simple sensitivity analysis to assess which of the four environmental predictors were most important for projections of future habitat gain or loss from the SDM. This involved re-scoring the environmental fields from ESM2M through the SDM, but holding one variable at a time constant between the two time periods (1971–2000 vs. 2071–2100). Projected patterns in habitat loss and gain were then compared between the original time period, and four addition model runs:

- (1) surface temperature held constant between the two time periods (i.e. no future warming),
- (2) 100 m temperature held constant,
- (3) 100 m oxygen held constant, and
- (4) surface chlorophyll held constant.

Results

Oxygen balance model

The GAM predicting metabolic rate from swimming speed and temperature explained 90.6% of the observed variability in the combined experimental data from Blank *et al.* (2007a, b) and Clark *et al.* (2013a, b). Both predictors, and a linear interaction term, were highly significant in the GAM model ($p < 0.001$). Metabolic rate increased with swimming speed, and was minimal between ~ 10 and 20°C (Figure 2). The interaction between swimming speed and temperature first described by Blank *et al.* (2007a) was strongly evident, with the effect of swimming speed on metabolic rate increasing at warmer temperatures.

The model of oxygen uptake through the gills largely depended on ambient oxygen concentrations, while the model of oxygen supply to tissues through the circulatory system depended on water temperature (Figure 3). We assumed that the minimum value from these two models in any given set of conditions would constitute the limiting factor for oxygen supply to offset metabolic demand. At a moderate swimming speed (2 BL/s), this resulted in the lowest predicted oxygen balance at $<5^{\circ}\text{C}$, and maximum oxygen balance at 10 – 25°C , depending on ambient oxygen concentrations (Figure 3).

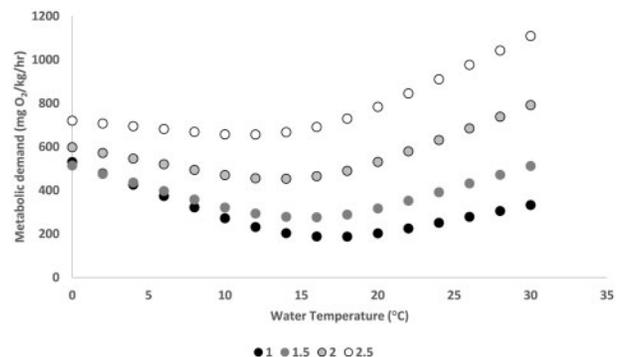


Figure 2. Results from a GAM to predict metabolic demand in ABFT from water temperature and swimming speed using data from published laboratory studies (Blank *et al.*, 2007a, b; Clark *et al.*, 2013a, b). Examples of predicted metabolic demand are shown for four swimming speeds: 1, 1.5, 2, and 2.5 BL/s.

Correlative species distribution model

Pelagic longline fishing activity in the US fleet from 1997 to 2010 (which we used to build the correlative habitat model) followed a seasonal distribution. There was more effort in the Sargasso Sea and east of the Bahamas in winter and more effort in the Mid-Atlantic Bight and the far north-western Atlantic during summer (Figure 4). Although ABFT are also targeted by other gears (e.g. rod and reel) in shallower areas in the Gulf of Maine and Mid-Atlantic Bight, pelagic longline activity was restricted to deeper waters. The northern limit of fishing roughly corresponded to the mean position of the surface 10 °C isotherm. The fleet primarily fished in waters with low to moderate chlorophyll at the surface (<0.25 mg/m³), with the exception of the Gulf Stream front and Grand Banks region southeast of Newfoundland during summer (Figure 4).

Optimization runs showed that the boosted regression tree SDM was best parameterized with a learning rate of 0.01, and a tree complexity of 7, resulting in a total of 2350 trees. Oxygen at 100 m and surface temperature were the most influential variables in the model (scores of 27.98 and 23.98, respectively), followed by temperature at 100 m (score of 20.68) and surface chlorophyll (score of 17.74). Moon phase was less influential, with a score of 9.61.

Partial plots from the SDM showed that ABFT were most likely to be encountered on longline sets when oxygen at 100 m was between 7 and 10 mg/L, and when sea surface temperatures were between 10 and 16 °C (Figure 5). Relationships with 100 m temperature were uncertain at very cold temperatures, but the probability of occurrence of ABFT generally decreased with

temperature between 6 and 28 °C. The effect of surface chlorophyll was not clear from the partial plot, but results suggested a lower probability of occurrence of ABFT when values were less than 0.7 or greater than 3.2 mg/m³ (note fourth root transformation in figure). Moon phase was the weakest predictor in the model, but the partial plot showed a generally elevated probability of occurrence of ABFT during the full moon (Figure 5).

Model comparison

The ICCAT 5° × 5° catch rate data showed that ABFT were most commonly encountered south of 50°N during winter and south of 60°N in summer (Figure 6). Highest catch rates in winter were observed in the Gulf of Mexico, Mid-Atlantic Bight, between Morocco and the Bay of Biscay, and the open Atlantic at equivalent latitudes. During summer, areas of highest catch rates generally moved north, with maximum values off the Gulf of Maine, Bay of Biscay, and nearly as far north as Iceland. Catch rates were also high in the Mediterranean Sea in both seasons (Figure 6).

The oxygen balance model run for a moderate swimming speed of 2 BL/s predicted a broad zone of suitable habitat roughly coincident with observed positive catch rates (Figure 6: upper panels). ABFT were rarely encountered in the equatorial Atlantic Ocean and Caribbean Sea, and these areas corresponded to low predicted oxygen balances. The oxygen balance model also predicted low habitat suitability in cold waters north of the Gulf Stream and North Atlantic Current, where no catch rate data were available. While ABFT were observed towards the northern boundary of theoretically favourable habitat in both seasons, some favourable habitat off western Africa had no positive catches recorded (Figure 6).

Predicted probabilities of occurrence from the SDM also generally agreed with observed catch rates from the ICCAT database (Figure 6: lower panels). In summer, the highest predicted probabilities were in the Mediterranean Sea, from Morocco up to Iceland in the northeast Atlantic Ocean, and offshore of the Gulf of Maine in the north-west. Regions with high probabilities of occurrence from the SDM agreed well with regions of modelled maximum oxygen balance in summer, although the SDM predicted slightly more favourable habitat east of the south-eastern U.S., and in the Gulf of Saint Lawrence (Canada). In contrast, predictions from the two models for winter were quite different (Figure 6). While regions of favourable habitat from the SDM broadly corresponded to regions of maximum oxygen balance, these were much patchier in the SDM, particularly in the western Atlantic. Predictions from the SDM were also more favourable across the 25°N parallel (Figure 6). ABFT were present in this area in both the ICCAT database and the pelagic longline logbooks (Figure 4), although catch rates were generally low. Both oxygen balance from the metabolic model, and probability of occurrence from the SDM, were low in the Gulf of Mexico during winter, despite moderate to high catch rates in this region.

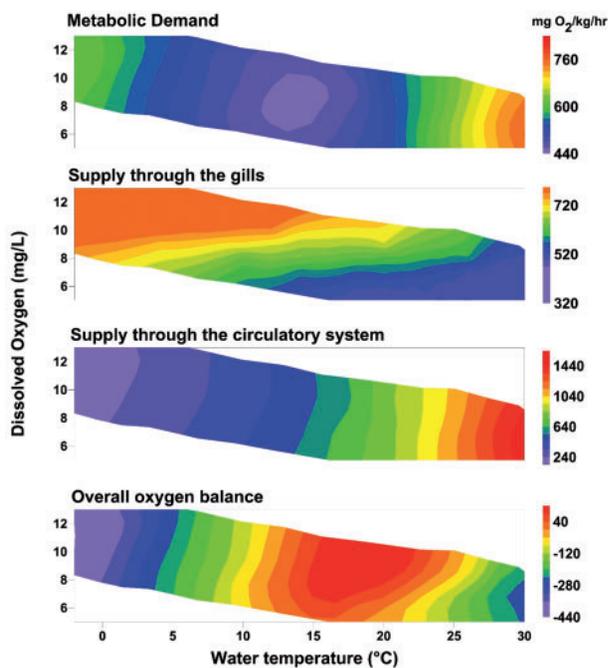


Figure 3. Modelled metabolic demand, oxygen supply through the gills, oxygen supply through the circulatory system, and the resulting overall oxygen balance for an ABFT swimming at 2 BL/s across a range of temperature and dissolved oxygen conditions. Results are constrained to upper 50 m temperature (1995–2014) and oxygen (long-term climatology) conditions observed in the WOA for the North Atlantic Ocean.

Climate change projections

ESM2M projected that the pelagic environment in the North Atlantic Ocean would warm ~2.5 °C between 1971–2000 and 2071–2100 in the region south of 40°N, at both the surface and 100 m depth (Figures 7 and 8). North of 40°N, the pattern was more complex, with strong cooling in a region south of Greenland, slight cooling around Iceland, and warming elsewhere. Oxygen at 100 m was projected to decrease by ~0.28 mg/m³

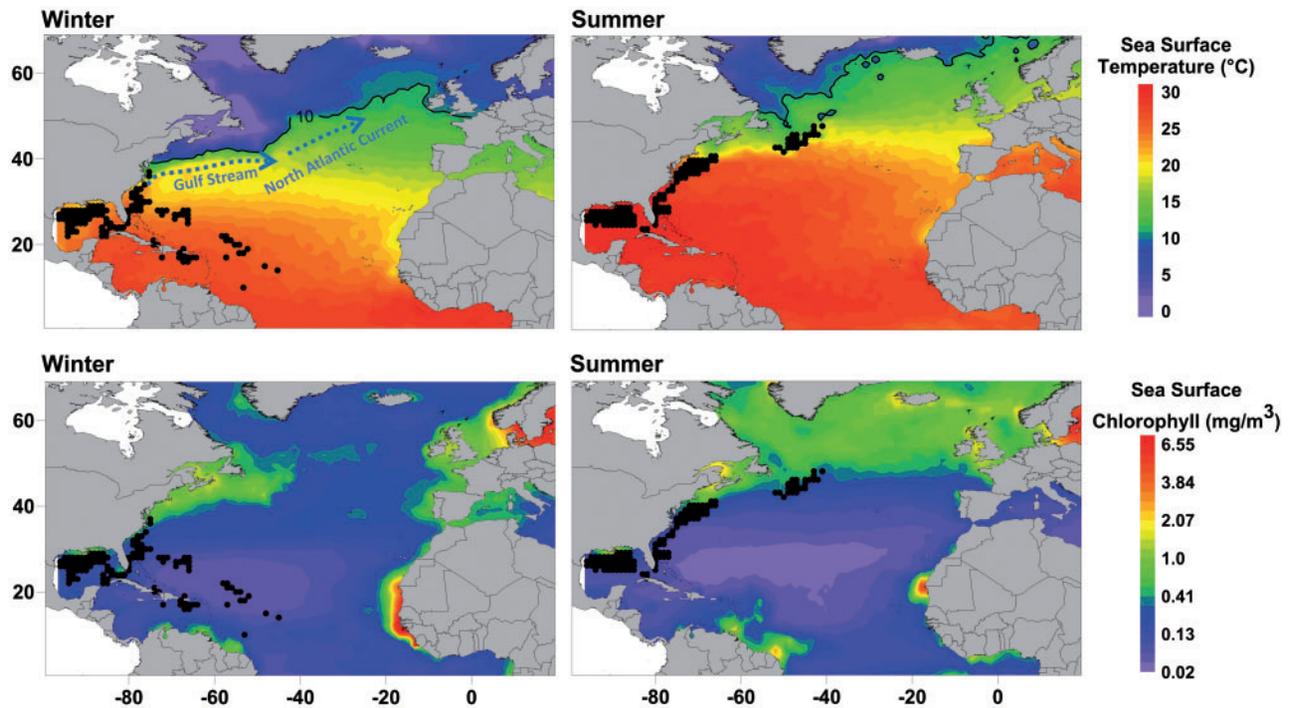


Figure 4. Fishing activity in summer and winter for the U.S. pelagic longline fleet. Rounded $1 \times 1^\circ$ locations with all environmental variables used in the SDM available for at least 10 sets from 1997 to 2010 are shown as black dots. Climatological surface temperature (WOA: 1995–2014) and surface chlorophyll (SeaWiFS: 1997–2010) are also shown, along with schematic representations of the Gulf Stream and North Atlantic Current. Note non-linear scale for chlorophyll.

throughout most of the region, with the exception of an increase south of Greenland in the area of projected cooling, as expected from a temperature-solubility control. Surface chlorophyll was projected to increase north of 40°N , and also in the Mediterranean Sea during winter, but to decrease throughout most of the region during summer (Figures 7 and 8).

These changes in the pelagic ocean environment resulted in shifts in projected habitat for ABFT. The oxygen balance model predicted a decrease in habitat suitability south of $35\text{--}40^\circ\text{N}$ in both seasons, due to warming waters and associated slight decreases in oxygen (Figure 9). The projected cooling south of Greenland and around Iceland also reduced the predicted oxygen balance in this area, with the negative influence of temperature on heart rate and blood oxygen transport outpacing the positive effect of increased oxygen concentrations. The oxygen balance model projected improved habitat elsewhere north of 40°N , as a result of warming ocean temperatures.

Projections from the SDM were broadly similar to those from the oxygen balance model, but more pessimistic in winter north of $\sim 40^\circ\text{N}$ (Figure 9). The SDM predicted that habitat throughout the North Atlantic Ocean would generally become less suitable for ABFT in both seasons, with the exception of a band of mostly improved conditions between 40 and 50°N , from the Gulf of Saint Lawrence across to the northern Bay of Biscay and Celtic Sea. The gains in habitat in these areas were mostly consistent with results from the oxygen balance model. However the SDM did not show a general improvement in habitat in the rest of the far North Atlantic, whereas the oxygen balance model did (Figure 9). When we compared projected changes in habitat suitability to the core habitats where ABFT catch rates are currently positive

(Figure 6), we noted a general loss of habitat projected for the southern and northern parts of the current range, with some gains in the central portion. While the oxygen balance model projected that some areas north of the current range would become more suitable, the SDM showed loss of habitat or neutral conditions in these areas (Figure 9).

As results from the oxygen balance model and the SDM were markedly different between waters north and south of $\sim 40^\circ\text{N}$, we calculated the sensitivity analysis results separately for these two regions (Figure 10). In the area north of 40°N , the SDM predicted an average 0.8% drop in probability of occurrence (6.1% down to 5.3%, $p < 0.01$, t -test) of ABFT on longline sets in winter, and a slight increase in summer (8.2% up to 8.6%, $p < 0.01$, t -test), between 1971–2000 and 2071–2100 (Figure 10). When either sea surface temperature or 100 m temperature was held constant, results became more optimistic for both seasons. If oxygen levels at 100 m were unchanged between the two time periods, summer projections became slightly more pessimistic; and if surface chlorophyll remained constant, winter projections became more optimistic. Our results suggested that the projected decrease in winter habitat north of 40°N was largely a result of ocean cooling south of Greenland, and that this cool area also limited the northward expansion of ABFT habitat in summer. There was a secondary, and unexpected, negative effect of increased chlorophyll during winter.

In contrast, model sensitivities for the region south of 40°N were more straightforward. The SDM run considering climate-induced changes across all variables projected a 1.4% decrease in probability of occurrence in winter (2.4% down from 3.8%, $p < 0.01$, t -test), and a 1.7% decrease in summer (1.9% down

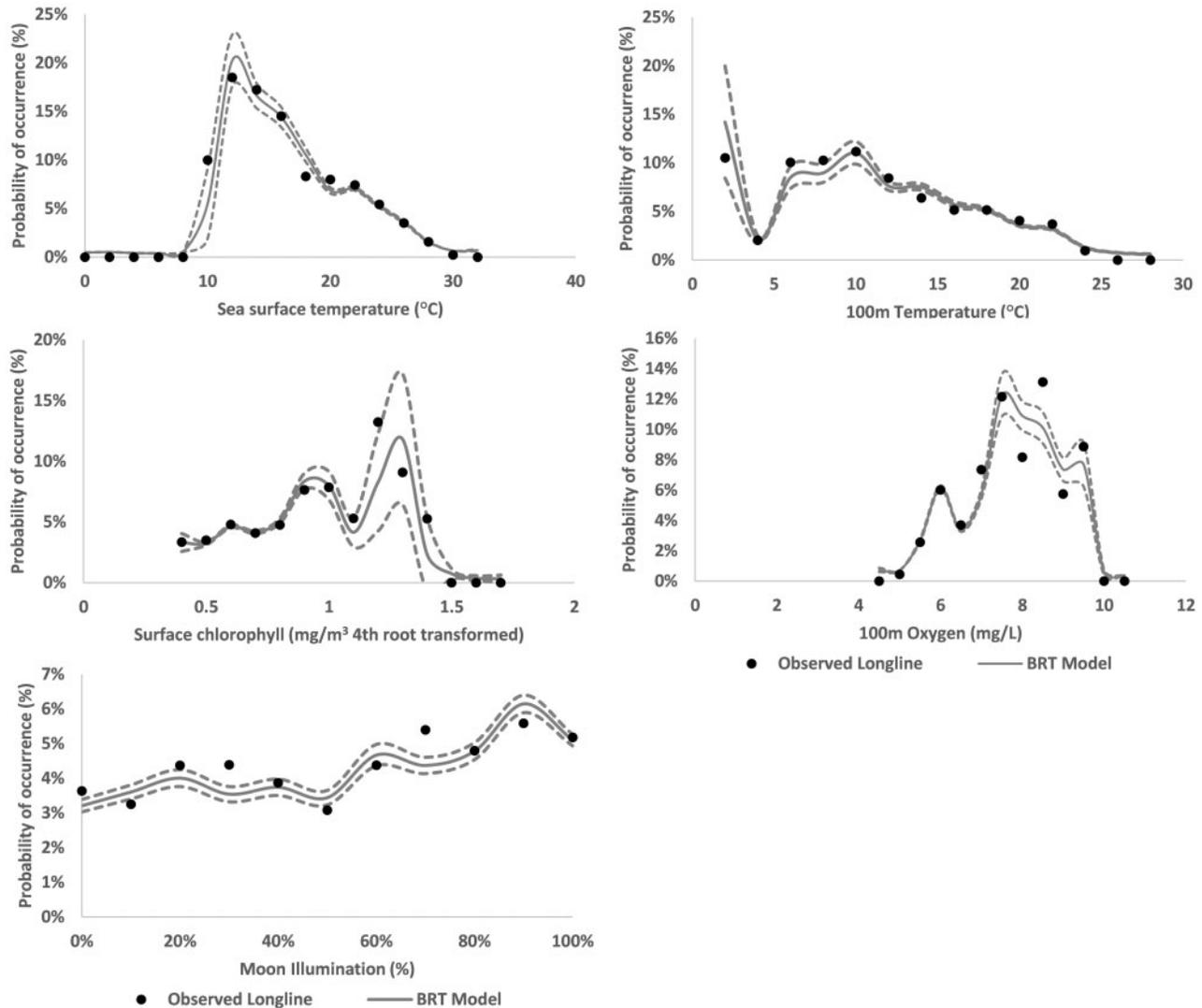


Figure 5. Boosted regression tree (BRT) modelled (line) and observed (dots) relationships between presence/absence of ABFT on pelagic longlines, and five environmental predictors from the SDM. Dashed lines show ± 1 standard error from SDM predictions within each bin plotted, thus representing variability (from all sources) in the model at different environmental conditions. Only results from the test data (i.e. those not used to build the SDM) are shown.

from 3.6%, $p < 0.01$, t -test) (Figure 10). Holding ocean temperatures constant resulting in more optimistic results, while holding 100 m oxygen or surface chlorophyll constant made minimal difference. The projected loss of habitat south of 35°N was therefore primarily a result of ocean warming, particularly at depth.

Discussion

Bluefin tuna spatial distributions

Our results suggest that ABFT are generally distributed within parts of the North Atlantic Ocean with favourable metabolic characteristics, and that these regions shift seasonally. Predicted suitable habitat from both the oxygen balance model and the correlative SDM matched reasonably well with spatial catch rate data, with the exception of the Gulf of Mexico. These were also consistent with known ABFT migration routes and habitat use from studies employing both conventional and electronic data

recording tags (Block *et al.*, 2001, 2005; Boustany *et al.*, 2008; Walli *et al.*, 2009; Wilson *et al.*, 2015). These data sources are complementary, as while fisheries-dependent catch-data may be easier to obtain than tagging data, the former cannot distinguish between fish which have been caught as they migrate through an area from those which are resident. Conversely, data from electronic tags show the spatial heterogeneity of habitat use, and directed migratory behaviour between feeding and spawning grounds (Block *et al.*, 2005; Teo *et al.*, 2007; Walli *et al.*, 2009; Neilson *et al.*, 2014). They are also less dependent on the spatial coverage of fishing fleets, and are not subject to many of the issues of bias associated with using fishery-dependent catch rate data (Walters, 2003; Bishop, 2006). However, in our study, the spatially restricted US pelagic longline data were still effective at training a SDM which was consistent with unseen, Atlantic-wide catch rate data (from ICCAT), and with the seasonal habitat use defined by previous electronic tagging studies (Block *et al.*, 2005; Walli *et al.*, 2009).

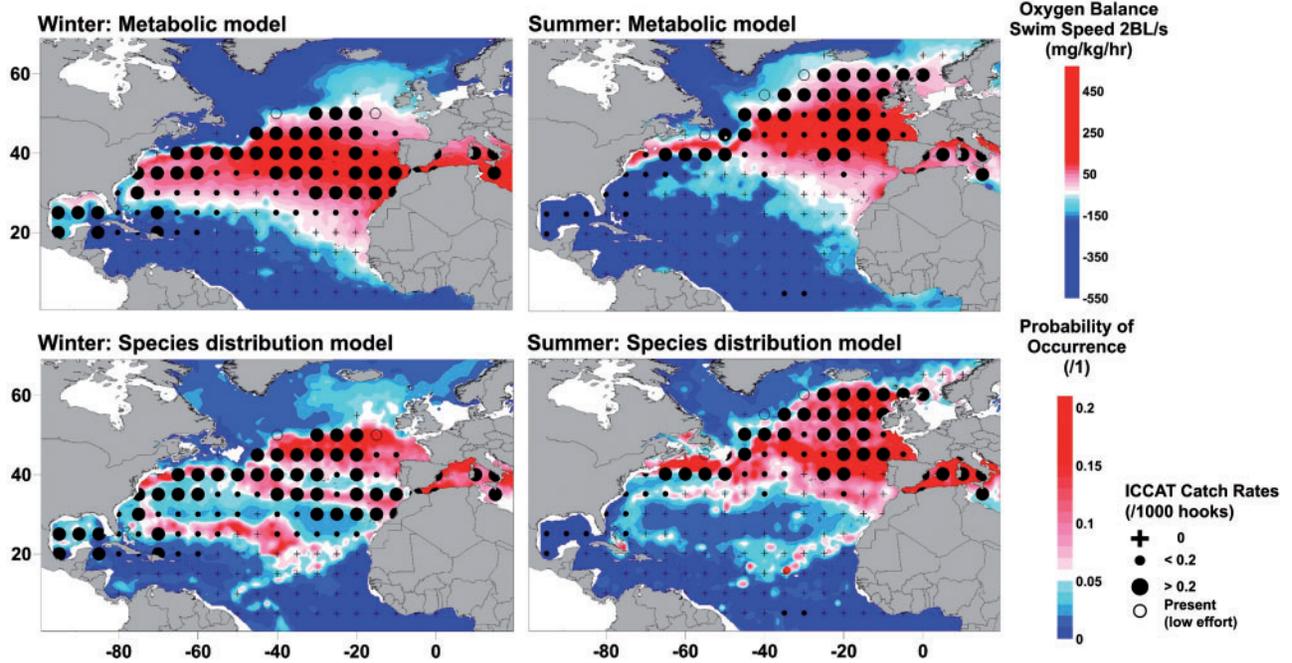


Figure 6. Predicted oxygen balance (top) and probability of occurrence (bottom) from the metabolic oxygen balance model and the SDM, respectively. Results from the oxygen balance model are shown for an ABFT swimming at 2 BL/s. Catch rate data from the ICCAT Task II database (1997–2014) are overlaid. Waters shallower than 50 m are masked for the metabolic model, and waters shallower than 100 m are masked for the SDM, as a function of predictor variables used in each model.

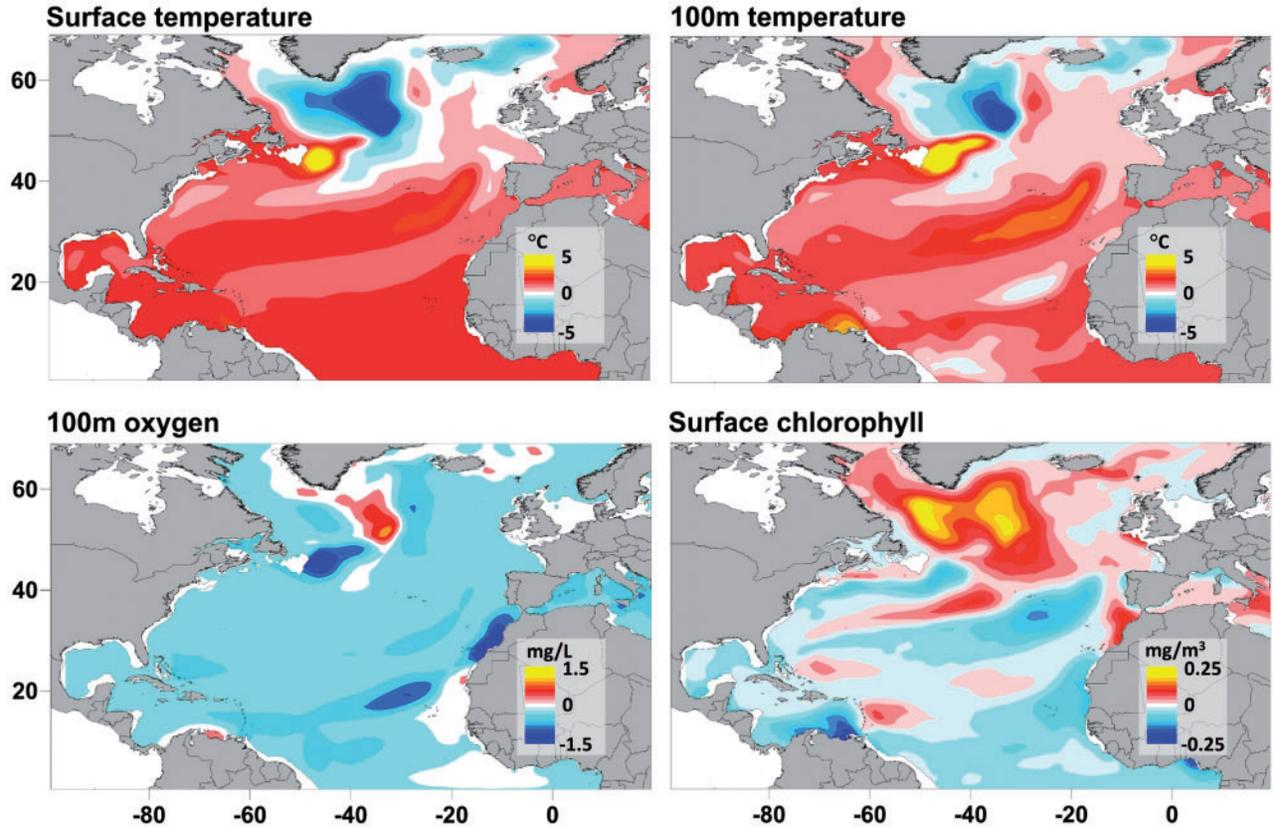


Figure 7. Projected winter (January–March) changes in surface temperature, 100 m temperature, 100 m oxygen, and surface chlorophyll from the ESM2M earth system model, 1971–2000 vs. 2071–2100.

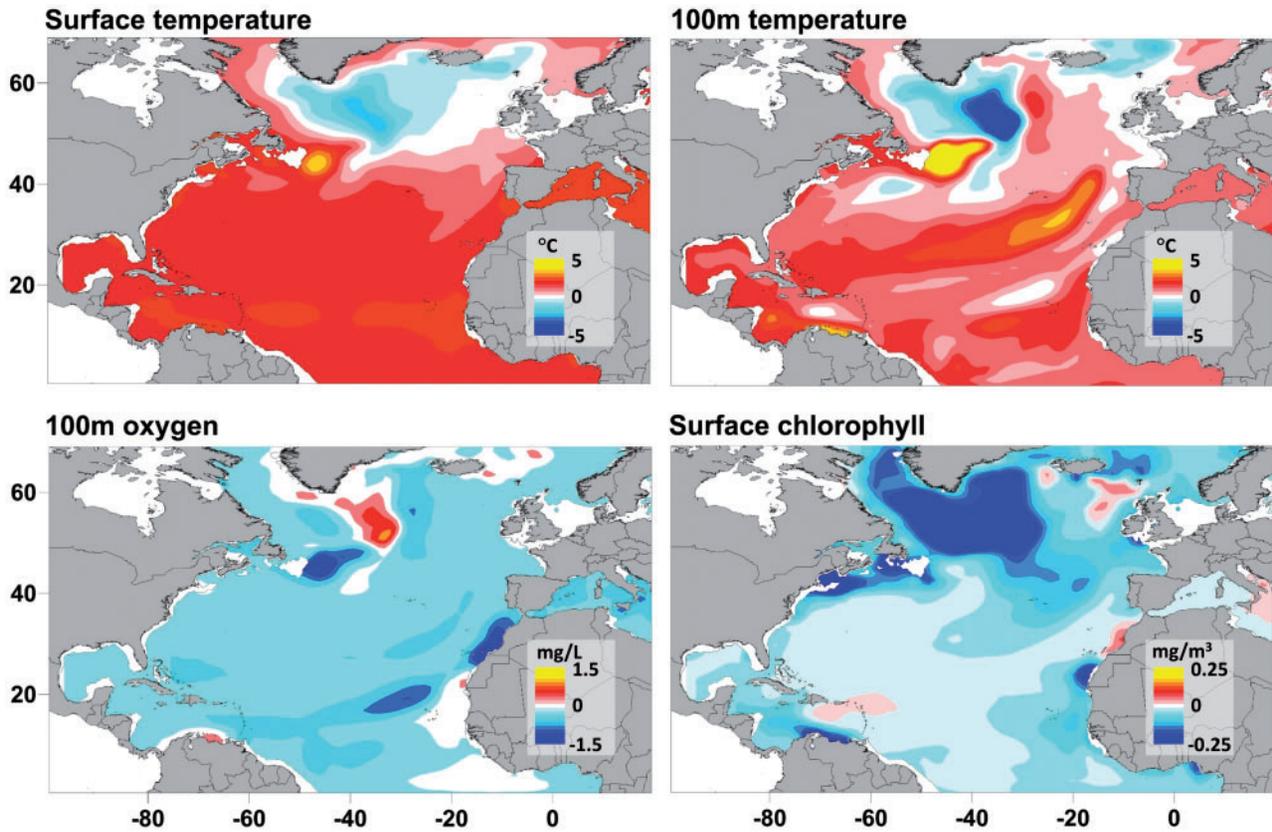


Figure 8. As for Figure 7, but for summer (July–September).

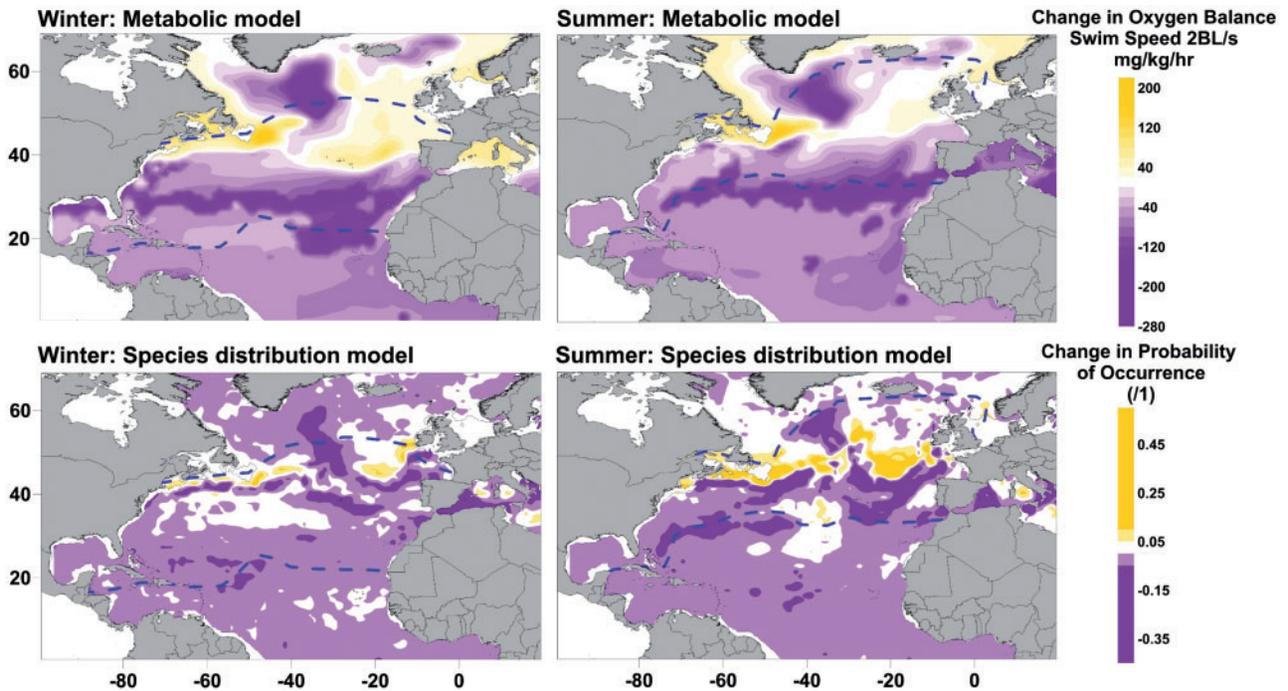


Figure 9. Projected change in oxygen balance (top) and probability of occurrence (bottom) for ABFT between 1971–2000 and 2071–2100, from the ESM2M earth system model. The regions where positive catch rates for ABFT have been recorded in the ICCAT Task II database (1997–2014: i.e. Figure 6) are shown as dashed polygons.

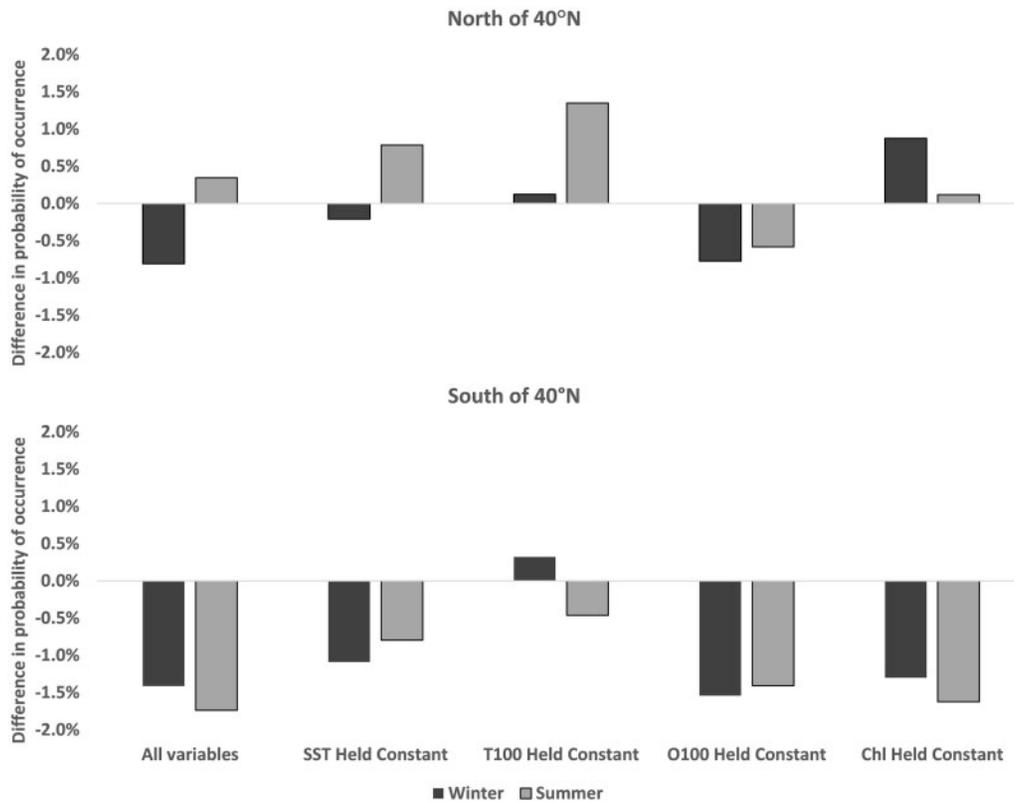


Figure 10. Sensitivity testing for the SDM. Projected change in probability of ABFT occurrence on pelagic longlines is shown for (L–R): the original model (i.e. Figure 9), for a model where surface temperature (SST) is held constant and does not change between 1971 and 2000, for a model where 100 m temperature (T_{100}) is held constant, for a model where 100 m oxygen (O_{100}) is held constant, and where surface chlorophyll (Chl) is held constant. Dark bars denote winter, light bars summer. Results are shown separately for the region of north 40°N, and south of 40°N.

Adult ABFT tagged in the North Atlantic Ocean migrate as far south as the Gulf of Mexico and northern Caribbean Sea, and as far north as Newfoundland, Iceland and Norway (Mather *et al.*, 1995; Block *et al.*, 2005; Walli *et al.*, 2009; Wilson *et al.*, 2015), with the northern boundary of their distribution synonymous with the northern wall of the Gulf Stream and the North Atlantic Current. Our results show that this distributional limit is associated with the northern boundary of favourable metabolic habitat. Both the oxygen balance model and the SDM predicted favourable habitat connecting the eastern and western North Atlantic in both winter and summer, which may facilitate trans-Atlantic migrations (Mather *et al.*, 1995; Block *et al.*, 2005; Rooker *et al.*, 2008).

One historical migratory route which was not supported by our results was the so-called “Brazilian episode”, where ABFT were found in sufficient numbers to support a fishery off Brazil in the 1950s and 1960s (Takeuchi *et al.*, 2009). Two ABFT tagged with conventional tags near the Bahamas during this time were recaptured off Brazil and Argentina, confirming a link between the Brazilian fish and the north Atlantic Ocean (Mather *et al.*, 1995). The oxygen balance model that we developed showed generally unfavourable habitat in the tropical Atlantic between the Bahamas and Brazil in both winter and summer. The SDM also showed low probabilities of occurrence in this area, with the exception of some small, marginally favourable areas in winter. Fromentin *et al.* (2014) hypothesized that ABFT habitat between

the Bahamas and South America was more favourable in the 1960s than the present day, primarily due to slightly cooler surface temperatures. This may have allowed easier migration across equatorial waters, with lower metabolic stress incurred.

ABFT distributions were not purely a function of predicted oxygen balance, however. Most large adult ABFT migrate to the Gulf of Mexico area from late winter to early summer to spawn (Mather *et al.*, 1995; Block *et al.*, 2005; Muhling *et al.*, 2010). This region is characterized by very warm sea surface temperatures, which may approach 28–30 °C by the end of the spawning season (Muller-Karger *et al.*, 2015; Wilson *et al.*, 2015). As a result, the oxygen balance model predicted that habitat suitability in this area was low or marginal, even during winter. Several authors have proposed that this environment may cause metabolic stress in ABFT, and noted that they adopt more extensive vertical movement patterns while on the spawning ground in order to thermoregulate, particularly while traversing the Loop Current (Blank *et al.*, 2004; Block *et al.*, 2005; Teo *et al.*, 2007).

Conversely, ABFT feeding grounds can include very cold waters in the northern North Atlantic. Adult ABFT have been caught near Iceland, Greenland and historically near Norway, where surface temperatures may be as low as 9–11 °C (Mather *et al.*, 1995; Mackenzie *et al.*, 2014). These areas are typically close to the northern limits of favourable metabolic habitat. Several authors (Brill, 1994; Brill and Lutcavage, 2001; Bernal *et al.*, 2010; Horodysky *et al.*, 2016) have argued that temperature, dissolved

oxygen and prey concentrations are the primary mechanisms driving distributions of large pelagic fishes, including tunas. They considered the first two variables to be physically limiting, and the last to be “permissive/attractive”, which is consistent with finer-scale use of feeding habitats within broader physiological limits. This concept was demonstrated in the field for the California Current ecosystem, where Pacific bluefin tuna were observed to target favourable foraging habitats within broadly suitable metabolic temperature ranges (Kitagawa *et al.*, 2007; Whitlock *et al.*, 2015). Walli *et al.* (2009) also noted that tagged ABFT ranged throughout much of the sub-tropical and temperate north Atlantic, but congregated in spatially restricted, high-use feeding areas, which shifted seasonally.

In the context of previous studies, our results thus suggest that ABFT do not preferentially occupy regions of absolute lowest metabolic stress, but rather complete necessary biological processes (spawning, feeding) within physiological limits, and sometimes near the boundaries of these. Areas of highest habitat use correspond closely to specific environmental conditions suitable for spawning or feeding, which are within theoretical metabolic limits, but more spatially restricted. The nature of conceptual models linking metabolic scope and species distributions and behaviours are still under some discussion (Clark *et al.*, 2013a; Farrell, 2016). However, tunas have relatively high standard metabolic rates, and require additional metabolic scope above these for digestion (specific dynamic action), somatic and gonadal growth, and repayment of oxygen debt incurred by descending into cold or oxygen-limited habitats to feed (Brill, 1987; Bushnell and Jones, 1994; Brill, 1996; Korsmeyer *et al.*, 1996; Clark *et al.*, 2010; Whitlock *et al.*, 2013; Estess *et al.*, 2014). The availability of oxygen to sustain essential physiological processes would therefore place limits on overall distributions, although not necessary patterns of abundance within these (Brill, 1994; Bestley *et al.*, 2009).

Comparison with other tuna species

The association of maximum oxygen balances with temperatures of 10–20 °C for ABFT were primarily a result of the unusual relationship between metabolic demand and temperature for bluefin tuna species. Pacific bluefin tuna metabolic oxygen demand in laboratory experiments has been shown to be at a minimum at ~15 to 20 °C at low or moderate swimming speeds, increasing as temperatures cooled or warmed beyond this range (Blank *et al.*, 2007a; Clark *et al.*, 2013b; Clark, 2016). This is in contrast to YFT, where metabolic rates have been shown to increase with temperature between 18 and 30 °C (Brill, 1987; Dewar and Graham, 1994). To the best of our knowledge, no studies have been completed at temperatures colder than 18 °C, but within this range, YFT do not show any evidence of the U-shaped relationship exhibited by ABFT. As a result, a metabolic scope model for YFT developed by Del Raye and Weng (2015), using experimental data and metabolic theory, showed that maximum metabolic scope for this species was at ~25 °C, rather than at the 10–20 °C suggested for bluefin tunas.

Pacific bluefin tuna also have higher overall metabolic rates than YFT at the same temperature and swimming speed (Blank *et al.*, 2007b). This suggests a fundamental physiological difference between the two species. If oxygen balance is an important determinant of metabolic stress in warm waters, bluefin tunas may be slightly disadvantaged in these habitats compared to YFT,

and other tuna species that primarily occupy tropical and subtropical areas. However, interactions between ambient temperature and oxygen, vertical movements and thermoregulation, and metabolic scope in different tunas as they relate to upper temperature tolerances are difficult to quantify. Early studies of warm-water species such as skipjack tuna (*Katsuwonus pelamis*) speculated that they would be prone to over-heating in warm regions as a consequence of their endothermy (Barkley *et al.*, 1978). However, it has since been shown that tuna are able to quickly adjust the efficacy of their vascular counter-current heat exchanger in response to water temperature (Dizon and Brill, 1979a,b; Holland *et al.*, 1992; Brill *et al.*, 1994; Dewar *et al.*, 1994), which complicates accurate modelling of thermal stress (Boye *et al.*, 2009). Bluefin tunas can maintain much warmer body temperatures than YFT, allowing them to forage in much colder waters (Carey and Teal, 1969; Graham and Dickson, 2001), although maintaining thermal excess in cold waters may be associated with significant metabolic costs (Blank *et al.*, 2007a; Kitagawa *et al.*, 2007). Previous studies have speculated that high mortality of ABFT caught on longline gear in the warm Gulf of Mexico may be due to oxygen stress (Blank *et al.*, 2004). However, exactly how ABFT physiology may contribute to intolerance of warm waters, and why this problem is not as severe for warm-water tunas caught in the same area (e.g. YFT, skipjack tuna), is not completely clear.

In contrast, the superior ability of bluefin tuna hearts to tolerate cold temperatures, in comparison to more tropical tunas, is well documented. Pacific bluefin tuna can maintain cardiac function in waters as cold as 2 °C, and have higher heart rates and cardiac output than YFT at temperatures of <15 °C (Blank *et al.*, 2004). This appears to be due to several physiological specializations of bluefin tuna hearts, which distinguishes them from other tuna species (Landiera-Fernandez *et al.*, 2004; Galli *et al.*, 2009; Madigan *et al.*, 2015). As a result, the poleward limits of favourable metabolic habitat in this study, which result primarily from the effects of cold temperatures on heart rates, can be considered to have higher confidence than the equatorward limits, which are due to very high modelled metabolic demands at warm temperatures.

Projection of climate change impacts

Application of the oxygen balance model and SDM to projections of future conditions from the ESM2M model showed general loss of habitat for ABFT under climate change. Strong warming and some deoxygenation south of ~40°N led to lower predicted oxygen balances, and lower predicted probabilities of occurrence. In contrast, habitat suitability from both the oxygen balance model and the SDM was projected to improve around the Gulf of Maine, Nova Scotia, and Newfoundland. This was primarily due to the future warming of cold waters which are currently north of the Gulf Stream, partially as a result of a northward shift in this circulation feature (Joyce and Zhang, 2010; Saba *et al.*, 2016). Waters near Greenland, Iceland and Norway were predicted to become more favourable in the oxygen balance model, but not in the SDM. The cooling projected for the region south of Greenland resulted in lower habitat suitability under future conditions in both predictive models. This cooling feature is present in many GCMs, but is particularly prominent in ESM2M. It is due to the influence of a weakening Atlantic Meridional Overturning Circulation, as well as reduced mixing, and increased

freshwater inflow from the Greenland ice sheet (Drijfhout *et al.*, 2012; Jahn and Holland, 2013; Kim and An, 2013; Agarwal *et al.*, 2014; Swingedouw *et al.*, 2014). In addition to these oceanographic changes, the shoaling of deep winter mixing and enhanced stratification in the far North Atlantic may partially alleviate the current light limitation on primary productivity in this region, resulting in a winter surface chlorophyll increase. Conversely, enhanced stratification during summer will likely exacerbate current nutrient limitation, leading to reduced surface chlorophyll, and potentially less favourable feeding conditions (Doney, 2006; Stock *et al.*, 2014).

Projections of future ABFT habitats are largely consistent with Muhling *et al.* (2015), who found that thermal habitat from correlative SDMs for adult for larval and adult ABFT is likely to decrease on the Gulf of Mexico spawning grounds as a result of anthropogenic warming. In contrast, Hazen *et al.* (2013) predict a future increase in core habitat for Pacific bluefin tuna in the North Pacific by the end of the 21st century, using projections from ESM2.1, under the A2 CO₂ emission scenario. This is largely due to the weak warming projected for core Pacific bluefin tuna habitat in the California Current region (<1 °C). Chlorophyll concentrations in this area are also projected to increase, potentially expanding favourable feeding habitat (Boustany *et al.*, 2010). Region-specific patterns of climate change effects on oceanographic environments can thus cause widely diverging projections of biological impacts, even for very closely related species.

Projections of future changes in habitat suitability in this study are reasonably similar between the oxygen balance model and the SDM, partially because of the importance of temperature and oxygen to both models. However, there are some differences between the two approaches. While both models projected a loss of ABFT habitat south of ~40°N, and south of Greenland, the SDM is more pessimistic in the rest of the far North Atlantic. This is partially because probabilities of ABFT occurrence from the SDM cannot be less than 0. Cold areas of the North Atlantic in winter, such as near Norway and Iceland, warm less than 1 °C in ESM2M between 1971–2000 and 2071–2100, remaining below 5 °C. Thus predicted probabilities of occurrence from the SDM remain near zero, and the change in habitat suitability will be near zero. However, some of the differences between the oxygen balance model and the SDM also result from the SDM attempting to extrapolate near or beyond the edges of conditions encountered in the training data. For example, winter chlorophyll concentrations north of 40°N are projected to increase into the future. The sensitivity analyses show that this contributes to a loss of winter habitat in the SDM. This is counter-intuitive, but resulted from the SDM attempting to extrapolate the effects of chlorophyll in very cold waters, which it had not previously “seen” in the training dataset. This was because the training dataset was sourced from fisheries-dependent logbook data, and so any predictions beyond the range of conditions fished by pelagic longline fishermen required extrapolation by the SDM.

This demonstrates an important weakness for the use of correlative SDMs: that they are only as good as their training data. Where suitable habitat is largely assumed to be related to temperature, SDMs will be the most successful where there is good information on both upper and lower limits. In our study, upper temperature limits are well defined, as the pelagic logbook data included extensive effort in warm sub-tropical and tropical waters where ABFT are largely absent. In contrast, lower temperature

limits had to be artificially forced in the SDM, which leads to high uncertainty in future projections for the far North Atlantic.

Key uncertainties

The two biological models we developed in this study give quite similar results when applied to both recent historical and potential future conditions, primarily because water temperature and oxygen are important to both. However, they did demonstrate some of the advantages and disadvantages with using correlative versus mechanistic biological models to assess climate change impacts. SDMs require relatively few input variables and no mechanistic understanding to parameterize, and there are standard methods available in most cases to assess model performance and predictive skill (Peck *et al.*, 2016). However, they rely on statistical methods to approximate biological processes, and must usually consider non-parametric, non-linear relationships, multiple predictor variables, and interaction terms in order to fit historical training datasets. This complexity can lead to unexpected or biologically unlikely results when applied to new datasets, particularly if extrapolation is required. In addition, different types of SDM can give widely varying results, and (as in our study), may require subjective adjustment or boundary clipping to force sensible results (Jones *et al.*, 2012; Jarnevich *et al.*, 2015; Cheung *et al.*, 2016a). It can also be challenging to identify the most biologically important factors that limit a species range, particularly if mechanistic understanding is limited. Even once these are identified statistically, projecting correlative SDMs forward in time assumes stationarity; in other words that relationships between a species and its environment will not change in the future (Dormann *et al.*, 2012; Horodysky *et al.*, 2015, 2016).

The oxygen balance model is more mechanistic than the SDM, although it still requires empirical estimation of physiological processes. The main uncertainties with this model are that physiological parameters are not well known for adult ABFT, and so had to be estimated from data obtained from juvenile Pacific bluefin tuna and YFT. Tuna physiology can change markedly with body size and with species, even among congeners (Lowe *et al.*, 2000; Korsmeyer and Dewar, 2001; Blank *et al.*, 2007b). There are also substantial differences in physiology among tuna species. These are most obvious for bluefin tunas versus YFT, as the former have more highly developed endothermic capabilities, and reach much larger sizes (Carey and Teal, 1969; Graham and Dickson, 2001). In addition, Clark *et al.* (2008) highlight several differences in haematological characteristics among different tuna species, including blood oxygen affinity (measured as P₅₀, or the oxygen partial pressure required to achieve 50% blood oxygen saturation), which Mislán *et al.* (2015) used as an indicator of oxygen-based vertical habitat availability. However, there may also be important differences even among the bluefin tunas. For example, although all three bluefin tuna species are relatively large and long-lived, both ABFT and Pacific bluefin tuna grow faster than Southern bluefin, and ABFT attain the largest size of all three species (Gunn *et al.*, 2008; Santamaria *et al.*, 2009; Shimose *et al.*, 2009). The effects of these differences on the validity of building a model for ABFT based on data from other species are unknown, but may be substantial. These issues demonstrate one of the main disadvantages with mechanistic models: their parameterization requires sufficient experimental data. Where the required information is not available, it must be drawn from other species (“parameter stealing”: Peck *et al.*, 2016), other regions, or other

life stages; and the contribution of this to overall uncertainty is difficult to quantify. These considerations highlight the need for more species-level experimental data across life stages, which can be challenging to obtain from large, rapidly swimming organisms such as tunas.

In addition, neither the SDM nor the oxygen balance model implicitly considered feeding dynamics, although the use of chlorophyll in SDMs is often considered to be a rough proxy (Robinson *et al.*, 2011; Hazen *et al.*, 2013). Recent studies have shown that poleward shifts in ABFT distributions in recent years are primarily attributable to shifts in prey abundance or quality, as well as the presence of tolerable water temperatures (Astthorsson *et al.*, 2012; Mackenzie *et al.*, 2014; Vanderlaan *et al.*, 2014; Golet *et al.*, 2015; Logan *et al.*, 2015; Jansen *et al.*, 2016). While more complex life-cycle models including feeding dynamics are becoming more common for climate change projections, and are likely the way of the future (Lehodey *et al.*, 2013, 2015; Dueri *et al.*, 2014), they may still result in high uncertainties in regions where food web dynamics are not yet well understood (Woodworth-Jefcoats *et al.*, 2015; Peck *et al.*, 2016).

Both the SDM and the oxygen balance model are essentially distribution models, only considering climate change impacts in terms of range shifts. While this is a good starting point, other factors influencing life history and phenology, including estimates of recruitment potential, stock productivity, interactions with other species, and adaptive capacity will eventually need to be incorporated if projections are to be useful for stock management (McIlgorm, 2010; Hartog *et al.*, 2011; Howell *et al.*, 2013; Peck *et al.*, 2016; Ward *et al.*, 2016). Our models are also very coarse in space and time, and do not consider fish behaviour in three dimensions, or finer-scale interactions between ABFT and local-regional oceanographic features. This is partly due to the coarse resolution of ESM2M. Climate models typically have spatial resolutions of ~ 1 degree, and therefore may not well represent important regional mesoscale and sub-mesoscale oceanographic circulation features (Liu *et al.*, 2015; Saba *et al.*, 2016). As the resolution of these models continues to improve, finer-scale projections will be possible. The representation of biogeochemical tracers in earth system models is also much less certain than physical variables such as temperature. There is significant spread among different earth system models, and regional biases can be large (Bopp *et al.*, 2013). As a result, we employed only one model (ESM2M), as it simulated historical surface chlorophyll in the North Atlantic much more realistically than the other models considered. However, future work should consider the contribution of spread in climate models to future projections across all variables, including temperature and oxygen, and include additional climate change scenarios (e.g. RCP4.5) (Cheung *et al.*, 2016b).

Our study also focused primarily on horizontal distributions of ABFT, rather than vertical behaviours. Water column structure, particularly the depth of oxygen minimum zones, has been shown to influence vertical movements in large pelagic fishes, and shoaling of these low-oxygen layers may vertically compress available habitat (Stramma *et al.* 2012; Deary *et al.* 2016). ABFT tolerate strong environmental gradients in the course of foraging and diving behaviours (Brill *et al.*, 2002; Block *et al.*, 2005; Walli *et al.*, 2009), and Teo *et al.* (2007) proposed that ABFT on the Gulf of Mexico spawning grounds use vertical movements to thermoregulate in warm waters. However, the ability of ABFT to adjust

these to minimize physiological stress as oceans continue to warm is not well known.

Despite these uncertainties, our results provide strong support for temperature and oxygen as important drivers of ABFT distribution in the North Atlantic Ocean. Observed range limits correlate closely with theoretical metabolic oxygen balance, although abundance within these limits is probably more driven by the targeted use of foraging and spawning environments. The unique physiology of bluefin tunas results in minimum metabolic costs at 10–20 °C, which led to the location of favourable habitats in temperate latitudes of the north Atlantic. Projections of climate change impacts showed a future loss of habitat in tropical and sub-tropical regions, but more complex changes in northern habitats. These have implications for future spatial distribution of ABFT, and thus availability to fishing fleets from different nations. Given the ecological and economic importance of ABFT, future work should continue to develop and refine mechanistic projections of climate change impacts on this, and other, tuna species.

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