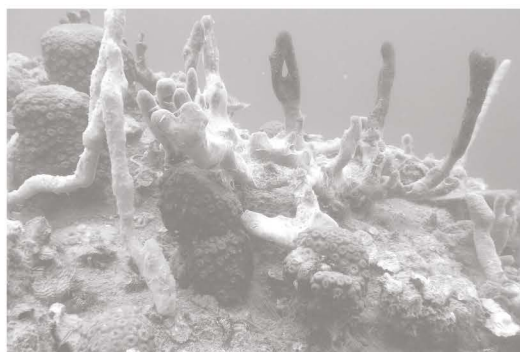# IUCN

Ocean deoxygenation: Everyone's problem

Causes, impacts, consequences and solutions

Edited by D. Laffoley and J.M. Baxter

8.2 The significance of ocean deoxygenation for open ocean tunas and billfishes

Shirley Leung, K. A. S. Mislan, Barbara Muhling and Richard Brill

8.2 The significance of ocean deoxygenation for open ocean tunas and billfishes

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Summary

- Tunas and billfishes should be especially sensitive to low ambient oxygen conditions given their high metabolic rates as well as the large differences between their resting and maximum metabolic rates. Although there are many behavioural similarities among the different species, there are also clear and demonstrable differences in growth rates, maximum adult size, physiological abilities, low-oxygen tolerances, and preferred environmental conditions.

- Climate change is projected to alter oxygen concentrations throughout the open ocean, with most regions undergoing decreases due to a slowdown in ocean ventilation and a decline in surface oxygen solubility. Between 200 and 700 m depth (a vertical range including depths to which tunas and billfishes commonly descend to forage), the greatest and most certain decreases in oxygen concentrations are projected to occur in the North Pacific and much of the Southern Ocean, while the smallest and least certain changes are projected to occur within the tropical Pacific Ocean. Along a north-south line through the middle of the Pacific Ocean (160°W longitude), projected oxygen concentration decreases are most pronounced from 15°N to 50°N between 250 and 750 m depth and south of 50°S between 50 and 300 m depth.

- The depth at which oxygen concentrations drop below 3.5 ml L^{-1} (a threshold hypoxic concentration for several tuna and billfish species including yellowfin and skipjack tunas, marlins, and sailfish) is projected to shoal throughout the global oceans, which may lead to widespread vertical habitat compression and changes in vertical movement patterns. Projected shoaling of the 3.5 ml L^{-1} threshold depth is especially pronounced within subtropical and mid-latitude Pacific Ocean regions. Oxycline depth is also projected to shoal by over 150 m in these same Pacific Ocean regions and throughout much of the Southern Ocean. Species residing in the temperate North Pacific, such as swordfish and yellowfin, bigeye, Pacific bluefin, and albacore tunas, may therefore be impacted by future oxygen changes more greatly than other species, as projected decreases in oxygen concentrations are greatest within their present-day ranges.

- Changes in temperature and oxygen content have the potential to alter the distribution and catchability of tunas and billfishes in three dimensions. Because they are highly mobile, tunas and billfishes can exhibit complex shifts in their distributions in response to changing environmental conditions. Where surface layer temperatures become too warm, they may spend more time at depth (assuming oxygen concentrations are sufficient); where low-oxygen layers shoal or expand, they may spend more time near the oxygenated surface (assuming temperatures are not too warm), increasing their vulnerability to surface fishing gears. If no vertical refuge from unsuitable conditions is available, they may shift their distributions horizontally. Because temperature and hypoxia tolerances of tunas and billfishes are species-specific, any changes in temperature and oxygen content within the water column may modify competition among different species as their vertical and horizontal habitats shift in different ways, potentially altering established food web dynamics, ecosystem structures, and bycatch rates. Differential responses of prey species to changes in environmental conditions could also affect food web structures, the ability of tunas and billfishes to find food, age at first reproduction, and mean body sizes.

- Future changes in the distributions of tunas and billfishes are likely to complicate stock assessments and to have important socio-economic effects. As spatial habitats of targeted tuna and billfish species shift, the ability of fishery-dependent, catch per unit effort (CPUE)-based abundance indices to capture stock dynamics accurately will be compromised, unless CPUE-standardization methods can adapt. Where populations of targeted tuna and billfish species decrease in abundance or move away from traditional fishing grounds, fishers will have to spend more resources to locate and catch these species or reconfigure their gear to target new ones. Economic, political, and regulatory constraints can, however, hinder the ability of fishers to effectively adapt, particularly if species move across management boundaries. Smaller-scale fisheries in developing nations and fisheries relying on vessels with limited range and low technological capabilities are likely to be most vulnerable to shifts in range or migratory patterns.

Ocean hypoxia effect	Potential consequences
Decreasing oxygen concentrations in current habitats may result in species-specific shifts in range and migratory patterns.	• Alters the ecological relationships between some tuna and billfish species and their prey. • Geographically redistributes catches and societal benefits from fisheries. • Complicates stock assessment and management, as changes in environmental conditions alter fish availability and subsequent fishery data-derived estimates of abundance.
Shallower oxyclines and hypoxic layers may result in species-specific changes in vertical movement patterns and compression of vertical habitat.	• Decreases vertical separation among tuna species, resulting in future increases in the frequency of competitive species interactions. • Alters coupling between predator and prey and thus foraging success. • Increases vulnerability to capture by surface fishing gears.
Changing oxygen concentrations may lead to changes in locations of spawning grounds.	• Alters spawning success and year class strength, which could modify the ability of tuna and billfish populations to withstand high rates of fishing mortality. • Albacore tuna in the South Pacific may be negatively affected by oxygen concentration decreases on their spawning grounds; other species may be either negatively or positively affected.
The temperate North Pacific Ocean is projected to undergo large decreases in oxygen content within the upper water column (above 1000 m).	• Species currently residing in this region (which include swordfish and yellowfin, bigeye, Pacific bluefin, and albacore tunas) are expected to experience the most dramatic decreases in oxygen concentrations and shoaling of hypoxic layers within their habitat.

8.2.1 Introduction

The effects of temperature and ambient oxygen on the behaviours and physiology of tunas (members of the family Scombridae, tribe Thunnini) and billfishes (members of the family Istiophoridae and Xiphiidae) (Figure 8.2.1) have been actively investigated over five decades (e.g. Barkley et al., 1978; Blackburn, 1965; Bushnell & Brill, 1991, 1992; Bushnell et al., 1990; Dizon, 1977; Dizon et al., 1974, 1976; Gooding et al., 1981; Sharp, 1975, 1978, 1983; Stevens, 1972; Stevens &

Fry, 1972; Sund et al., 1981). Variations in temperature and ambient oxygen with depth have long been known to influence species-specific vertical movement patterns which, in turn, affect vulnerability to different types of fishing gear (Figure 8.2.2). Understanding changes in the vulnerability of fish to specific gear types under different oceanographic conditions defined by temperature and oxygen content is important for standardizing catch-per-unit effort (CPUE) indices used in stock assessments and management decisions (e.g. Bigelow et al., 2002; Bigelow & Maunder, 2006; Brill,
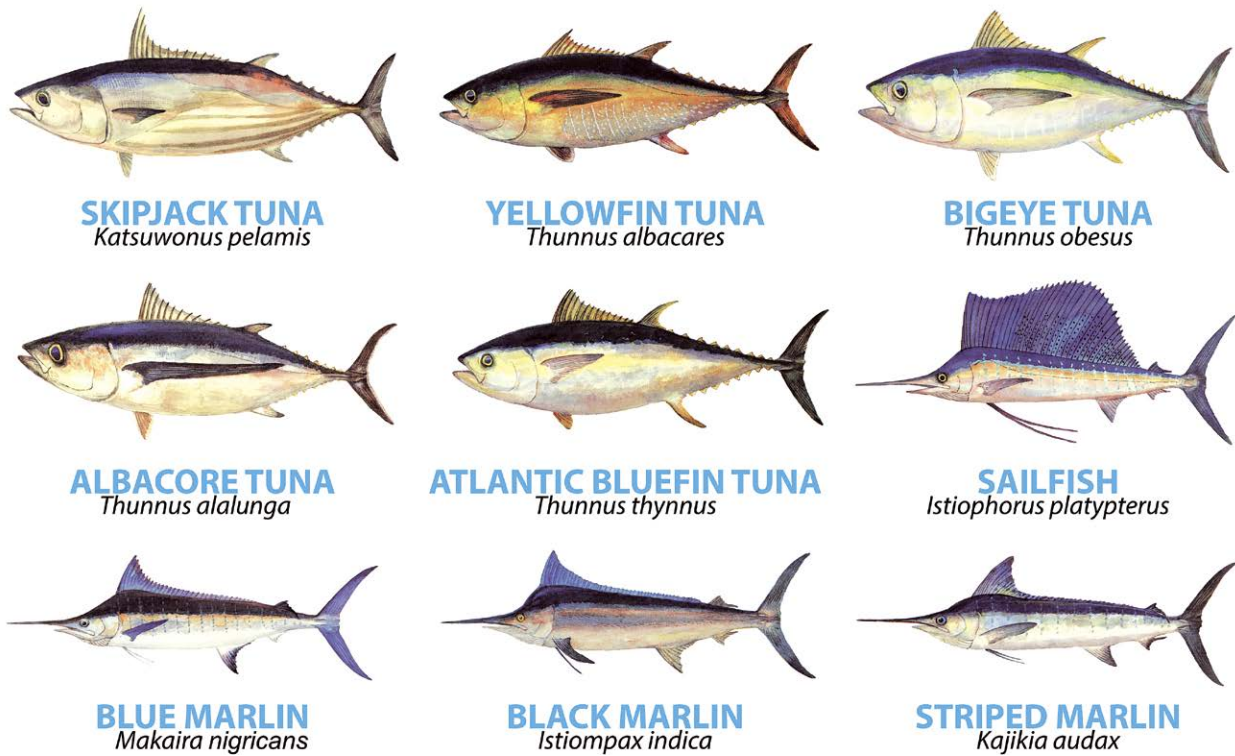
Figure 8.2.1 Tuna and billfish species. (Paintings by George Mattson).

1994; Hinton & Deriso, 1998; Hinton & Nakano, 1996; Sharp, 1995, 2001). Horizontal migrations away from traditional habitats and fishing grounds can also result from changes in environmental conditions (Block et al., 2011; Pinsky et al., 2013), with important downstream effects on the food security and economic development of regions dependent on tuna and billfish fisheries.

On theoretical grounds alone, tunas and billfishes should be especially sensitive to low oxygen concentrations given their unique anatomical and physiological characteristics, which permit high routine and maximum metabolic rates and large absolute metabolic scopes (e.g. Bernal et al., 2009; Brill & Bushnell, 1991, 2001; Brill & Chin Lai, 2016; Bushnell & Jones, 1994; Deutsch et al., 2015; Killen et al., 2016; Korsmeyer & Dewar, 2001; Stoffels, 2015; Wegner et al., 2013). Metabolic rates of billfishes have never been measured but are assumed to be similar to those of tunas because of the high degree of convergent evolution (Bernal et al., 2001, 2009; Wegner et al., 2013). The limiting effects of hypoxia in the marine environment appear, however, to be highly species-specific (e.g. Childress & Seibel, 1998; Deutsch et al., 2015; Seibel, 2011, 2013). An understanding of basic mechanistic principles (i.e. species-specific physiological abilities and tolerances and the resultant behavioural responses to environmental conditions)

is therefore needed to better predict species-specific movement patterns (e.g. Hobday et al., 2013; Horodysky et al., 2015, 2016; McKenzie et al., 2016). The ability to predict the effects of environmental conditions on the movements of large and economically important fish species is becoming even more critical as the effects of directional global climate change become increasingly apparent in the pelagic environment – including but not limited to increasing upper ocean temperature[1], expansion of oxygen minimum zones, and the resultant interaction of these two factors (e.g. Breitburg et al., 2018; Deutsch et al., 2015; Gilly et al., 2013; Mislan et al., 2017; Muhling et al., 2017a; Prince & Goodyear, 2006, 2007; Prince et al., 2010; Stramma et al., 2010a, 2012).

This section aims to summarize the main effects of projected changes in ocean oxygen content on species-specific tuna and billfish habitats and populations, as well as the resulting ecosystem and societal consequences. We begin by defining the tuna and billfish species of interest and comparing limits of hypoxia tolerance and

1   The effects of ocean warming *per se* on the geographic distributions and vertical movement patterns of large pelagic tunas have been extensively investigated and the conclusions reviewed elsewhere (e.g. Gilman et al., 2016; Hobday et al., 2013, 2017; Lehodey et al., 2011) and therefore have not been extensively discussed here.

Table 8.2.1 Relative importance of the principal market species of tunas based on annual landings (FAO. Fishery Statistical Collections. Global Tuna Catches by Stock. 2014; Available at: http://www.fao.org/fishery/statistics/tuna-catches/en. Accessed: 30/12/2014.)

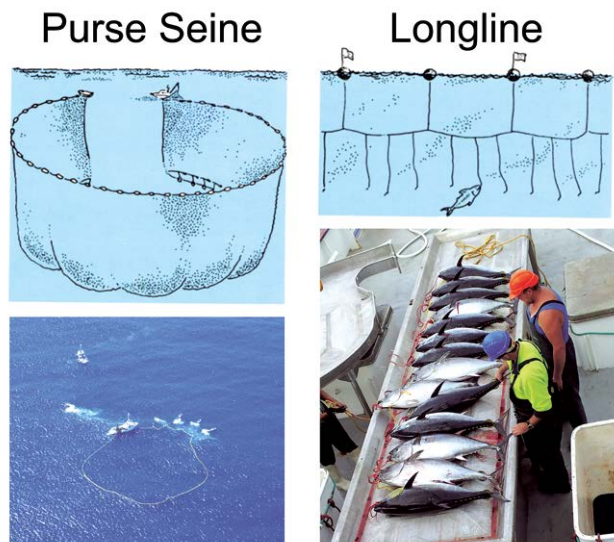| Species	Percentage of Total Tuna Catch
Skipjack tuna	58.1%
Yellowfin tuna	26.8%
Bigeye tuna	8.2%
Albacore	5.9%
Atlantic bluefin tuna	less than 1%
Pacific bluefin tuna	less than 1%
Southern bluefin tuna	less than 1%

Figure 8.2.2 Common types of fishing gear used to commercially capture tuna and billfish. (Conceptual drawings from Joseph et al. (1980). Left photograph © Jessica Farley. Right photograph © Alistair Hobday).

resultant movement behaviours among these species. We then analyse projected changes in oxygen content within current habitat spaces and summarize projected oxygen-induced habitat suitability changes calculated from four different types of models. Lastly, we highlight the potential effects of these oxygen-induced habitat suitability changes on ecosystems and human society.

Throughout this section, we will discuss oxygen content and conditions in terms of either dissolved concentrations (units of ml L^{-1} or mg L^{-1}) or partial pressures (units of kPa), depending on the context. Oxygen content within the ocean has historically been expressed in terms of dissolved concentrations rather than partial pressures because unlike partial pressures, dissolved concentrations do not depend on temperature, salinity, or depth in the water column and are thus useful for mass balance calculations and numerical models. The driving force for molecular oxygen transfer (both from water to blood in the gills and from blood through tissues to the mitochondria) is, however, controlled by the partial pressure of oxygen (Hofmann et al., 2011). To characterize the oxygen environment experienced by

tunas and billfishes more completely, we therefore also report oxygen conditions in terms of partial pressures whenever possible. Because partial pressures depend on both dissolved oxygen concentrations and oxygen solubility (which in turn depends on temperature, salinity, and depth), we will avoid conversion to partial pressures when comparing results with historical thresholds or measurements expressed in dissolved concentration units and lacking simultaneous temperature, salinity, and depth data.

8.2.2 Definition of species group

Various species of billfish and tuna are discussed, but emphasis is placed on the seven principal market species of tunas (Table 8.2.1) both because of their importance and the availability of data. Tunas in aggregate support the world's largest fisheries with an economic value of ~US\$9 billion, landing ~6.5 x 10^6

Figure 8.2.3 (A) Yellowfin tuna *Thunnus albacares* © Juniors Bildarchiw / Alamy stock photo; (B) Skipjack tuna *Katsuwonus pelamis* © Paulo Oliveira / Alamy stock photo.

Figure 8.2.4 Atlantic blue fin tuna (*Thunnus thynnus*) shoal © Paolo Oliveira / Alamy stock photo.

Figure 8.2.5 Swordfish (*Xiphias gladius*) © Paulo Oliveira / Alamy stock photo.

metric tons annually. The seven principal market species collectively account for ~66% of the global tuna landings (FAO, 2014; Guillotreau et al., 2017; Sumaila et al., 2007) (Table 8.2.1). Yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas (Figure 8.2.3) collectively account for ~85% of the landings of the seven principal market species. Albacore (*Thunnus alalunga*), bigeye (*Thunnus obesus*), and bluefin tunas collectively account for >10% of the landings, but the latter two have high economic value because they dominate the fresh fish (i.e. sashimi-grade) market (Guillotreau et al., 2017). Because of the especially high political profile of Atlantic (*Thunnus thynnus*) (Figure 8.2.4), Pacific (*Thunnus orientalis*), and Southern (*Thunnus maccoyii*) bluefin tunas (e.g. Safina, 2001), these three species have received significant scientific attention, especially with regard to the effects of climate change on their movements, distributions and spawning areas (e.g. Hazen et al., 2013; Kitagawa & Kimura, 2015; Muhling et al., 2015, 2017a, b). The aggregate landings of billfishes (~136 x 10³ metric tons in 2015) (FAO, 2017) are approximately three orders of magnitude less than

those of the primary market species of tunas, with swordfish (*Xiphias gladius*) (Figure 8.2.5) constituting most of the billfish catch. Other billfishes are, however, highly prized by recreational anglers because of their acrobatic ability and because some species (e.g. blue and black marlin, *Makaira nigricans* and *Istiompax indica*, respectively) achieve extraordinary body sizes.

Tunas and billfishes are highly mobile, top-level carnivores (though trophic level varies with age class) that live predominately in the energy-depauperate pelagic environment, where rates of primary productivity (per unit area) are approximately one-tenth of those in coastal areas (e.g. Antoine et al., 1996; Westberry et al., 2008) and where forage-species are highly aggregated (such as at fronts) and these aggregations are heterogeneously distributed (e.g. Lehodey et al., 1998; Polovina et al., 2001). Though several tuna species also inhabit coastal waters where productivity is higher overall, it is tunas' unique anatomical, biological, and physiological attributes (e.g. Block & Stevens, 2001; Brill, 1996; Brill & Hobday, 2017) that allow their now well-documented

SECTION 8.2

Table 8.2.2 (From Lehodey et al. (2011)): Lower lethal oxygen levels for four of the seven principal market species of tunas based on the ratio of minimum speed needed to sustain hydrostatic equilibrium (i.e. to keep these negatively buoyant fish from sinking) (Magnuson, 1978; Magnuson & Weininger, 1978). Values are shown for a 50 cm and 75 cm skipjack, yellowfin, bigeye, and albacore tuna. Percentage saturation data for skipjack, yellowfin, and bigeye tunas were calculated using oxygen solubility in sea water at 25 °C and data for albacore using oxygen solubility in sea water at 15 °C.

	Fork length (cm)	Lower lethal oxygen levels		
		mg L⁻¹	ml L⁻¹	% saturation
Skipjack tuna	50	2.45	1.87	37
	75	2.83	2.16	43
Yellowfin tuna	50	1.49	1.14	23
	75	2.32	1.77	35
Bigeye tuna	50	0.52	0.40	8
	75	0.65	0.50	10
Albacore	50	1.67	1.23	21
	75	1.39	1.03	18

extraordinary growth and reproductive rates (Gaertner et al., 2008; Gaikov et al., 1980; Schaefer, 2001; Wild, 1986). These extraordinary growth and reproductive rates in turn permit simultaneous high rates of natural (Murphy & Sakagawa, 1977) and fisheries mortality. Less is known about the physiological abilities of billfishes because, in contrast to tunas (Farwell, 2001), they have never been maintained in shore-side facilities and therefore have never been available for laboratory

studies involving whole animals. There is, however, considerable evidence for rapid somatic and gonadal growth rates and high fecundity in billfishes (e.g. Hopper, 1990; Prince & Pulos, 1983).

Although there are many behavioural similarities among the principal market species of tunas, there are also clear and demonstrable species-specific differences in growth rates (Fromentin & Fonteneau, 2001; Murua et

Table 8.2.3 Summary of oxygen conditions encountered in present-day, species-specific tuna and billfish habitats. For simplicity, we assumed a constant, frequently-visited vertical range throughout each species' horizontal extent to delineate present-day, three-dimensional habitat. Species-specific horizontal ranges were taken directly from the IUCN Red List (IUCN, 2011, 2014), while depth ranges were taken from the IUCN Red List (IUCN, 2011, 2014) with six modifications as follows: (1) IUCN lists 10 m as the lower depth limit for longtail tuna, but the minimum depth interval for our analysis was 25 m depth, which is therefore the frequently-visited lower depth used here; (2) IUCN lists 2743 m as the absolute lower depth limit for Southern bluefin tuna, but we deemed 600 m to be a more reasonable frequently-visited lower depth based on tagging data (Patterson et al., 2008); (3) IUCN lists 50 m as the upper depth limit for Southern bluefin tuna, but there is evidence that they spend large amounts of time much closer to the surface (Patterson et al., 2008); we therefore used 0 m as the frequently-visited upper depth here; (4) IUCN lists 1500 m as the absolute lower depth limit for bigeye tuna but mention that they are mostly found above 500 m, which is therefore the frequently-visited lower depth used here; (5) IUCN lists 1000 m as the absolute lower depth limit for blue marlin but mention that they remain mostly within the upper 40 m, which is therefore the frequently-visited lower depth used here; (6) IUCN lists 2878 m as the absolute lower depth limit for swordfish but mention that its typical range is from the surface to 550 m, which is therefore the frequently-visited lower depth used here. Next, we computed present-day annual mean oxygen partial pressure (PO_2) values over the entire ocean using data from World Ocean Atlas 2013 (WOA, 2013) on a 1° x 1° horizontal grid at 25-m depth intervals. From these gridded PO_2 values analysed over each species' assumed three-dimensional range, we then calculated the spatial means and standard deviations of minimum PO_2 values in the water column encountered by each species and the depths at which these minimum PO_2 values occur. Lastly, we also calculated the spatial mean and standard deviation of the oxycline depth within each species' assumed habitat. For reference, 1 kPa = 7.5 mmHg.

| Common Name	Scientific Name	Frequented Depth Range (m)	Minimum PO_2 (kPa)	Depth of Minimum PO_2 (m)	Depth of Oxycline (m)
Skipjack tuna	*Katsuwonus pelamis*	0 - 260	12±6	236±37	117±94
Albacore tuna	*Thunnus alalunga*	0 - 600	9±5	533±107	128±95
Yellowfin tuna	*Thunnus albacares*	0 - 464	9±5	407±82	121±95
Blackfin tuna	*Thunnus atlanticus*	0 - 200	15±3	185±46	99±39
Southern bluefin tuna	*Thunnus maccoyii*	0 - 600	15±2	575±90	106±97
Bigeye tuna	*Thunnus obesus*	0 - 500	9±5	454±82	122±93
Pacific bluefin tuna	*Thunnus orientalis*	0 - 550	7±4	522±75	178±146
Atlantic bluefin tuna	*Thunnus thynnus*	0 - 500	13±4	460±109	80±31
Longtail tuna	*Thunnus tonggol*	0 - 25	21±1	20±8	77±50
Black marlin	*Istiompax indica*	0 - 100	17±5	98±12	127±102
Sailfish	*Istiophorus platypterus*	0 - 40	21±2	29±15	118±92
White marlin	*Kajikia albida*	0 - 150	16±4	146±18	88±42
Striped marlin	*Kajikia audax*	0 - 289	11±6	255±45	126±101
Blue marlin	*Makaira nigricans*	0 - 40	21±2	28±15	124±94
Shortbill spearfish	*Tetrapturus angustirostris*	0 - 200	12±6	196±13	133±104
Roundscale spearfish	*Tetrapturus georgii*	0 - 200	14±4	195±23	93±44
Longbill spearfish	*Tetrapturus pfluegeri*	0 - 240	13±5	218±30	93±44
Swordfish	*Xiphias gladius*	0 - 550	10±6	494±98	117±93
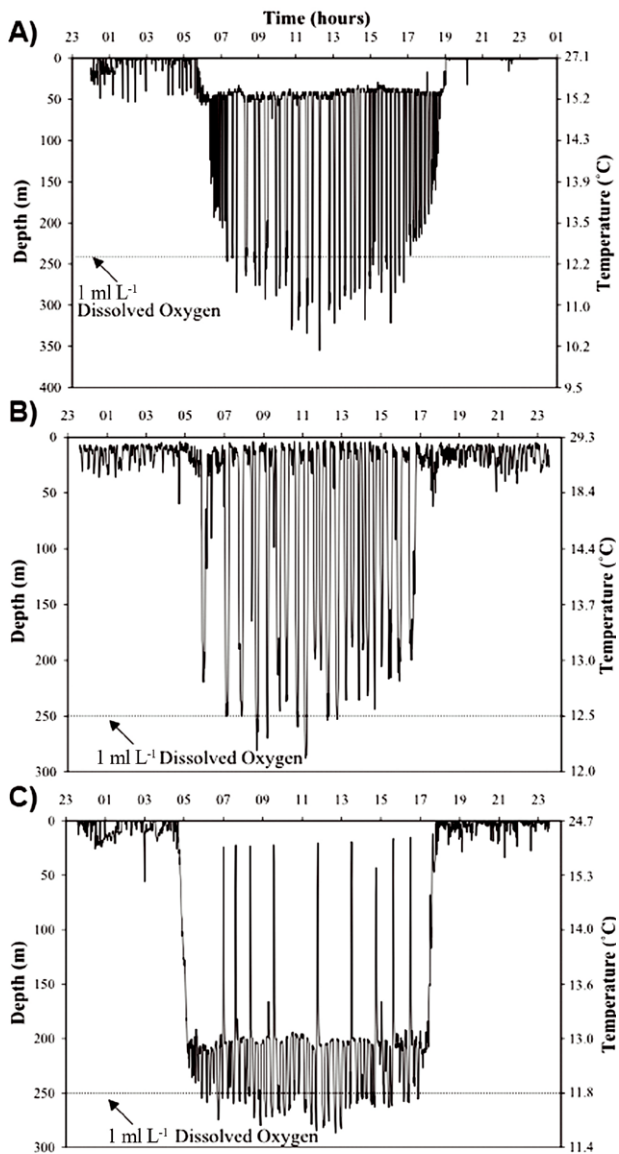
Figure 8.2.6 Representative daily vertical movement patterns of (A) skipjack tuna (66-cm), (B) yellowfin tuna (52-cm), (C) bigeye (88-cm) tunas. Tuna dive to deep depths during the day to forage for prey in the deep sound scattering layer. Skipjack and yellowfin tunas stay for short periods <15 minutes whereas bigeye tuna remain for much longer periods (>2 hours). The 1 ml L^{-1} oxygen line indicates a tuna hypoxic threshold. At 12 °C, 1 ml L^{-1} = 1.3 mg L^{-1}. Adapted from Schaefer et al. (2009a).

(Figure 8.2.8), migratory patterns (which take some species from temperate feeding areas to tropical spawning areas), and apparent resource partitioning (e.g. Bernal et al., 2009, 2017; Block et al., 2001; Boustany et al., 2010; Carey, 1990; Carey & Robison, 1981; Muhling et al., 2017b; Musyl et al., 2003; Schaefer & Fuller, 2002; Schaefer et al., 2009a; Wilson et al., 2005, 2015). These species-specific movements have been reviewed extensively for tunas, billfishes and sharks by Bernal et al. (2009), and more recently and specifically for tunas and billfishes by Horodysky et al. (2016) and Bernal et al. (2017). These reviews show that tuna species can be categorized into groups exhibiting distinct vertical movement behaviours (Figure 8.2.7). For example, the extensive vertical movements of bigeye tuna (and other species in Group 3, Figure 8.2.7) and their ability to remain at depth for extended periods are in stark contrast to the vertical movement patterns of skipjack and yellowfin tunas (Schaefer & Fuller, 2002, 2007, 2010; Schaefer et al., 2007, 2009a, b, 2014). The latter species also make forays to depths of ~500 m, but times spent in these cold and hypoxic waters are brief compared to time spent at depth by bigeye tuna, which include long periods (~45-60 minutes) below the thermocline (~500 m depth) during daylight hours, where water temperatures may be below 6 °C and oxygen levels ~1 mg L^{-1} (~0.7 ml L^{-1}, assuming 5 °C) (Figure 8.2.6) (Evans et al., 2008; Fuller et al., 2015; Hanamoto, 1987; Musyl et al., 2003; Schaefer & Fuller, 2002, 2010). Albacore also exhibit vertical movements to depths below 400 m, but their vertical forays are generally brief (<32 minutes), like those of skipjack and yellowfin tunas (Childers et al., 2011; Williams et al., 2015). Tracking data show that albacore usually experience oxygen levels >5 mg L^{-1} (> ~3.7 ml L^{-1}, assuming 15 °C) (Laurs & Lynn, 1977) and shipboard experiments on swimming showed that aerobic metabolism declined below this oxygen level, all of which imply that albacore are relatively hypoxia-intolerant compared to bigeye tuna (Bushnell et al., 1990; Graham et al., 1989). Similarly, although there are extensive records of the vertical movements of both Atlantic and Pacific bluefin tunas, these data do not allow inferences with respect to the hypoxia tolerance of these species. Both species do, however, make forays to depth where water temperature is ~10 °C and lower (Bauer et al., 2017; Block et al., 2005; Boustany et al., 2010; Kitagawa et al., 2004, 2007a, b; Patterson et al., 2008). Atlantic bluefin tuna reportedly reach depths of ~1000 m and water temperatures of ~5 °C (Block et al., 2001), but the accompanying oxygen levels at the depths and areas routinely occupied by Atlantic bluefin

al., 2017), maximum adult size, physiological abilities, and tolerances of temperature and oxygen reductions that occur with increasing depth (e.g. Bernal et al., 2009, 2017; Blank et al., 2004; Galli et al., 2009, 2011; Lowe et al., 2000; Shiels et al., 1999, 2015; Sibert et al., 2006) (Tables 8.2.2 & 8.2.3). It is primarily differences in adult body size, thermoregulatory ability, and cardio-respiratory function that determine species-specific thermal and hypoxic tolerances, which in turn account for documented differences in daily vertical mobility patterns (Figures 8.2.6 & 8.2.7), spatial distributions
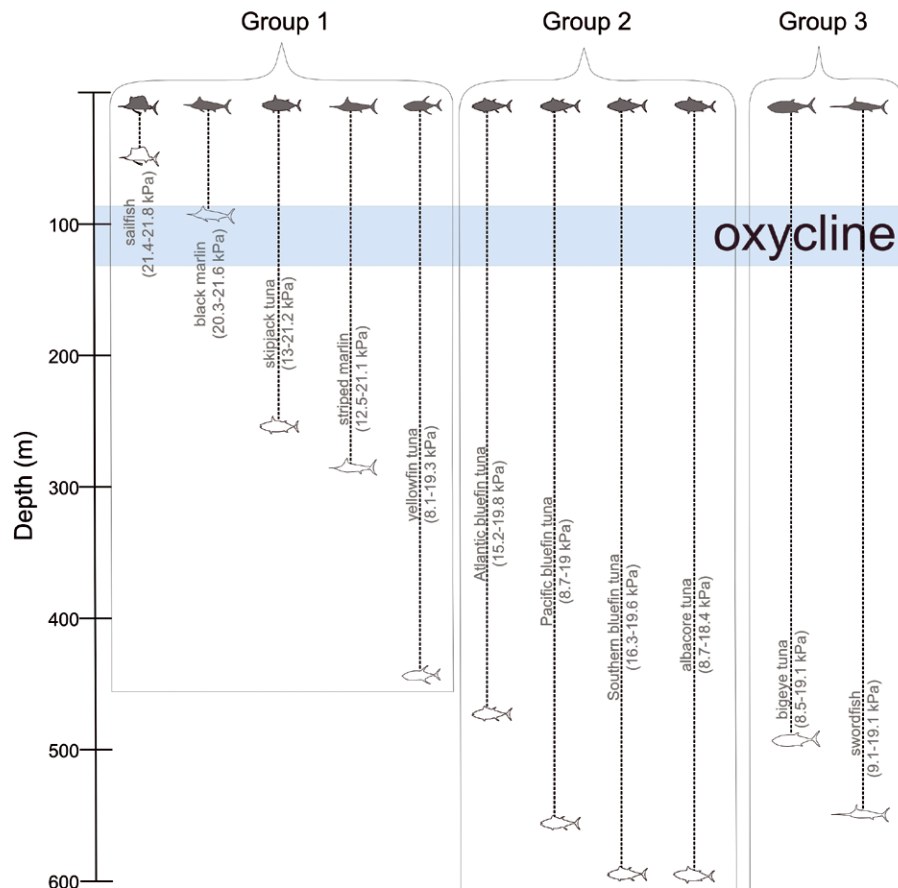
Figure 8.2.7 Schematic diagram of approximate depth ranges frequented by various tuna and billfish species. Depth ranges were taken and sometimes modified (see Table 8.2.3 caption) from the IUCN Red List (IUCN, 2011, 2014). Species are grouped by relative hypoxia tolerance, with Group 1 being least hypoxia-tolerant and Group 3 being most hypoxia-tolerant. The range (25th through 75th percentile) of oxygen partial pressure (PO_2) values encountered by each species within their assumed present-day habitats (delineated by the constant depth ranges listed in Table 8.2.3 and IUCN Red List horizontal distributions) is shown. Note that the amounts of time spent at depth by each species, as well as the environmental conditions within each species' range, differ. Drawing adapted from Figure 1 in Bernal et al. (2009).

tuna are unlikely to be limiting (Gilly et al., 2013; Teo & Boustany, 2016). Southern bluefin tuna can also spend periods of over 10 hours below ~400 m at temperatures <10 °C (Patterson et al., 2008), but oxygen levels in these same areas are relatively high (Mislan et al., 2017).

Tracking studies employing sonic telemetry and electronic data recording tags have shown that billfishes likewise display species-specific vertical movement patterns. Marlins and sailfishes (*Istiophorus platypterus*) (Figure 8.2.9) largely remain in the uniform temperature surface layer, although like skipjack and yellowfin tunas, they do make brief descents below the thermocline (Block et al., 1993; Brill et al., 1993; Holland et al., 1990; Hoolihan et al., 2005; Horodysky et al., 2007; Pepperell & Davis, 1999; Pohlot & Ehrhardt, 2017; Prince & Goodyear, 2006, 2007; Prince et al., 2010). Their vertical movements do, however, appear

to be strongly constrained to water with oxygen concentrations >3.5 ml L^{-1} (Braun et al., 2015). In contrast, swordfish tracked in the Pacific and Atlantic Oceans and Mediterranean Sea have been shown to regularly descend and stay for up to eight hours below 550-600 m, where temperatures are ~5 °C and oxygen levels are below ~1.4 mg L^{-1} (~1 ml L^{-1}, assuming 5 °C) (Figure 8.2.7) (Abascal et al., 2010; Canese et al., 2008; Carey, 1990; Carey & Robison, 1981; Dewar et al., 2011; Evans et al., 2014; Sepulveda et al., 2010; Takahashi et al., 2003). This result is congruent with the vertical movement patterns of bigeye tuna described above. The maximum depths reached by bigeye tuna and swordfish, and the concomitant reductions in temperature and low ambient oxygen, obviously imply similarly extraordinary physiological tolerances of both species; some convergent evolution in cardiac function between the two species has indeed been confirmed (Galli et al., 2009).
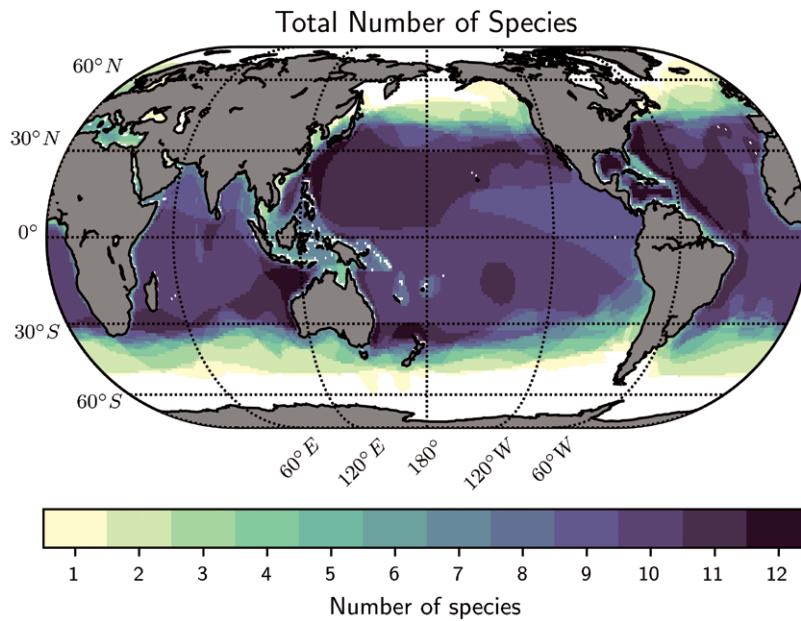
Total Number of Species

Figure 8.2.8 Global distribution of the number of species of tuna and billfish based on horizontal range data from the IUCN Red List (IUCN, 2011, 2014).

8.2.3 Trends and impacts

Climate change is projected to alter oxygen concentrations throughout the ocean, with most regions undergoing projected decreases owing to a slowdown in ocean ventilation and a decline in surface oxygen solubility (e.g. Bopp et al., 2013; Cabré et al., 2015; Cocco et al., 2013; Frölicher et al., 2009; Keeling et al., 2010). Agreement among models over how oxygen concentrations will change is greatest in the North Pacific and much of the Southern Ocean, and lowest in the tropical Pacific (Bopp et al., 2013; Cabré et al., 2015), though observations in the latter region indicate that oxygen concentrations have been decreasing there over the last several decades (Czeschel et al., 2012; Helm et al., 2011; Ito et al., 2017; Schmidtko et al., 2017; Stramma et al., 2008, 2010a, b).

Figure 8.2.9 Sailfish (*Istiophorus platypterus*) feeding on shoal of sardines © Nature Picture Library / Alamy stock photo.

8.2.3.1 Projecting oxygen changes in present-day tuna and billfish habitats

Output from Earth System Models included in the Coupled Model Intercomparison Project 5 (CMIP5) (Taylor et al., 2012) was used to project changes in global oceanic oxygen content set to occur by the end of the 21st century. These models, which simulate physical, chemical and biological processes, are run into the future under various plausible greenhouse gas emissions scenarios. Model output from years 2071–2100 within the RCP8.5 scenario, which represents a "business-as-usual" situation in which climate change goes unmitigated were utilized. To simulate present-day conditions, output from years 1971–2000 within the historical scenario was used, which is forced with historically observed atmospheric CO_2 emissions and concentrations. To calculate projected future changes, multi-model mean simulated differences between the RCP8.5 and historical scenarios were computed. The six models included here were CESM1-BGC (Gent et al., 2011; Lindsay et al., 2014), GFDL-ESM2G, GFDL-ESM2M (Dunne et al., 2012, 2013), HadGEM2-ES (Collins et al., 2011; Jones et al., 2011; Palmer & Totterdell, 2001), IPSL-CM5A-LR (Dufresne et al., 2013), and MPI-ESM-LR (Giorgetta et al., 2013; Ilyina et al., 2013).

Average oxygen concentrations between 200 and 700 m depth, where many tuna and billfish species forage, are projected to decrease throughout the mid- and

Annual Mean Oxygen Concentration between 200 and 700 m

A) Present Day (WOA 2013)

B) Future Change (CMIP5 Multi-Model Mean)

Average O$_2$ [ml L^{-1}]

ΔAverage O$_2$ [ml L^{-1}]

Annual Mean Hypoxic Threshold Depth

C) Present Day (WOA 2013)

D) Future Change (CMIP5 Multi-Model Mean)

Depth of O$_2$ threshold [m]

Shallower ◄ ► *Deeper*

ΔDepth of O$_2$ threshold [m]

Annual Mean Oxycline Depth

E) Present Day (WOA 2013)

F) Future Change (CMIP5 Multi-Model Mean)

Depth of oxycline [m]

Shallower ◄ ► *Deeper*
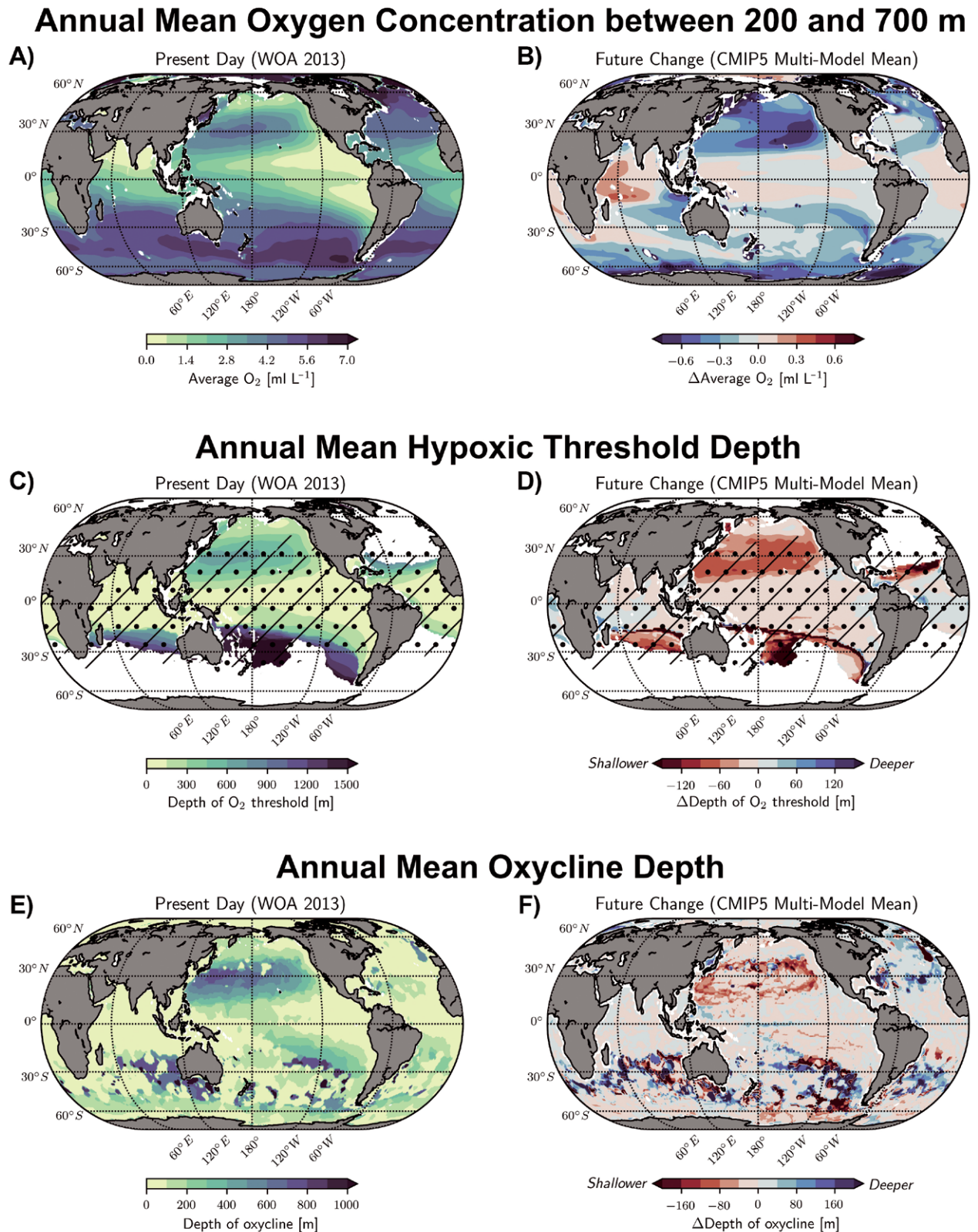
ΔDepth of oxycline [m]

Figure 8.2.10 Historical and projected changes in annual mean (A-B) average oxygen concentrations between 200 and 700 m, (C-D) threshold hypoxic depths (where oxygen concentrations decrease below 3.5 ml L^{-1}), and (E-F) upper oxycline depths (lower row). Historical oxygen data are from WOA 2013. Projected changes (RCP8.5 scenario, 2071–2100 minus 1971–2000) are from six Earth System Models included in the Coupled Model Intercomparison Project Phase 5 (CMIP5), interpolated onto the same grid as WOA 2013 (1˚ x 1˚ horizontal grid with 25-m depth intervals). Hatching and stippling denote skipjack and yellowfin tuna habitat, respectively (IUCN, 2011, 2014). Threshold hypoxic and upper oxycline depths are shallowest in tropical regions and deepest in temperate regions. They are projected to be shallower in the North and South Pacific and the Southern Indian Ocean by 2100.

high-latitudes (Figure 8.2.10A-B). The greatest and most coherent decreases are projected to occur in the eastern North Pacific Ocean (Figure 8.2.10A-B), which already has lower mean oxygen concentrations compared to the western half of the basin (Figure 8.2.10A). Within the eastern North Pacific between 20-40°N, average oxygen concentrations between 200-700 m depth are projected to decrease by as much as 0.6 ml L^{-1} from 1971–2000 to 2071–2100 (Figure 8.2.10B). The depth at which oxygen concentrations drop to 3.5 ml L^{-1} (a threshold hypoxic concentration for several species of tuna and billfish including yellowfin and skipjack tunas, marlins, and sailfish) is also projected to shoal throughout most of the global ocean, reducing available oxygenated vertical habitat space for many species (Figure 8.2.10C-D). By 2071-2100, projected shoaling of the 3.5 ml L^{-1} oxygen level is greatest in the North Pacific and parts of the Southern Ocean, moving upward by 60-100 m from a historical average of about 450-600 m depth in the former and by over 150 m from a historical average of >1,000 m depth in the latter. Projected changes in oxycline depth are spatially similar to those of the 3.5 ml L^{-1} hypoxic depth, with a predicted shoaling of

over 150 m in some places within the North Pacific and Southern Oceans (Figure 8.2.10E-F). Along 160°W in the North Pacific, the largest projected decreases in oxygen concentration (between 0.8-1 ml L^{-1}) are centred around ~450 m depth, with the greatest potential impacts on swordfish and yellowfin, bigeye, Pacific bluefin, and albacore tunas residing in the area (Figure 8.2.11). Oxygen concentrations are projected to decrease greatly throughout most of the present-day range of Pacific bluefin tuna in particular. Comparisons between current and future oxygen conditions experienced by Pacific bluefin tuna within their present-day habitats (based on depth limits listed in Table 8.2.3) further support the notion that this species will likely experience some of the largest decreases in oxygen content, assuming that they maintain their present-day range (Figure 8.2.12).

It is important to note here (specifically, in the discussion of subsection 8.2.3.1 and in generating Table 8.2.3, Figure 8.2.7, Figure 8.2.11 and Figure 8.2.12) that all species-specific, present-day habitats are assumed to be rectangular boxes. In other words, we apply a single static, oft-frequented depth range (listed in Table 8.2.3)

Cross Section of Annual Mean Oxygen Concentration Along 160°W in the Pacific Ocean

1) Sailfish, **2)** Blue marlin , **3)** Black marlin , **4)** Shortbill spearfish, **5)** Skipjack tuna
6) Striped marlin, **7)** Yellowfin tuna, **8)** Bigeye tuna, **9)** Pacific bluefin tuna, **10)** Swordfish,
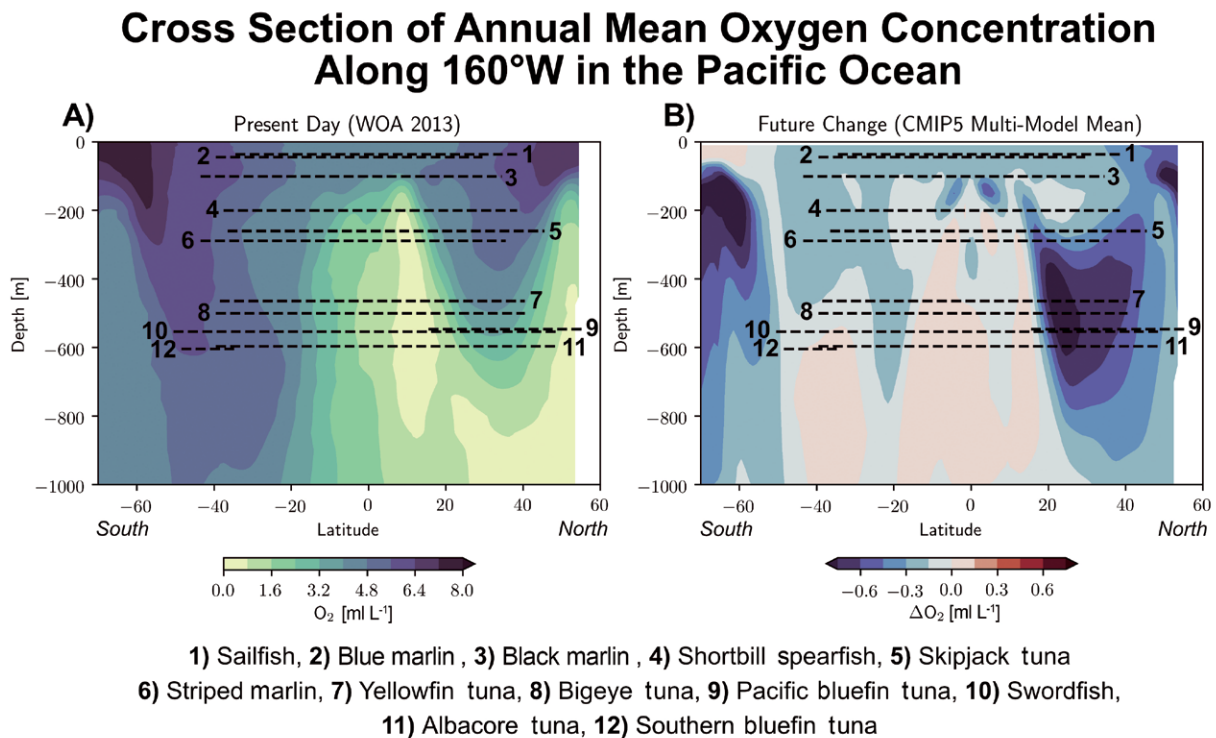**11)** Albacore tuna, **12)** Southern bluefin tuna

Figure 8.2.11 (A) Historical and (B) projected changes in annual mean oxygen concentrations along 160°W in the Pacific. Each species' present-day, frequently-visited lower depth range (as described in the caption of Table 8.2.3) is plotted across its latitudinal extent at this longitude. Historical oxygen data are from WOA 2013. Projected changes (RCP8.5 scenario, 2071–2100 minus 1971–2000) are from six Earth System Models included in CMIP5, interpolated onto the same grid as WOA 2013. Oxygen concentrations are the lowest in the tropics. The greatest decreases in oxygen concentrations by 2100 are projected to occur at temperate latitudes within the depth ranges of various tuna and billfish species.
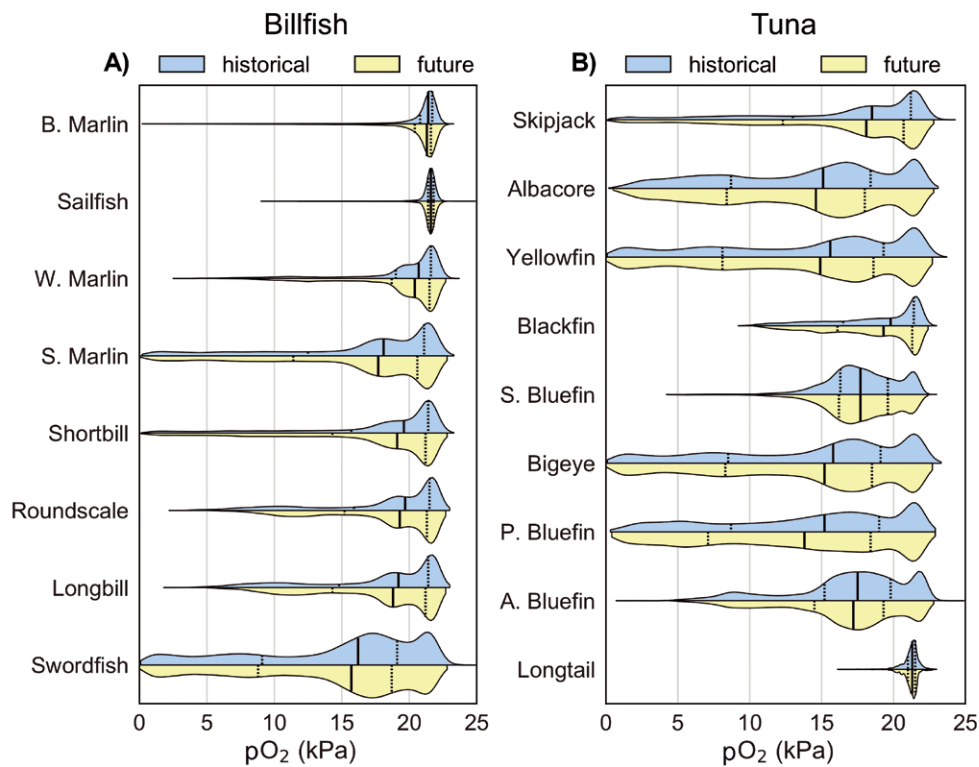
Oxygen Distributions in Present-Day Habitats

Figure 8.2.12 Historical and projected oxygen distributions encountered in present-day, species-specific (A) billfish and (B) tuna habitats. For simplicity, we assumed a constant, frequently-visited vertical range throughout each species' horizontal extent to delineate present-day, three-dimensional habitat. Species-specific horizontal ranges were taken directly from the IUCN Red List (IUCN, 2011, 2014), while depth ranges were taken from the IUCN Red List (IUCN, 2011, 2014) with six modifications, as detailed in the caption of Table 8.2.3. Historical oxygen partial pressure (PO$_2$) data are from WOA 2013. Future PO$_2$ projections were generated by adding CMIP5-modelled changes (RCP8.5 scenario, 2071–2100 minus 1971–2000) to WOA 2013 historical values. The two vertical dashed black lines within each distribution curve indicate the 25th and 75th percentiles of PO$_2$ encountered (as listed for each species in Figure 8.2.7), while the vertical solid black line indicates the 50th percentile. Oxygen partial pressures encountered vary greatly among the different species. Oxygen pressures are projected to decrease in the habitats of most tuna and billfish species by 2100.

over each species' horizontal habitat to represent its three-dimensional distribution (using data from IUCN, 2011, 2014 with minor modifications). In reality, each species-specific depth range (as well as the amount of time spent at each depth) varies greatly over space and time (e.g. Barkley et al., 1978; Block et al., 2001; Schaefer & Fuller, 2002, 2007, 2010; Schaefer et al., 2009a, b, 2014; Wilson et al., 2005, 2015). This is because temperature and oxygen levels also exhibit large spatio-temporal variabilities, and vertical movements are constrained by temperature and oxygen levels themselves rather than depth *per se* (Bernal et al., 2017; Prince et al., 2010). There are, however, currently not enough data to properly resolve the spatial and temporal variations of each species' vertical movements over its entire horizontal range. For simplicity, we therefore choose a spatio-temporally constant, oft-frequented depth range throughout each species' horizontal distribution to define its present-day three-dimensional habitat. Without more and better standardized data,

it is also difficult to distinguish between the absolute maximum depth to which each species can descend, the deepest average descent, and the depth above which they spend the majority of their time. Within these constraints, we attempt to define a reasonable depth range that each species frequently occupies, based on IUCN data and results from tagging studies (Table 8.2.3). We acknowledge, however, that there may be minor inconsistencies among species in how the depth range most frequently occupied is defined.

8.2.3.2 Projecting oxygen-induced habitat suitability changes with statistical models

One of the most straightforward and common approaches for projecting future habitat changes is to use statistical methods to relate present-day species distributions to observed environmental conditions, and to then apply these relationships to projections of future environmental conditions (Coro et al., 2016; Hartog et

Figure 8.2.13 Bigeye tuna (*Thunnus obesus*) © WaterFrame / Alamy stock photo.

al., 2011; Hazen et al., 2013; Muhling et al., 2015; Peck et al., 2016; Stock et al., 2011). The main advantages of these models are that they allow for multivariate, non-linear relationships among variables; require relatively few input variables; and are conceptually simple as they require no explicit parametrizations of physiology, behaviour, or ecosystem dynamics (Dormann et al., 2012; Peck et al., 2016). Because key mechanistic processes are not included in the models, however, present-day empirical relationships are assumed to hold into the future, which may not be a valid assumption in all cases (Dormann et al., 2012; Horodysky et al., 2015, 2016; Peck et al., 2016). Most statistical models also rely more on temperature than oxygen, due to the greater availability of temperature data (both environmental and from electronic tracks), and the abundance of studies showing the importance of thermal limits in determining the distributions of tuna and billfish species. Muhling et al. (2017a) were, however, able to use temperature and chlorophyll measurements at the surface, temperature and oxygen concentrations at 100 m depth, and concurrent data on the presence or absence of adult Atlantic bluefin tuna to create a statistical model capable of predicting this species' distributions in the North Atlantic Ocean. They found that oxygen concentration at 100 m depth was the most important predictor of habitat suitability out of the four variables considered. Application of the model to future projections from GFDL-ESM2M (one of the CMIP5 Earth System Models, using the RCP8.5 scenario and comparing 1971–2000 to 2071–2100) showed a general loss of habitat with climate change, especially south of ~40°N as well as in the region south of Greenland, which was in agreement with projections from an oxygen balance model (as discussed in subsection 8.2.3.4) applied to the same GFDL-ESM2M projections.

8.2.3.3 projecting oxygen-induced habitat suitability changes with a P_{50} depth-based trait analysis model

Blood oxygen affinity (quantified by the partial pressure of oxygen required to bring blood oxygen content to 50% of the maximum oxygen carrying capacity, and commonly referred to as the 'P_{50}') can predict hypoxia tolerance in a range of fish species (Farrell & Richards, 2009; Mandic et al., 2009; Wells, 2009). Hypoxia-tolerant species (including bigeye tuna) have blood with high oxygen affinity (i.e. low P_{50}) (Lowe et al., 2000). While this high blood oxygen affinity allows species like bigeye (Figure 8.2.13) to be more tolerant of low ambient oxygen conditions, it may also lead to slower rates of oxygen delivery if blood oxygen affinity remains too high at the tissues (Yang et al., 1992). Blood oxygen affinity at tissues also depends, however, on whether arterial blood undergoes temperature changes as it passes through gills (i.e. 'open system' temperature changes where the blood is free to exchange oxygen and CO_2 with the respiratory medium) or as it passes through the vascular countercurrent heat exchangers possessed by tunas (i.e. 'closed system' temperature changes where blood is not free to exchange oxygen and CO_2 with the respiratory medium) (Brill & Bushnell, 1991, 2006; Carey & Gibson, 1977, 1983; Clark et al., 2008; Jones et al., 1986; Lowe et al., 2000; Rossi-Fanellai & Antoninie, 1960; Stevens, 1982; Stevens & Carey, 1981). These countercurrent heat exchangers allow tunas to maintain muscle temperatures significantly above ambient water temperatures and can therefore help lower blood oxygen affinity at muscles, where oxygen off-loading and delivery is required. Bigeye tuna are particularly adept at maintaining elevated muscle temperatures during deep descents (into water as cold as ~5 °C) by controlling the efficacy of their vascular countercurrent heat exchangers before making rapid ascents back to the warm uniform temperature surface layer to get a 'gulp' of heat in a way analogous to a marine mammal returning to the surface to get a breath (Boye et al., 2009; Holland & Sibert, 1994). At depth where muscle temperatures are significantly above ambient temperature, arterial blood in bigeye tuna is thus subjected to 'closed system' temperature changes. The net result is large decreases in blood oxygen affinity from high (low P_{50}) to low (high P_{50}) values that are more characteristic of less hypoxia-tolerant species such as skipjack, yellowfin, and bluefin tunas (Brill & Bushnell, 1991, 2006; Clark et al., 2008). These large decreases in blood oxygen affinity (increases in P_{50}) as the blood
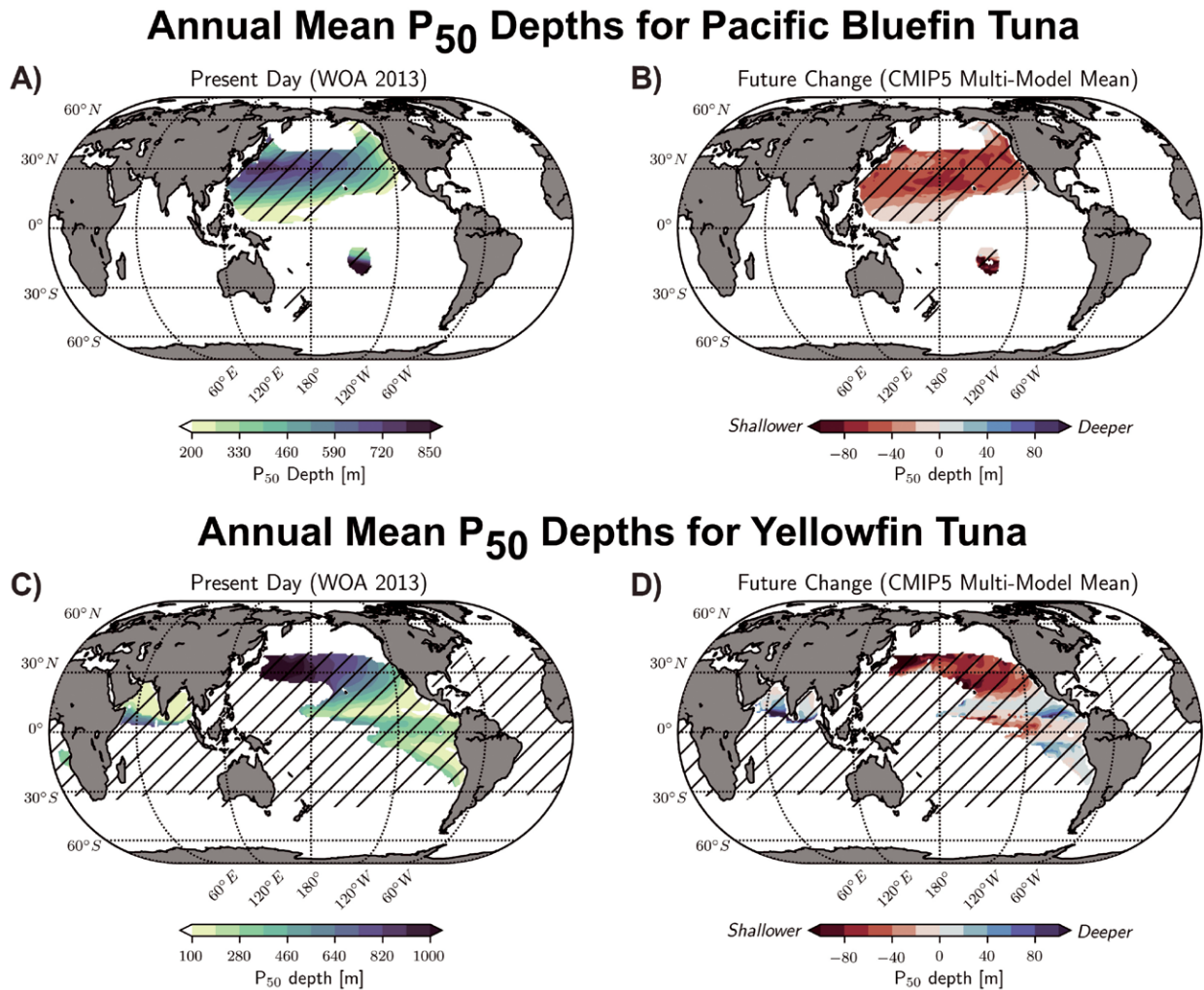
SECTION 8.2

Annual Mean P$_{50}$ Depths for Pacific Bluefin Tuna

A) Present Day (WOA 2013)

B) Future Change (CMIP5 Multi-Model Mean)

P$_{50}$ Depth [m]
200 330 460 590 720 850

Shallower ◄───► *Deeper*
−80 −40 0 40 80
P$_{50}$ depth [m]

Annual Mean P$_{50}$ Depths for Yellowfin Tuna

C) Present Day (WOA 2013)

D) Future Change (CMIP5 Multi-Model Mean)

P$_{50}$ depth [m]
100 280 460 640 820 1000

Shallower ◄───► *Deeper*
−80 −40 0 40 80
P$_{50}$ depth [m]

Figure 8.2.14 Historical and projected changes in P$_{50}$ depths within the present-day habitats of Pacific bluefin tuna (A-B) and yellowfin tuna (C-D). P$_{50}$ depth is the shallowest depth at which blood is <50% oxygenated. Historical data are from WOA 2013. Projected changes (RCP8.5 scenario, 2071–2100 minus 1971–2000) are from six Earth System Models included in CMIP5, interpolated onto the same grid as WOA 2013. White regions of the ocean do not contain P$_{50}$ depths for the given species. Hatching denotes the given species' habitat, based on IUCN geographic ranges (IUCN, 2011, 2014). P$_{50}$ depths in Pacific bluefin tuna habitats are projected to be universally shallower in 100 years. Changes in P$_{50}$ depths within yellowfin tuna habitats are projected to vary spatially.

travels from gills to warm tissues ensures adequate rates of oxygen delivery in the swimming muscles of bigeye tuna. Studies quantifying the oxygen affinity of isolated haemoglobin (Sharp, 1975, 1983) and whole blood (Cech et al., 1984) from albacore all suggest that this species is relatively hypoxia-intolerant (although more hypoxia-tolerant than yellowfin or skipjack tunas).

P$_{50}$ depth is the shallowest depth in the water column where the partial pressure of oxygen (PO$_2$) drops below the minimum value required for blood to reach its P$_{50}$ value. It thus denotes the depth below which oxygen becomes limiting and serves as a mechanistic way of estimating species-specific vertical habitat range in regions where hypoxic conditions exist at depths reachable by tunas (Mislan et al., 2016). The spatial

distribution and extent of P$_{50}$ depths vary greatly among tuna species. For example, the vertical movements of more hypoxia-tolerant species (e.g. bigeye tuna) are constrained by P$_{50}$ depth over smaller geographic areas than less hypoxia-tolerant species (e.g. yellowfin or Pacific bluefin tunas) (Mislan et al., 2017) (Figure 8.2.14). The shallowest P$_{50}$ depths are in the tropics, occurring above 100 m in some areas for the least hypoxia-tolerant tuna species, including yellowfin tuna (Figure 8.2.14) (Mislan et al., 2017).

By the end of the 21st century, P$_{50}$ depths of multiple tuna species are projected (under the RCP8.5 scenario, using the six CMIP5 models listed in subsection 8.2.3.1) to shoal in temperate regions, and to either shoal or deepen within the tropics depending on the specific

location. Multi-species P_{50} depths are projected to become shallower in the subtropical and mid-latitude North Pacific Ocean in particular (Figure 8.2.14), where the greatest decreases in oxygen content are projected to occur (Bopp et al., 2013; Mislan et al., 2017). For Pacific bluefin tuna, whose geographic range is almost entirely in the North Pacific, P_{50} depths are projected to be shallower throughout its range (Figure 8.2.14). Yellowfin tuna, on the other hand, have a broader geographic range than Pacific bluefin tuna, with populations in the temperate and tropical Pacific as well as the Arabian Sea and the Bay of Bengal. The P_{50} depths of yellowfin tuna are very shallow in the tropics but are projected to become deeper by 2100 in the areas where they are currently shallowest (i.e. between 5°N-20°N and 5°S-20°S in the eastern Pacific) (Figure 8.2.14). In other regions within the eastern Pacific (poleward of 20°N and within 5° of the equator), P_{50} depths of yellowfin tuna are projected to be shallower by 2100. These bidirectional changes could potentially alter the vertical range of yellowfin tuna over large geographic areas. Projections of oxygen levels in the eastern Pacific within 20° of the equator are not considered to be robust (Bopp et al., 2013; Cabre et al., 2015), however, and may change as models are improved. Changes in spawning regions are another factor that needs to be considered. P_{50} depths of southern bluefin tuna are projected to be 80 to 600 m shallower by 2100 in their main spawning region off the west coast of Australia (Mislan et al., 2017). P_{50} depths are likely key in determining billfish habitat use as well, but physiological parameters needed to calculate species-specific P_{50} depths for billfish are not available. Based on their similar vertical ranges and hypoxic tolerances (Figure 8.2.7), however, we hypothesize that future changes in P_{50} depths of marlin will be closer to those of yellowfin tuna and those of swordfish will be closer to those of bigeye tuna. In summary, P_{50} depth analysis is important for understanding how climate change-driven alterations in oxygen levels within the pelagic environment will impact individual species with different hypoxic tolerances.

8.2.3.4 Projecting oxygen-induced habitat suitability changes with metabolic oxygen balance models

The oxygen balance model used to evaluate future changes in Atlantic bluefin tuna habitat by Muhling *et al.* (2017a) includes three sub-components: an oxygen demand model, an oxygen supply model, and a cardiac transport model. Overall 'oxygen balance' is calculated by subtracting metabolic oxygen demand from estimates of oxygen supply, both of which are influenced by water temperature, the amount of dissolved oxygen in the water, and fish swimming speed. All three sub-models were parameterized using published studies on captive tunas (yellowfin, skipjack and bluefin tunas). Muhling et al. (2017a) show a case study for Atlantic bluefin tuna, but the oxygen balance model has also been modified for yellowfin tuna. Projections for both species groups (i.e. combined bluefin tunas, yellowfin tuna) are thus shown here. As experimental data are from juvenile fish (due to difficulties keeping adults in captivity), the oxygen balance models may be overly conservative at cooler temperatures (Graham & Dickson, 2001).

Metabolic oxygen demand (MO_2) with water temperature and swimming speed is estimated from Generalized Additive Models (GAMs) trained on experimental data (Blank et al., 2007; Brill, 1987; Clark et al., 2010; Dewar & Graham, 1994). Yellowfin tuna MO_2 is assumed to be constant when temperature is <15 °C, as no measurements are available from lower temperatures. Bluefin tuna MO_2 increases when temperatures fall below ~15 °C, but there is no evidence that tuna species predominately caught in tropical and subtropical areas (e.g. skipjack and yellowfin tunas) respond similarly. The oxygen supply model is adapted from equations reported by Bushnell and Brill (1991). The volume of water passing through the gills (ventilation volume) depends on swimming speed and mouth gape, with the latter increasing under hypoxic conditions. Oxygen delivery is then dependent on ambient dissolved oxygen concentration, ventilation volume, and percentage utilization (i.e. the percentage of the oxygen content in the inhaled water stream removed by the cardio-respiratory system). Delivery of oxygen to tissues is dependent on cardiac output, and the difference in oxygen content of arterial and venous blood (Brill & Bushnell, 2001). These equations are parameterized by combining results from Blank et al. (2002, 2004), Korsmeyer et al. (1997 a, b) and Clark et al. (2008, 2013) into a multivariate exponential relationship, where both temperature and swimming speed determine heart rate, and thus cardiac output (assuming the volume of blood pumped per heartbeat remains constant, which is true in tunas; Brill & Bushnell, 2001). Oxygen balance (i.e. surplus or deficit) is determined by subtracting metabolic demand from the lesser of oxygen delivery through the gills, and oxygen delivery via the circulatory system.

SECTION 8.2

Annual Mean Bluefin Tuna Oxygen Balance (0-50 m)

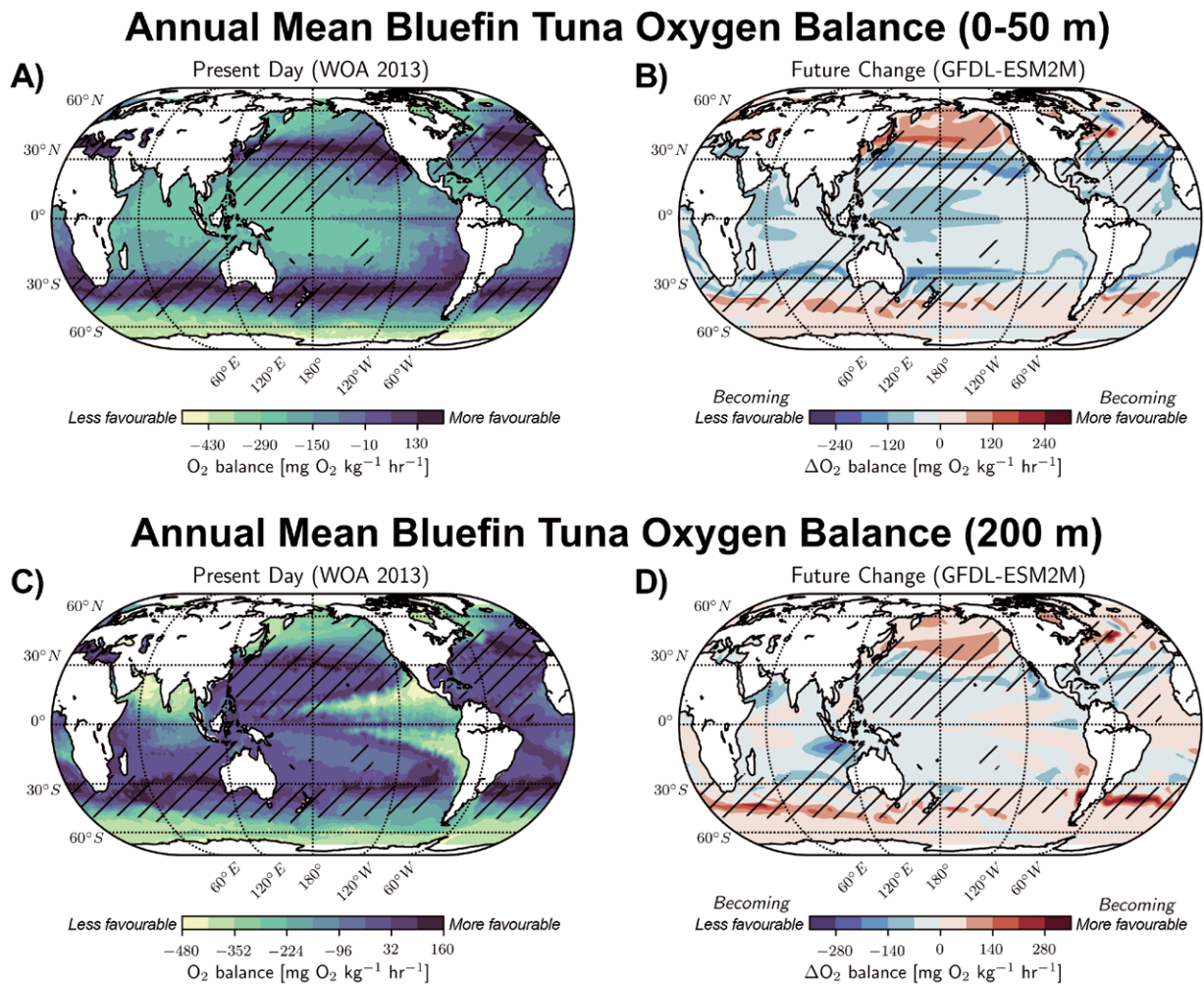## Annual Mean Bluefin Tuna Oxygen Balance (200 m)

Figure 8.2.15 Annual mean bluefin tuna (all three species combined) oxygen balance. Hatching represents current bluefin (all three species) tuna habitat (IUCN, 2011, 2014). (A) 0-50 m depth oxygen balance in recent historical past (from World Ocean Atlas, temperature climatology 1995–2012, oxygen climatology 1900–2012). (B) Future change in 0-50 m depth oxygen balance from GFDL-ESM2M (RCP8.5 scenario, 2071–2100 minus 1971–2000). (C) Same as (A), but at 200 m depth. (D) Same as (B), but at 200 m depth.

Application of the oxygen balance model (Muhling et al., 2017a) to annual temperature and dissolved oxygen climatologies from the World Ocean Atlas (Garcia et al., 2014; Locarnini et al., 2013) shows that regions of highest oxygen balance in the upper 50 m of the water column correspond closely to regions of highest catch for both yellowfin and bluefin tunas (FAO, 2017). In particular, favourable conditions are present on Atlantic bluefin tuna fishing grounds in the north-east Atlantic Ocean and Mediterranean Sea (Teo & Boustany, 2016), on southern bluefin tuna fishing grounds along 40°S between South Africa and New Zealand (Hobday et al., 2016), and along migratory pathways used by Pacific bluefin tuna to cross between Japan and the California Current region (Fujioka et al., 2016) (Figure 8.2.15A, C). Metabolic stress in the upper ocean is thought to be higher on Atlantic and Pacific bluefin tunas' spawning

grounds in the Gulf of Mexico, south of Indonesia, and between Taiwan and Japan, due to warm upper ocean conditions in these areas. Conditions at 200 m are, however, more favourable and it has been proposed that adult Atlantic bluefin tuna may thermoregulate by descending to cooler depths in these areas (Teo et al., 2007).

Projections from GFDL-ESM2M (one of the CMIP5 Earth System Models, using the RCP8.5 scenario and comparing 1971–2000 to 2071–2100) show poleward shifts in annual mean favourable metabolic habitat for all three species of bluefin tunas in the upper 50 m of the water column as a result of warming and deoxygenation (Figure 8.2.15B). There is also a projected reduction in suitability at 200 m depth on southern bluefin tuna spawning grounds south of Indonesia and in Pacific

bluefin tuna habitat in the southern California Current, primarily due to stronger deoxygenation at depth in these areas (Figure 8.2.15D). Conversely, some parts of the Southern Ocean may become more favourable, both in the upper 50 m of the water column and at 200 m depth. The P_{50} depth-based trait analysis model discussed in subsection 8.2.3.3 projected a shoaling of Pacific bluefin tuna P_{50} depth throughout the North Pacific, while the oxygen balance model discussed here suggests that habitat suitability in the upper water column may decline as a result of warming and deoxygenation. In some parts of the North Pacific, it is therefore possible that certain species, such as Pacific bluefin tuna, may experience habitat loss at both the upper and lower bounds of their vertical habitat within their current range.

In contrast to the three species of bluefin tunas, present-day favourable metabolic habitat for yellowfin tuna covers most of the tropics and subtropics between 40°N and 40°S, with some lower suitability near the equator (Figure 8.2.16A). This corresponds well with the observed distribution of yellowfin tuna, which are caught on various fishing gears between these latitudes in all oceans, except for some parts of the eastern Pacific Ocean (FAO, 2017). Conditions at 200 m depth also appear to be favourable for yellowfin tuna throughout much of the subtropics, with the exception of the oxygen minimum zones in the eastern equatorial Atlantic and Pacific Oceans as well as the northern Indian Ocean (Figure 8.2.16C). Projections of future conditions suggest a loss of yellowfin tuna habitat in near-surface waters within the tropics, due to warming and deoxygenation, though this may be partially offset by poleward habitat expansion (Figure 8.2.16B). Habitat suitability at 200 m depth of some subtropical regions may improve, with warming temperatures and weaker deoxygenation. The area south of Indonesia may, however, become less habitable in association with stronger deoxygenation (Figure 8.3.16D).

8.2.3.5 Projecting oxygen-induced habitat suitability changes with process-based models (SEAPODYM and APECOSM-E)

Based on advection-diffusion-reaction equations, the spatial ecosystem and population dynamics model (SEAPODYM) was developed to investigate spatial tuna population dynamics under the influence of both environmental conditions and fishing (Lehodey et al., 2003). It has undergone various refinements since its

initial development and includes all of the following features: (1) forcing by temperature, currents, primary production, and oxygen concentration; (2) predictions of spatio-temporal distributions of mid-trophic level micronekton; (3) predictions of spatio-temporal distributions of tuna populations by age; (4) predictions of total catch size by fleet; and (5) parameter estimation (Lehodey et al., 2010, 2013, 2015). Tunas' spatial and population dynamics are determined using modelled habitat indices, growth rates, and mortality rates. Feeding habitat is determined by the accessibility of prey, while spawning habitat is determined by temperature preferences, availability of food suitable for larvae, and predator pressure. Larval recruitment is assumed to be a function of spawning stock biomass, the extent of spawning habitat, larval food availability, and larval mortality during advection by currents.

Using SEAPODYM and future biogeochemical changes from IPSL-CM4 (an older CMIP3, rather than CMIP5, Earth System Model) under scenario A2 (similar to scenario RCP8.5, but reaching ~850 ppm CO_2 rather than ~950 ppm by 2100), Lehodey et al. (2013) projected that skipjack tuna habitat will expand within the central and eastern Pacific as well as towards higher latitudes, but will shrink within the increasingly warm and decreasingly productive west-central tropical Pacific by the end of the 21st century. A simulation replacing projected oxygen concentrations with present-day climatologies did not change these results, indicating that the projected changes in skipjack tuna habitat are principally driven by changes in temperature, primary productivity, and currents (Lehodey et al., 2013). Similar projections of future albacore habitat, on the other hand, indicate that oxygen concentration decreases in the South Pacific projected by IPSL-CM4 in the next half-century will lead to weaker recruitment here, with a strong negative impact on the abundance of young South Pacific albacore (Lehodey et al., 2015). Projected changes in bigeye tuna habitats and populations are also likely to be heavily influenced by spatially variable changes in oxygen concentrations by 2100 (Lehodey et al., 2010). For example, the feeding habitat of adult bigeye tuna is projected to improve in the eastern tropical Pacific because subsurface increases in dissolved oxygen concentrations will allow for access to deeper prey. At the same time, natural mortality rates of older bigeye tuna are projected to increase within the western-central Pacific due to decreasing oxygen concentrations (along with overly warm temperatures and decreases in food supply) (Lehodey et al., 2010).

SECTION 8.2

Annual Mean Yellowfin Tuna Oxygen Balance (0-50 m)

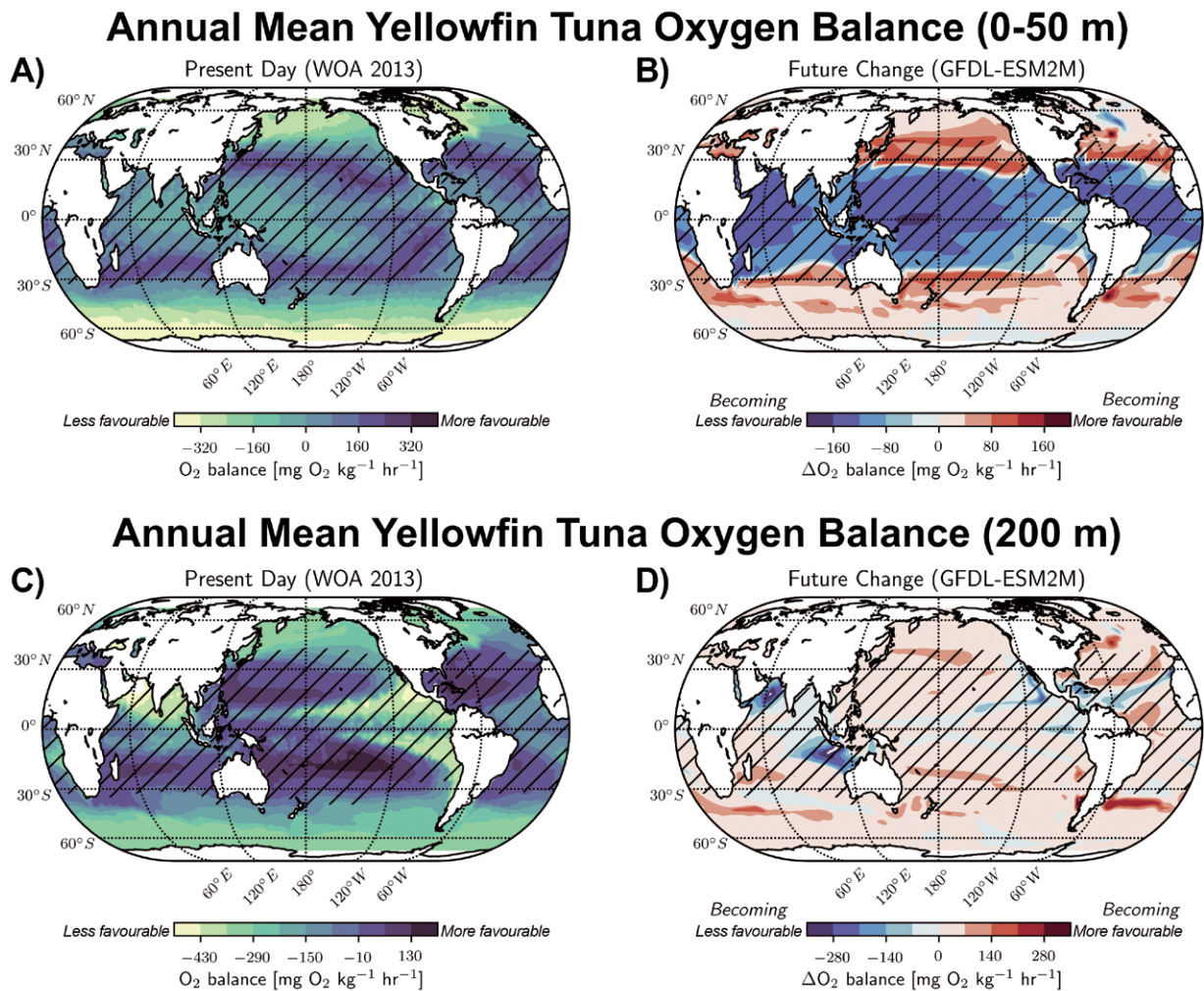## Annual Mean Yellowfin Tuna Oxygen Balance (200 m)

Figure 8.2.16 Annual mean yellowfin tuna oxygen balance. Hatching represents current yellowfin tuna habitat (IUCN, 2011, 2014). (A) 0-50 m depth oxygen balance in recent historical past (from World Ocean Atlas, temperature climatology 1995–2012, oxygen climatology 1900–2012). (B) Future change in 0-50 m depth oxygen balance from GFDL-ESM2M (RCP8.5 scenario, 2071–2100 minus 1971–2000). (C) Same as (A), but at 200 m depth. (D) Same as (C), but at 200 m depth.

This increase in mortality, coupled with the migration of surviving fish to more favourable habitat in the east, may lead to declining adult biomass in the western Pacific by the end of the 21st century.

Like SEAPODYM, the Apex Predator ECOSystem Model - Estimation (APECOSM-E) simulates both spatial and temporal dynamics of skipjack tuna biomass and abundance. Unlike SEAPODYM, however, APECOSM-E mechanistically (rather than empirically) links environmental factors, metabolic rates, and behavioural responses via dynamic energy budget theory. This technique involves tracking the energy budget of an individual organism throughout its life stages (Dueri et al., 2014). Despite their different methods of representing biological processes and the slightly different Earth System Models driving their ocean

biogeochemistry (APECOSM-E uses CMIP5 model IPSL-CM5A-MR and scenario RCP8.5), both models exhibit similar changes in skipjack tuna distribution within the Pacific Ocean by 2100, projecting shifts away from the western Pacific and expansions into the eastern Pacific and towards higher latitudes. In both models, changes in temperature and access to food were the dominant factors driving these distribution shifts, while changes in oxygen content played a relatively minor or insignificant role.

8.2.4 Ecosystem consequences

A thorough understanding of the ecological relationships that exist within the modern-day ocean is needed to better predict how species-specific responses to three-dimensional changes in temperature and oxygen will

affect ecosystem structure and dynamics. Currently available data suggest that species-specific vertical movements result in niche partitioning in areas where different species are sympatric (e.g. Bernal et al., 2009, 2017). For example, the vertical movement patterns of swordfish and bigeye tuna appear to directly follow the diurnal vertical movements of the squid, euphausiids, and mesopelagic fish that are associated with the deep sound scattering layer (SSL) (Bertrand et al., 1999, 2002a, b; Carey, 1990; Carey & Robison, 1981; Dagorn et al., 2000a, b, c; Grudinin, 1989; Josse et al., 1998; Longhurst, 1976; Marchal et al., 1993; Marchal & Lebourges, 1996; Nakamura, 1993; Roger & Grandperrin, 1976; Yatsu et al., 1999). This is in contrast to the shallower habitat use of yellowfin and skipjack tunas, although both of these species do appear to make descents, albeit brief, to depths occupied by SSL organisms during the daytime (Schaefer & Fuller, 2007; Schaefer et al., 2007, 2009a, b). This apparent resource partitioning is supported by stomach content analyses, which show that bigeye tuna generally select mesopelagic prey from the SSL, while yellowfin tuna feed primarily on epipelagic prey from the mixed layer when the two tuna species are caught in the same areas (Holland & Grubbs, 2007; King & Ikehara, 1956; Kornilova, 1981; Pelczarski, 1988; Portier et al., 2004, 2007). The fishes and crustaceans of the SSL migrate downward during the day into cold, dark, low-oxygen waters as a refuge against predation, and can do so due to a suite of morphological, physiological, and biochemical adaptations (e.g. Belman & Childress, 1975; Childress, 1971; Childress & Nygaard, 1974; Sanders & Childress, 1990). Bigeye tuna and swordfish have, however, also obviously evolved physiological abilities to sustain extended forays into the SSL organisms' predator refuge.

Tunas and billfishes are likely to display species-specific three-dimensional habitat changes due to future climate change, just as they currently display species-specific movement patterns and ecological niches. Differential changes in hypoxia-induced vertical habitat extents, in particular, can either decouple or enhance competition among different species. For example, in the North Pacific Ocean, projected decreases in vertical separation among several pairs of tuna species due to species-specific changes in P_{50} depths suggest future increases in the frequency of competitive interactions between tuna here (Mislan et al., 2017). Species-specific responses to climate-driven changes in oxygen and other environmental conditions may also impact

bycatches (i.e. unintended catches) of tunas, billfishes, and other species (Hobday et al., 2015; Komoroske & Lewison, 2015). To our knowledge, there are currently no studies exploring the effects of climate-driven oxygen changes on bycatches of tuna and billfish in fisheries targeting other species, nor on bycatches of other non-targeted species in tuna and billfish fisheries. Hartog et al. (2011), however, suggest that a temperature-driven increase in overlapping habitats of yellowfin and southern bluefin tunas in the yellowfin-targeting, eastern Australian longline fishery may lead to increased bycatches of southern bluefin tuna if current management policies do not adapt.

Future oxygen-driven changes in vertical movements and spatial distributions of prey species exploited by tunas and billfish will also play an important role in determining the overall ecosystem effects induced by oxygen changes. As is the case for tunas and billfishes, changing oxygen concentrations may impact prey in species-specific ways, potentially altering established ecosystem structures and food web dynamics (e.g. Gallo & Levin, 2016; Koslow et al., 2011). Koslow et al. (2011) showed that the abundance of mesopelagic prey species decreased by 63% during periods of reduced oxygen concentration within the oxygen minimum zone of the southern California Current. This likely occurred because the prey species were forced to occupy better-oxygenated shallow (and subsequently more well-lit) waters, rendering them more vulnerable to visually orienting predators such as tunas and billfishes. Changes in populations of these mid-trophic level mesopelagic prey species (which are both major consumers of zooplankton and major food sources for tunas, billfishes, and a wide range of other fish, squids, seabirds, and marine mammals) could have far-reaching impacts on the abundance of tunas and billfishes in particular, and the structure of pelagic food webs in general, which may be either positive or negative. Future changes in vertical habitat usage driven by changes in oxygen content may also alter population structures via changes in species size and productivity. For example, Prince and Goodyear (2006) showed that enhanced coupling between predator and prey likely leads to increased foraging opportunities and therefore larger mean body sizes of sailfish in the hypoxia-compressed habitats of the eastern tropical Pacific and Atlantic Oceans, as compared to the well-oxygenated western North Atlantic Ocean. Whether climate change will lead to enhanced or decreased coupling between predator and prey will depend on region-specific changes

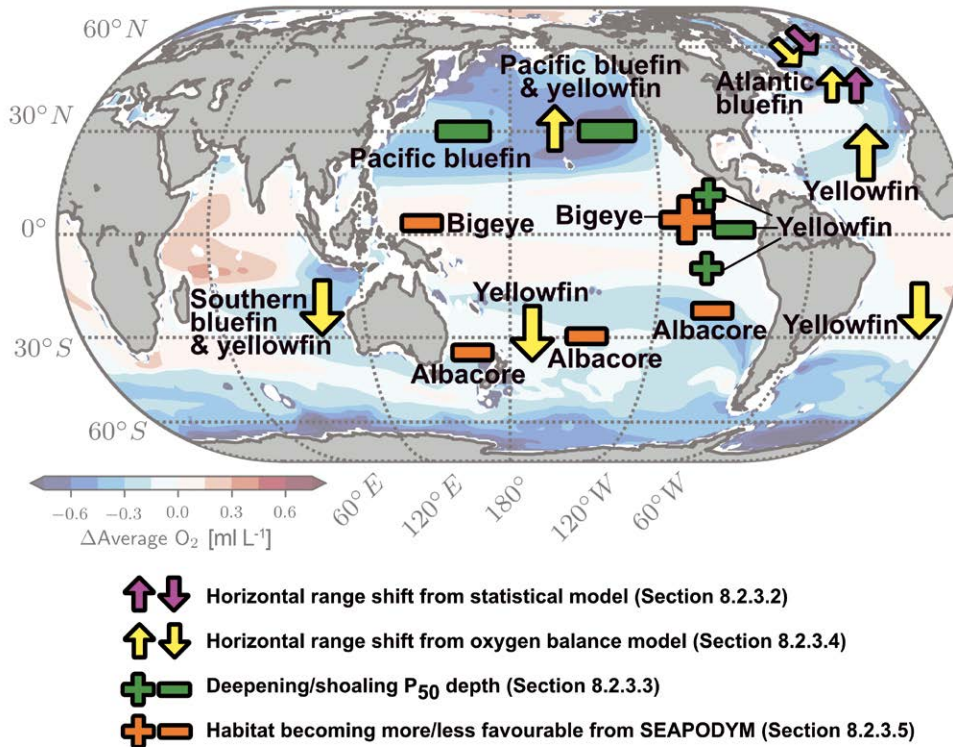## Summary of Projected Oxygen-Driven Tuna Habitat Changes

Figure 8.2.17 Summary of projected changes in species-specific tuna habitats by the end of the 21st century, driven (at least partially) by projected changes in oxygen content. The background map of projected changes in average oxygen concentrations between 200 and 700 m depth is taken from Figure 8.2.10B. Changes in habitat driven by factors unrelated to or not including oxygen are not shown here. For example, changes in skipjack tuna distributions within the Pacific Ocean are expected to be driven primarily by temperature and access to food; because oxygen plays an insignificant role in this case, these projected distributional shifts are not depicted here. It is important to note that there are substantial uncertainties associated with each habitat projection. Uncertainties are especially large in the eastern tropical Pacific, due mainly to lack of model agreement on how oxygen concentrations will change within this region. For more information on uncertainties, see the subsections cited in the figure.

in oxygen and temperature distributions, as well as species-specific differences in hypoxic and thermal tolerances.

8.2.5 Societal consequences

Different tuna and billfish species are fished by different gears, depending on targeted species size and depth range, vessel capacity, and applicable regulations, among other factors (ICCAT, 2016; Ward & Hindmarsh, 2007; Williams & Terawasi, 2011). Skipjack and yellowfin tunas (the two tuna species dominating worldwide landings, Table 8.2.1) are primarily taken by purse seine fisheries (Figure 8.2.2), which are concentrated in the tropical waters of the Pacific, Atlantic, and Indian Oceans (FAO Fisheries & Aquaculture "Global Capture Production" and "Global Catches by Stock" databases consulted on 20/12/2017). Purse seines largely target the upper water column and may fish down to ~200 – 300 m depth depending on the target species (ICCAT, 2016; Lennert-Cody et al., 2008). Purse seining thus

depends on oxycline and/or thermocline depths (below which skipjack and yellowfin tunas do not frequently dive) being shallower than ~200 – 300 m. Pelagic longline gear primarily catches larger fish (ICCAT, 2016) and can be placed in different configurations in order to set the majority of hooks at the desired depths. For example, hooks are set to occupy 50 – 100 m depth to target swordfish (at night, when this species occupies the upper water column) and 200 – 300 m depth to target tunas (Bigelow et al., 2006; Nakano et al., 1997; Ward & Myers, 2005). In general, skipjack tuna and billfishes are caught on shallower set hooks, while albacore and bigeye tunas are more likely to be caught on deep-set gear, due to their species-specific vertical movement patterns (described in subsection 8.2.2). Yellowfin tuna longline catchability is less correlated with depth within their vertical range (above about 300 - 500 m) (Nikolic et al., 2017; Prince et al., 2010; Ward & Myers, 2005). Surface gears including trolling and hook-and-line are used to catch smaller or juvenile tunas in some areas, such as the juvenile albacore fishery off of the western

United States and the juvenile Atlantic bluefin tuna fishery in the north-eastern Atlantic Ocean (Fromentin, 2009; Nikolic et al., 2017; Xu et al., 2015). Other gears, such as fixed traps, drift gillnets, and harpoons, are also used to target tunas and billfishes, but fishing effort and landings are generally small compared to purse seine and longline fisheries (Miyake et al., 2010).

Ocean warming and deoxygenation have the potential to change the distribution and catchability of tunas and billfishes in three dimensions. Because tunas and billfishes are highly mobile and patchily aggregated, they are likely to exhibit complex shifts in their distributions in response to changing environmental conditions. Where surface layer temperatures become too warm, they may spend more time at depth (assuming oxygen concentrations are sufficient), potentially decreasing their vulnerability to surface-oriented fishing gears. In contrast, if oxygen minimum layers expand and shoal, relatively hypoxia-intolerant species (e.g. skipjack and yellowfin tunas) may be pushed towards the surface (assuming temperatures are not too warm), potentially increasing their vulnerability to surface-oriented fishing gears (e.g. Stramma et al., 2012). If no vertical refuge from unsuitable conditions is available, the fish may shift their distributions horizontally, moving towards areas with temperatures or oxygen levels that are more tolerable. To maintain their livelihoods, fishers will need to adapt to potential changes in species distributions, vulnerabilities to different gear types or fishing fleets, and efficiencies of supply chains, which can be further exacerbated by factors such as rising fuel prices and decreasing government subsidies (Jones et al., 2015). Where populations of target species decrease or move away from traditional fishing grounds, fishers will have to spend more resources to catch the same species or adapt their gear and vessel configurations to target new ones. Economic and regulatory constraints can, however, hamper the ability of fishers to effectively adapt to changing species availability, particularly if species movements cross management boundaries (Pinsky & Fogarty, 2012). Smaller-scale fisheries in developing nations and fisheries relying on vessels with limited range and low technological capabilities are likely to be most vulnerable, particularly if their exposures to the effects of climate change are also high (Guillotreau et al., 2012; Ommer et al., 2009). Communities that are strongly economically dependent on these types of small-scale fisheries for livelihoods and incomes are therefore likely to be hardest hit by climate-driven changes to fish distributions.

Climate-driven changes in habitat suitability and population structures are also likely to complicate stock assessment and management. Most current stock assessment models use standardized indices of abundance derived from fishery-dependent catch per unit effort (CPUE) data to infer changes in stock size. Environmentally-driven changes in species distribution, range, or population structure can, however, lead to trends in catchability and subsequently CPUE data that are unrelated to abundance (Bigelow & Maunder, 2006; Link et al., 2011). If not accounted for, these types of changes in CPUE data can bias estimates of abundance used in population assessment models (Wilberg et al., 2010). Some newer stock assessment methods can incorporate effects of time-varying selectivity (Methot & Wetzel, 2013), however, and spatio-temporal models are becoming more feasible (Berger et al., 2017). In addition, indices derived from survey or fisheries data can be standardized to account for environmental effects (e.g. Cao et al., 2017; Lynch et al., 2012). Misspecification of these processes can, however, lead to biases (Hulson et al., 2013). Increasing model complexity to deal with changing environmental factors thus requires caution. Managers will have to carefully adapt their stock assessment strategies in the face of climate change in order to remain effective and ensure resource sustainability.

8.2.7 Conclusions / Recommendations

We conclude (as have numerous other authors cited here) that climate change occurring over the next 100 years will drive species-specific changes in the population structures and (more importantly) the horizontal and vertical movement patterns of tunas and billfishes in the open ocean through changes in habitat suitability. We contend that a major factor contributing to these changes will be altered oxygen distributions throughout the global ocean. The temperate North Pacific Ocean is projected to undergo some of the largest overall decreases in oxygen content within the upper water column across ocean basins, as well as some of the most pronounced shoaling of hypoxic layers (subsection 8.2.3.1). Species which currently reside in this region (e.g. swordfish and yellowfin, bigeye, Pacific bluefin, and albacore tunas) are thus expected to experience the most dramatic decreases in oxygen content and shoaling of P_{50} depths in their present-day habitat (subsection 8.2.3.3). In response to these changes in oxygen (and temperature), Pacific bluefin tuna are expected to shift northward toward

more favourable oxygen conditions and to adjust their vertical habitat usage to avoid oxygen limitation from shoaling P_{50} depths (subsections 8.2.3.3 and 8.2.3.4). Atlantic bluefin tuna are projected to shift northward as well, propelled by warming, unfavourable oxygen balances (subsection 8.2.3.4), and a loss of habitat south of ~40°N (subsection 8.2.3.2). Yellowfin tuna are likewise expected to shift poleward toward habitats with more favourable temperature and oxygen balances (subsection 8.2.3.4), as well as to potentially move upward in the water column within the temperate North Pacific due to shoaling P_{50} depths (subsection 8.2.3.3). Skipjack tuna, on the other hand, are less likely to be affected by future changes in oxygen concentrations at depth because they generally remain within the well-oxygenated surface layer (subsection 8.2.3.5). The combined effects of warming and slight deoxygenation of the upper mixed layer in tropical regions on species such as skipjack tuna remain uncertain, however. The effects of future oxygen changes on bigeye tuna population dynamics are more mixed, in that projected changes in subsurface oxygen concentrations in the eastern and western tropical Pacific drive both increases and decreases, respectively, in SEAPODYM-predicted adult biomass (subsection 8.2.3.5). In the South Pacific, SEAPODYM projects that younger cohorts of South Pacific albacore will be negatively affected by decreases in oxygen concentrations within their spawning grounds (subsection 8.2.3.5). These projected changes are summarized in Figure 8.2.17.

Each type of model used to predict the effects of future oxygen changes on tunas and billfishes has its own advantages and disadvantages. The trait-based, oxygen balance, and statistical models we describe here account for only the direct effects of oxygen (and temperature) changes on tuna and billfish physiology and therefore movements. The more complex process-based models (SEAPODYM and APECOSM-E), on the other hand, account for these direct effects as well as the indirect effects of potential oxygen-driven food-web and population structure changes. Additionally, the trait analysis, oxygen balance, and statistical models are distribution models that only consider climate change impacts in terms of potential horizontal and vertical range shifts, while SEAPODYM and APECOSM-E takes into account life histories and phenologies to produce more detailed projections of population and age structures. More complex models can be more difficult to parameterize, however, which can lead to greater uncertainty in projections. Continued work on all types

of species-specific models will therefore be necessary for generating more accurate projections and reducing uncertainties.

Improvements in Earth System Models used to project future environmental conditions will also help increase the accuracy of projections related to tuna and billfish distributions in response to climate change. Current Earth System Models, including the ones used in this report, typically have horizontal resolutions of 1° or coarser. This coarse resolution cannot distinguish many important meso- and sub-mesoscale processes that can oftentimes drive observed species distributions. Furthermore, projections of biogeochemical variables (such as oxygen concentration) can be highly uncertain within these models compared to projections of purely physical variables (such as temperature). Projections of changes in oxygen concentrations in the tropical Pacific Ocean, where the interactions between biology and the physics of ocean circulation are complicated, are especially uncertain. Part of the reason for these uncertainties is the relative lack of actual biogeochemical measurements that can be used for calibration and improvements in mechanistic understanding. Increased *in situ* monitoring of oxygen concentrations throughout the global oceans is therefore crucial for improving Earth System Model predictions of biogeochemistry.

To further improve projections of future habitat and population changes, greater numbers of *in situ* observations of tuna and billfish habitat use are also needed. More *in situ* habitat observations, along with more laboratory studies of physiological traits, will lead to a better understanding of the environmental conditions that can predict species-specific movement patterns and therefore species-specific responses to climate change. Data products that synthesize and standardize multiple sources of information would be particularly useful. For example, contradictory records for the depth ranges frequented by various tunas and billfishes sometimes occur because a standard method for calculating these ranges does not exist. In addition, the development of a four-dimensional (three spatial dimensions and time) gridded atlas documenting the spatio-temporally variable habitats of tunas and billfishes, derived from tagging data and species-specific physiological abilities and tolerances, would be invaluable for analysing how regional and seasonal variations in habitat usage will be impacted by deoxygenation. More detailed *in situ* observations of prey abundances and behaviours would also help improve projections of future habitat suitability

changes by improving our understanding of the effects of oxygen and other environmental conditions on prey distributions and predator-prey interactions.

The most obvious way to slow or prevent projected changes in global oxygen content and resultant changes in the populations and distributions of tunas and billfishes is to reduce greenhouse gas emissions. Besides preventing climate change, however, we can also adapt to and prepare for potential future effects. A sound mechanistic understanding of how tunas and billfishes respond to their ocean environment is key to successful adaptation. We thus argue (as have others, e.g. Brill & Hobday, 2017; Hobday et al., 2013; Lehodey et al., 2011; Mislan et al., 2016; Watters et al., 2003) that illuminating the interactions between fishes, fisheries, and climate change is, and will continue to be, critical for ensuring the sustainability of tunas and billfishes into the 21st century.

8.2.8 References

Abascal, F.J., Mejuto, J., Quintans, M., & Ramos–Cartelle, A. (2010). Horizontal and vertical movements of swordfish in the Southeast Pacific. *ICES Journal of Marine Science, 67,* 466–474. https://doi.org/10.1093/icesjms/fsp252

Antoine, D., André, J.M., & Morel, A. (1996). Oceanic primary production: 2. Estimation at global scale from satellite (coastal zone color scanner) chlorophyll. *Global Biogeochemical Cycles, 10,* 57–69. https://doi.org/10.1029/95GB02832

Barkley, R.A., Neill, W.H., & Gooding, R.M. (1978). Skipjack tuna, *Katsuwonus pelamis*, habitat base on temperature and oxygen requirement. *Fishery Bulletin USA, 76,* 653–662.

Bauer, R.K., Fromentin, J.–M., Demarcq, H., Brisset, B., & Bonhommeau, S. (2015). Co–Occurrence and habitat use of fin whales, striped dolphins and Atlantic bluefin tuna in the Northwestern Mediterranean Sea. *PLoS ONE*, *12*, e0139218. https://doi.org/10.1371/journal.pone.0139218

Bauer, R.K., Fromentin, J.–M., Demarcq, H., & Bonhommeau, S. (2017). Habitat use, vertical and horizontal behaviour of Atlantic bluefin tuna (*Thunnus thynnus*) in the Northwestern Mediterranean Sea in relation to oceanographic conditions. *Deep Sea Research Part II: Topical Studies in Oceanography, 147*, 248–261. https://doi.org/10.1016/j.dsr2.2017.04.006

Belman, B.W., & Childress, J.J. (1975). Circulatory adaptations to the oxygen minimum layer in the bathypelagic mysid *Gnathophausia ingens*. *Biological Bulletin, 150*, 15–37. https://doi.org/10.2307/1540586

Berger, A.M., Goethel, D.R., Lynch, P.D., Quinn, T., Mormede, S., McKenzie, J., & Dunn, A. (2017). Space oddity: The mission for spatial integration. *Canadian Journal of Fisheries and Aquatic Sciences, 74*, 1698–1716. https://doi.org/10.1139/cjfas-2017-0150

Bernal, D., Dickson, K.A., Shadwick, R.E., & Graham, J.B. (2001). Review: analysis of the evolutionary convergence for high performance swimming in lamnid sharks and tunas. *Comparative Biochemistry and Physiology, 129A*, 695–726. https://doi.org/10.1016/S1095-6433(01)00333-6

Bernal, D., Sepulveda, C., Musyl, M., & Brill, R. (2009). The ecophysiology of swimming and movement patterns of tunas, billfishes, and large pelagic sharks. In P. Domenici, & B.G. Kapoor (Eds.). *Fish locomotion: an etho–ecological approach*. Science Publishers, Enfield. pp. 436–483. https://doi.org/10.1201/b10190-15

Bernal, D., Dickson, K., Shields, H., & Brill, R. (2017). Sharing the water column: physiological mechanisms underlying species specific habitat use. *Reviews in Fish Biology and Fisheries, 27*, 843–880. https://doi.org/10.1007/s11160-017-9497-7

Bertrand, A., Josse, E., Bach, P., Gros, P., & Dagorn, L. (2002a). Hydrological and trophic characteristics of tuna habitat: consequences on tuna distribution and longline catchability. *Canadian Journal of Fisheries and Aquatic Sciences, 59*, 1003–1013. https://doi.org/10.1139/f02-073

Bertrand, A., Bard, F.–X., & Josse, E. (2002b). Tuna food habits related to the micronekton distribution in French Polynesia. *Marine Biology, 140*, 1023–1037. https://doi.org/10.1007/s00227-001-0776-3

Bertrand, A., Le Borgne, E., & Josse, E. (1999). Acoustic characterisation of micronekton distribution in French Polynesia. *Marine Ecology Progress Series, 191*, 127–140. https://doi.org/10.3354/meps191127

Bigelow, K.A., Hampton, J., & Naozumi, M.N. (2002). Application of a habitat–based model to estimate effective longline fishing effort and relative abundance of Pacific bigeye tuna (*Thunnus obesus*). *Fisheries Oceanography, 11*, 143–155. https://doi.org/10.1046/j.1365-2419.2002.00196.x

Bigelow, K.A., & Maunder, M.N. (2006). Does habitat or depth influence catch rates of pelagic species? *Canadian Journal of Fisheries and Aquatic Sciences, 64*, 1581–1594. https://doi.org/10.1139/f07-115

Bigelow, K., Musyl, M.K., Poisson, F., & Kleiber, P. (2006). Pelagic longline gear depth and shoaling. *Fisheries Research, 77*, 173–183. https://doi.org/10.1016/j.fishres.2005.10.010

Blackburn, M. (1965). Oceanography and the ecology of tunas. *Oceanography and Marine Biology Annual Review, 2*, 299–322.

Blank, J.M., Farwell, C.J., Morrissette, J.M., Schallert, R.J., & Block, B.A. (2007). Influence of swimming speed on metabolic rates of juvenile Pacific bluefin tuna and yellowfin tuna. *Physiological and Biochemical Zoology, 80*, 167–177. https://doi.org/10.1086/510637

Blank, J.M., Morrissette, J.M., Davie, P.S., & Block, B.A. (2002). Effects of temperature, epinephrine and Ca^{2+} on the hearts of yellowfin tuna (*Thunnus albacares*). *Journal of Experimental Biology, 205*, 1881–1888.

Blank, J.M., Morrissette, J.M., Landeira–Fernandez, A.M., Blackwell, S.B., Williams, T.D., & Block, B.A. (2004). In situ cardiac performance of Pacific bluefin tuna hearts in response to acute temperature change. *Journal of Experimental Biol*ogy, *207*, 881–890. https://doi.org/10.1242/jeb.00820

Block, B.A., Booth, D.T., & Carey, F.G. (1993). Depth and temperature of the blue marlin *Makaira nigricans*, observed by

acoustic telemetry. *Marine Biology, 114*, 175–183. https://doi.org/10.1007/BF00349517

Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., … Fudge, D. (2001). Electronic tags reveal migratory movements, depth preferences and thermal biology of Atlantic bluefin tuna. *Science, 293*, 1310–1314. https://doi.org/10.1126/science.1061197

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., … Ganong, J.E. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature, 475*, 86–90. https://doi.org/10.1038/nature10082

Block, B.A., & Stevens, E.D. (2001). *Fish Physiology, Volume 19, Tuna — Physiology, Ecology and Evolution*. Academic Press, San Diego. https://doi.org/10.1016/S1546-5098(01)19001-1

Block, B.A., Teo, S.L.H., Walli, A., Boustany, A., Stokesbury, M.J.W., Farwell, C.J., … Williams, T.D. (2005). Electronic tagging and population structure of Atlantic bluefin tuna. *Nature, 434*, 1121–1127. https://doi.org/10.1038/nature03463

Bopp, L., Resplandy, L., Orr, J.C., Doney, S.C., Dunne, J.P., Gehlen, M., …Tjiputra, J. (2013). Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences, 10*, 6225–6245. https://doi.org/10.5194/bg-10-6225-2013

Boustany, A.M., Matteson, R., Castleton, M., Farwell, C., & Block, B.A. (2010). Movements of Pacific bluefin tuna (*Thunnus orientalis*) in the Eastern North Pacific revealed with archival tags. *Progress in Oceanography, 86*, 94–104. https://doi.org/10.1016/j.pocean.2010.04.015

Boye, J., Musyl, M., Brill, R., & Malte, H. (2009). Transectional heat transfer in thermoregulating bigeye tuna (*Thunnus obesus*) – a 2D heat flux model. *Journal of Experimental Biology, 212*, 3708–3718. https://doi.org/10.1242/jeb.031427

Braun, C.D., Kaplan, M.B., Horodysky, A.Z., & Llopiz, J.K. (2015). Satellite telemetry reveals physical processes driving billfish behavior. *Animal Biotelemetry, 3:2.* https://doi.org/10.1186/s40317–014–0020–9

Breitburg, D., Levin, L.A., Oschlies, A., Grégoire, M., Chavez, F.P., Conley, D.J., … Zhang, J. (2018). Declining oxygen in the global ocean and coastal waters. *Science, 359*, eaam7240. https://doi.org/10.1126/science.aam7240

Brill, R.W. (1987). On the standard metabolic rate of tropical tunas, including the effect of body size and acute temperature change. *Fishery Bulletin, U.S., 85*, 25–35.

Brill, R.W. (1994). A review of temperature and oxygen tolerances studies of tunas, pertinent to fisheries oceanography, movement models, and stock assessments. *Fisheries Oceanography, 3*, 206–216. https://doi.org/10.1111/j.1365-2419.1994.tb00098.x

Brill, R.W. (1996). Selective advantages conferred by the high performance physiology of tunas, billfishes, and dolphin fish. *Comparative Biochemistry and Physiology, 113A*, 3–15. https://doi.org/10.1016/0300-9629(95)02064-0

Brill, R.W., & Bushnell, P.G. (1991). Metabolic and cardiac scope of high energy demand teleosts, the tunas. *Canadian Journal of Zoology, 69*, 2002–2009. https://doi.org/10.1139/z91-279

Brill, R.W., & Bushnell, P.G. (2001). The cardiovascular system of tunas. In B.A. Block, & E.D. Stevens (Eds.). *Fish Physiology, Volume 19, Tuna — Physiology, Ecology and Evolution.* Academic Press, San Diego. pp. 79–120. https://doi.org/10.1016/S1546-5098(01)19004-7

Brill, R.W., & Bushnell, P.G. (2006). Effects of open– and closed–system temperature changes on blood O_2 –binding characteristics of Atlantic bluefin tuna (*Thunnus thynnus*). *Fish Physiology and Biochemistry, 32*, 283–294. https://doi.org/10.1007/s10695-006-9104-7

Brill, R.W., & Chin Lai, N. (2016). Elasmobranch cardiovascular system In R.E. Shadwick, A.P. Farrell, & C.J. Brauner (Eds.), *Fish Physiology, Vol. 34B, Physiology of Elasmobranch Fishes – Internal Processes.* Academic Press, San Diego, CA. pp. 2–83.

Brill, R.W., & Hobday, A.J. (2017). Tunas and their fisheries: safeguarding sustainability in the twenty–first century. *Reviews in Fish Biology and Fisheries, 27*, 691–695. https://doi.org/10.1007/s11160-017-9500-3

Brill, R.W., Holts, D.B., Chang, R.K.C., Sullivan, S., Dewar, H., & Carey, F.G. (1993). Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the main Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurement of oceanic currents. *Marine Biology, 117*, 567–574. https://doi.org/10.1007/BF00349767

Bushnell, P.G., & Brill, R.W. (1991). Responses of swimming skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tunas exposed to acute hypoxia, and a model of their cardio–respiratory function. *Physiological Zoology, 64*, 787–811. https://doi.org/10.1086/physzool.64.3.30158207

Bushnell, P.G., & Brill, R.W. (1992). Oxygen transport and cardiovascular responses in skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) exposed to acute hypoxia. *Journal of Comparative Physiology B, 162*, 131–143. https://doi.org/10.1007/BF00398338

Bushnell, P.G., Brill, R.W., & Bourke, R.E. (1990). Cardiorespiratory responses of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*) to acute reductions of ambient oxygen. *Canadian Journal of Zoology, 68*, 1857–1865. https://doi.org/10.1139/z90-265

Bushnell, P.G., & Jones, D.R. (1994). Cardiovascular and respiratory physiology of tuna: adaptations for support of exceptionally high metabolic rates. *Environmental Biology of Fishes, 40*, 303–318. https://doi.org/10.1007/BF00002519

Cabré, A., Marinov, I., Bernardello, R., & Bianchi, D. (2015). Oxygen minimum zones in the tropical Pacific across CMIP5 models: mean state differences and climate change trends. *Biogeosciences, 12*, 5429–5454. https://doi.org/10.5194/bg-12-5429-2015

Canese, S., Garibaldi, F., Orsi Relini, L., & Greco, S. (2008). Swordfish tagging with pop–up satellite tags in the Mediterranean Sea. *ICCAT Collective Volume of Scientific Papers, 64*, 1052–1057.

Cao, J., Thorson, J.T., Richards, R.A., & Chen, Y. (2017). Spatiotemporal index standardization improves the stock assessment of northern shrimp in the Gulf of Maine. *Canadian Journal of Fisheries and Aquatic Sciences, 74*, 1781–1793. https://doi.org/10.1139/cjfas-2016-0137

Carey, F.G. (1990). Further acoustic telemetry observations on the biology of swordfish. In R.H. Stroud (Ed.). *Planning the Future*

of Billfishes. National Coalition for Marine Conservation Inc., Savannah, GA. pp. 103–122.

Carey, F.G., & Gibson, Q.H. (1983). Heat and oxygen exchange in the rete mirable of the bluefin tuna, *Thunnus thynnus*. *Comparative Biochemistry and Physiol*ogy, *74A*, 333–342. https://doi.org/10.1016/0300-9629(83)90612-6

Carey, F.G., & Gibson, Q.H. (1977). Reverse temperature dependence of tuna hemoglobin oxygenation. *Biochemical Biophysical Research Communications, 78*, 1376–1382. https://doi.org/10.1016/0006-291X(77)91444-9

Carey, F.G., & Robison, B.H. (1981). Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fishery Bulletin, 79*, 277–292.

Cech, J.J., Laurs, R.M., & Graham, J.B. (1984). Temperature induced changes in blood gas equilibria in the albacore, *Thunnus alalunga*, a warm–bodied tuna. *Journal of Experimental Biology, 109*, 21–34.

Childress, J.J. (1971). Respiratory adaptations to the oxygen minimum layer in the bathypelagic mysid *Gnathophausia ingens*. *Biological Bulletin, 141*, 109–121. https://doi.org/10.2307/1539995

Childress, J.J., & Nygaard, M.H. (1974). The chemical composition and relative buoyancy of midwater crustaceans as a function of depth off Southern California. *Marine Biology, 27*, 225–238. https://doi.org/10.1007/BF00391948

Childress, J.J., & Seibel, B.A. (1998). Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. *Journal of Experimental Biology, 201*, 1223–1232.

Childers, J., Snyder, S., & Kohin, S. (2011). Migration and behavior of juvenile North Pacific albacore (*Thunnus alalunga*). *Fisheries Oceanography, 20*, 157–173. https://doi.org/10.1111/j.1365-2419.2011.00575.x

Clark, T.D., Brandt, W.T., Nogueira, J., Rodriguez, L.E., Price, M., Farwell, C.J., & Block, B.A. (2010). Postprandial metabolism of Pacific bluefin tuna (*Thunnus orientalis*). *Journal of Experimental Biology, 213*, 2379–2385. https://doi.org/10.1242/jeb.043455

Clark, T.D., Farwell, C.J., Rodriguez, L.E., Brandt, W.T., & Block, B.A. (2013). Heart rate responses to temperature in free–swimming Pacific bluefin tuna (*Thunnus orientalis*). *Journal of Experimental Biology, 216*, 3208–3214. https://doi.org/10.1242/jeb.086546

Clark, T.D., Seymour, R.S., Wells, R.M.G., & Frappell, P.B. (2008). Thermal effects on the blood respiratory properties of southern bluefin tuna, *Thunnus maccoyii. Comparative Biochemistry and Physiology, 150A*, 239–246. https://doi.org/10.1016/j.cbpa.2008.03.020

Cocco, V., Joos, F., Steinacher, M., Frölicher, T.L., Bopp, L., Dunne, J., …Tjiputra, J. (2013). Oxygen and indicators of stress for marine life in multi–model global warming projections. *Biogeosciences, 10*, 1849–1868. https://doi.org/10.5194/bg-10-1849-2013

Collins, W.J., Bellouin, N., Doutriaux–Boucher, M., Gedney, N., Halloran, P., Hinton, T., & Woodward, S. (2011). Development and evaluation of an Earth–System model – HadGEM2. *Geoscientific Model Development, 4*, 1051–1075. https://doi.org/10.5194/gmd-4-1051-2011

Coro, G., Magliozzi, C., Ellenbroek, A., Kaschner, K., & Pagano, P. (2016). Automatic classification of climate change effects on marine species distributions in 2050 using the AquaMaps model.

Environmental and Ecological Statistics, 23, 155–180. https://doi.org/10.1007/s10651-015-0333-8

Czeschel, R., Stramma, L., & Johnson, G.C. (2012). Oxygen decreases and variability in the eastern equatorial Pacific. *Journal of Geophysical Research: Oceans, 117*, C11019. https://doi.org/10.1029/2012JC008043

Dacie, J.V., Lewis, S.N., Childers, J., Snyder, S., & Kohin, S. (2011). Migration and behavior of juvenile north Pacific albacore (*Thunnus alalunga*). *Fisheries Oceanography, 20*, 157–173. https://doi.org/10.1111/j.1365-2419.2011.00575.x

Dagorn, L., Bach, P., & Josse, E. (2000a). Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean determined using ultrasonic telemetry. *Marine Biology, 136*, 361–371. https://doi.org/10.1007/s002270050694

Dagorn, L., Josse, E., & Bach, P. (2000b). Individual differences in horizontal movements of yellowfin tuna (*Thunnus albacares*) in near–shore areas in French Polynesia, determined using ultrasonic telemetry. *Aquatic Living Resources, 13*, 193–202. https://doi.org/10.1016/S0990-7440(00)01063-9

Dagorn, L., Josse, E., Bach, P., & Bertrand, A. (2000c). Modeling tuna behaviour near floating objects: from individuals to aggregations. *Aquatic Living Resources, 13*, 203–211. https://doi.org/10.1016/S0990-7440(00)01065-2

Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H.–O., & Huey, R. (2015). Climate change tightens a constraint on marine habitats. *Science, 348*, 1132–1136. https://doi.org/10.1126/science.aaa1605

Dewar, H., & Graham, J. (1994). Studies of tropical tuna swimming performance in a large water tunnel – Energetics. *Journal of Experimental Biology, 192*, 13–31.

Dewar, H., Graham, J.B., & Brill, R.W. (1994). Studies of tropical tuna swimming performance in a large water tunnel – Thermoregulation. *Journal of Experimental Biology, 192*, 33–44.

Dewar, H., Prince, E.D., Musyl, M.K., Brill, R.B., Sepulveda, C., Luo, J., … McNaughton, L.M. (2011). Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop–up satellite archival tags. *Fisheries Oceanography, 20*, 219–241. https://doi.org/10.1111/j.1365-2419.2011.00581.x

Dizon, A.E. (1977). Effect of dissolved oxygen concentration and salinity on swimming speed of two species of tunas. *Fishery Bulletin U.S., 75*, 649–653.

Dizon, A.E., Stevens, E.D., Neill, W.H., & Magnuson, J.J. (1974). Comparative sensitivity of restrained skipjack tuna (*Katsuwonus pelamis*) to abrupt increases in temperature. *Biochemistry and Physiology Part A, 49*, 291–299. https://doi.org/10.1016/0300-9629(74)90120-0

Dizon, A.E., Byles, T.C., & Stevens, E.D. (1976). Perception of abrupt temperature decrease by restrained skipjack tuna, *Katsuwonus pelamis. Journal of Thermal Biology, 1*, 185–187. https://doi.org/10.1016/0306-4565(76)90012-7

Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., … Singer, A. (2012). Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography, 39*, 2119–2131. https://doi.org/10.1111/j.1365-2699.2011.02659.x

Dueri, S., Bopp, L., & Maury, O. (2014). Projecting the impacts of climate change on skipjack tuna abundance and spatial distribution. *Global Change Biology*, 20, 742–753. https://doi.org/10.1111/gcb.12460

Dufresne, J.L., Foujols, M.–A., Denvil, S., Caubel, A., Marti, O., Aumont, Y., … Vuichard, N. (2013). Climate change projections using the IPSL–CM5 Earth System Model: From CMIP3 to CMIP5. *Climate Dynamics, 40*, 2123–2165. https://doi.org/10.1007/s00382-012-1636-1

Dunne, J.P., John, J.G., Adcroft, A.J., Griffies, S.M., Hallberg, R.W., Shevliakova, E., … Zadeh, N. (2012). GFDL's ESM2 Global Coupled Climate–Carbon Earth System Models. Part I: Physical formulation and baseline simulation characteristics. *Journal of Climate, 25*, 6646–6665. https://doi.org/10.1175/JCLI-D-11-00560.1

Dunne, J.P., John, J.G., Shevliakova, E., Stouffer, R.J., Krasting, J.P., Malyshev, S.L., … Zadeh, N. (2013). GFDL's ESM2 global coupled climate–carbon earth system models. Part II: Carbon system formulation and baseline simulation characteristics. *Journal of Climate, 26*, 2247–2267. https://doi.org/10.1175/JCLI-D-12-00150.1

Evans, K., Langley, A., Clear, N.P., Williams, P., Patterson, T., Sibert, J., … Gunn, J.S. (2008). Behaviour and habitat preferences of bigeye tuna (*Thunnus obesus*) and their influence on longline fishery catches in the western Coral Sea. *Canadian Journal of Fisheries and Aquatic Sciences, 65*, 2427–2443. https://doi.org/10.1139/F08-148

Evans, K., Abascal, F., Kolody, D., Sippel, T., Holdsworth, J., & Marud, P. (2014). The horizontal and vertical dynamics of swordfish in the South Pacific Ocean. *Journal of Experimental Marine Biology and Ecology, 450*, 55–67. https://doi.org/10.1016/j.jembe.2013.10.025

FAO – Fishery Statistical Collections. Global Tuna Catches by Stock. (2014). Available at: http://www.fao.org/fishery/statistics/tuna–catches/en (Accessed: 12/18/2017).

FAO – Fisheries and Aquaculture Information and Statistics Branch. (2017). Available at: http://www.fao.org/figis/servlet/SQServlet?file=/usr/local/tomcat/8.5.16/figis/webapps/figis/temp/hqp_8098547457917812592.xml&outtype=html (Accessed: 19/12/2017).

Farwell, C.J. (2001). Tunas in captivity. In B.A. Block, & E.D. Stevens (Eds.). *Fish Physiology, Volume 19, Tuna — Physiology, Ecology and Evolution*. Academic Press, San Diego. pp. 319–413. https://doi.org/10.1016/S1546-5098(01)19011-4

Farrell, A.P., & Richards, J.G. (2009). Defining hypoxia: An integrative synthesis of the responses of fish to hypoxia. In J.G. Richards, A.P. Farrell, & C.J. Brauner (Eds.). *Fish Physiology Volume 27, Hypoxia*. Elsevier, London. pp. 487–503. https://doi.org/10.1016/S1546-5098(08)00011-3

Frölicher, T.L., Joos, F., Plattner, G.–K., Steinacher, M., & Doney, S.C. (2009). Natural variability and anthropogenic trends in oceanic oxygen in a coupled carbon cycle–climate model ensemble. *Global Biogeochemical Cycles, 23*, GB1003. https://doi.org/10.1029/2008GB003316

Fromentin, J.-M., & Fonteneau, A. (2001). Fishing effects and life history traits: a case study comparing tropical versus temperate tunas. *Fisheries Research, 53*, 133–150. https://doi.org/10.1016/S0165-7836(00)00299-X

Fromentin, J.-M. (2009). Lessons from the past: investigating historical data from bluefin tuna fisheries. *Fish and Fisheries, 10*, 197–216. https://doi.org/10.1111/j.1467-2979.2008.00311.x

Fujioka, K., Masujima, M., Boustany, A.M., & Kitagawa, T. (2016). Horizontal movements on Pacific bluefin tuna. In T. Kitagawa, & S. Kimura (Eds.). *Biology and Ecology of Bluefin Tuna*. CRC Press, Boca Raton, FL. pp. 101–122. https://doi.org/10.1201/b18714-9

Fuller, D.W., Schaefer, K.M., Hampton, J., Caillot, S., Leroy, B.M., & Itano, D.G. (2015).Vertical movements, behavior, and habitat of bigeye tuna (*Thunnus obesus*) in the equatorial central Pacific Ocean. *Fisheries Research, 172*, 57–70. https://doi.org/10.1016/j.fishres.2015.06.024

Galli, G.L.J., Lipnick, M.S., Shiels, H.A., & Block, B.A. (2011). Temperature effects on Ca^{2+} cycling in scombroid cardiomyocytes: a phylogenetic comparison. *Journal of Experimental Biology, 214*, 1068–1076. https://doi.org/10.1242/jeb.048231

Galli, G.L.J., Shiels, H.A., & Brill, R.W. (2009). Temperature sensitivity of cardiac function in pelagic fishes with different vertical mobilities: yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*), mahimahi (*Coryphaena hippurus*), and swordfish (*Xiphias gladius*). *Physiological and Biochemical Zoology, 82*, 280–290. https://doi.org/10.1086/597484

Gallo, N.D., & Levin, L.A. (2016). Chapter three – Fish ecology and evolution in the world's oxygen minimum zones and implications of ocean deoxygenation. *Advances in Marine Biology, 74*, 117–198. https://doi.org/10.1016/bs.amb.2016.04.001

Gaertner, D., Delgado de Molina, A., Ariz, J., Pianet, R., & Hallie, J. (2008). Variability of the growth parameters of the skipjack tuna (*Katsuwonus pelamis*) among areas in the eastern Atlantic: analysis from tagging data within a meta–analysis approach. *Aquatic Living Resources, 21*, 349–356. https://doi.org/10.1051/alr:2008049

Gaikov, V.V., Chur, V.N., Zharov, V.L., & Fedoseev, P.Y. (1980). On age and growth of the Atlantic bigeye tuna. *International Commission for the Conservation of Atlantic Tunas, Collective Volume of Scientific Papers, 9*, 294–302.

Graham, J.B., & Dickson, K.A. (2001). Anatomical and physiological specializations for endothermy. In: B.A. Block & E.D. Stevens (Eds.). *Fish Physiology, Volume 19, Tuna — Physiology, Ecology and Evolution*. Academic Press, San Diego, pp. 167–225. https://doi.org/10.1016/S1546-5098(01)19005-9

Garcia, H.E., Locarnini, R.A., Boyer, T.P., Antonov, J.I., Baranova, O.K., Zweng, M.M., … Johnson, D.R. (2014). *World Ocean Atlas 2013, Volume 3: Dissolved Oxygen, Apparent Oxygen Utilization, and Oxygen Saturation*. S, Levitus (Ed.), A Mishonov (Technical Ed.). NOAA Atlas NESDIS 75, 27 pp.

Gent, P.R., Danabasoglu, G., Donner, L.J., Holland, M.M., Hunke, E.C., Jayne, S.R., … Zhang, M. (2011). The Community Climate System Model Version 4. *Journal of Climate, 24*, 4973–4991. https://doi.org/10.1175/2011JCLI4083.1

Giorgetta, M.A., Jungclaus, J., Reick, C.H., Legutke, S., Bader, J., Böttinger M., & Stevens, B. (2013). Climate and carbon cycle changes from 1850 to 2100 in MPI–ESM simulations for the Coupled Model Intercomparison Project phase 5. *Journal of Advances in Modeling Earth Systems, 5*, 572–597. https://doi.org/10.1002/jame.20038

Gilly, W.F., Beman, J.M., Litvin, S.Y., & Robison, B.H. (2013). Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annual Review of Marine Science, 5*, 393–420. https://doi.org/10.1146/annurev-marine-120710-100849

Gilman, E., Allain, V., Collette, B., Hampton, J., & Lehodey, P. (2016). Effects of Ocean Warming on Pelagic Tunas, a Review. In D. Laffoley & J.M. Baxter (Eds.). *Explaining Ocean Warming: Causes, Scale, Effects and Consequences*. IUCN – International Union for the Conservation of Nature, Gland, Switzerland. pp. 254-270. https://doi.org/10.2305/IUCN.CH.2016.08.en

Gooding, R.M., Neill, W.H., & Dizon, A.E. (1981). Respiration rates and low–oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*. *Fishery Bulletin, 79*, 31–48.

Graham, J.B., Lowell, W.R., Chin Lai, N., & Laurs, R.M. (1989). O₂ tension, swimming–velocity, and thermal effects on the metabolic rate of the Pacific albacore *Thunnus alalunga*. *Experimental Biology, 48*, 89–94.

Grudinin, V.B. (1989). On the ecology of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*). *Journal of Ichthyology, 29*, 22–29.

Guillotreau, P., Campling, L., & Robinson, J. (2012). Vulnerability of small island fishery economies to climate and institutional changes. *Current Opinion in Environmental Sustainability, 4*, 1–5. https://doi.org/10.1016/j.cosust.2012.06.003

Guillotreau, P., Squires, D., Sun, J., & Compeán, G.A. (2017). Local, regional and global markets: what drives the tuna fisheries? *Reviews in Fish Biology Fisheries, 27*, 909–929. https://doi.org/10.1007/s11160-016-9456-8

Hanamoto, E. (1987). Effect of oceanographic environment on bigeye tuna distribution. *Bulletin Japanese Society of Fisheries Oceanography, 51*, 203–216.

Hartog, J.R., Hobday, A.J., Matear, R., & Feng, M. (2011). Habitat overlap between southern bluefin tuna and yellowfin tuna in the east coast longline fishery—implications for present and future spatial management. *Deep Sea Research Part II: Topical Studies in Oceanography, 58*, 746–752. https://doi.org/10.1016/j.dsr2.2010.06.005

Hazen, E.L., Jorgensen, S., Rykaczewski, R.R., Bograd, S.J., Foley, D.G., Jonsen, I.D., … Block, B.A. (2013). Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change, 3*, 234–238. https://doi.org/10.1038/nclimate1686

Helm, K.P., Bindoff, N.L., & Church, J.A. (2011). Observed decreases in oxygen content of the global ocean. *Geophysical Research Letters, 38*, L23602. https://doi.org/10.1029/2011GL049513

Hinton, M.G., & Deriso, R.D. (1998). Distribution and stock assessment of swordfish, *Xiphias gladius*, in the eastern Pacific Ocean from catch and effort data standardized on biological and environmental parameters. In I. Barrett, O. Sosa–Nishizaki, & N. Bartoo (Eds.). *Biology and Fisheries of Swordfish, Xiphias gladius.* In: *Papers from the International Symposium on Pacific Swordfish*. NOAA Technical Report NMFS 142, 161–179.

Hinton, M.G., & Nakano, H. (1996). Standardizing catch and effort statistics using physiological, ecological, or behavioral constraints and environmental data, with an application to blue marlin *(Makaira nigricans)* catch and effort data from Japanese longline fisheries in the Pacific. *Inter–American Tropical Tuna Commission Bulletin, 21*, 171–200.

Hobday, A.J., Young, J.W., Abe, O., Costa, D.P., Cowen, R.K., Evans, K., … Weng, K.C. (2013). Climate impacts and oceanic top predators: moving from impacts to adaptation in oceanic systems. *Reviews in Fish Biology and Fisheries, 23*, 537–546. https://doi.org/10.1007/s11160-013-9311-0

Hobday, A.J., Bell, J.D., Cook, T.R., Gasalla, M.A., & Weng, K.C. (2015). Reconciling conflicts in pelagic fisheries under climate change. *Deep Sea Research Part II: Topical Studies in Oceanography, 113*, 291-300. https://doi.org/10.1016/j.dsr2.2014.10.024

Hobday, A.J., Evans, K., Eveson, J.P., Farley, J.H., Hartog, J.R., Basson, M., & Patterson, T.A. (2016). Distribution and migration – Southern bluefin tuna (*Thunnus maccoyii*). In T. Kitagawa, & S. Kimura (Eds.). *Biology and Ecology of Bluefin Tuna*. CRC Press, Boca Raton, FL. pp. 189–210. https://doi.org/10.1201/b18714-12

Hobday, A., Arrizabalaga, J.H., Evans, K., Scales, K.L., Senina, I., & Weng, K.C. (2017). International collaboration and comparative research on ocean top predators under CLIOTOP. *Deep Sea Research Part II: Topical Studies in Oceanography, 140*, 1–8. https://doi.org/10.1016/j.dsr2.2017.03.008

Hofmann, A.F., Peltzer, E.T., Walz, P.M., & Brewer, P.G. (2011). Hypoxia by degrees: Establishing definitions for a changing ocean. *Deep Sea Research Part I: Oceanographic Research Papers, 58*, 1212–1226. https://doi.org/10.1016/j.dsr.2011.09.004

Holland, K., Brill, R., & Chang, R.K.C. (1990). Horizontal and vertical movements of Pacific blue marlin tagged and released using sportfishing gear. *Fishery Bulletin U.S., 88*, 397–402.

Holland, K.N., & Grubbs, R.D. (2007). Fish visitors to seamounts: Tunas and billfish at seamounts. In T.J. Pitcher, T. Morato, P.J.B. Hart, M.R. Clark, N. Haggan, & R.S. Santos (Eds.). *Seamounts: Ecology, Fisheries & Conservation*. Blackwell Publishing Ltd, Oxford, UK. pp. 198–201.

Holland, K.N., & Sibert, J.R. (1994). Physiological thermoregulation in bigeye tuna, *Thunnus obesus*. *Environmental Biology of Fishes, 40*, 319–327. https://doi.org/10.1007/BF00002520

Hopper, C.N. (1990). Patterns of Pacific blue marlin reproduction in Hawaiian waters. In R.H. Stroud (Ed.). *Planning the Future of Billfishes*. National Coalition for Marine Conservation Inc., Savannah, GA. pp. 29–40.

Hoolihan, J.P. (2005). Horizontal and vertical movements of sailfish (*Istiophorus platypterus*) in the Arabian Gulf, determined by ultrasonic and pop–up satellite tagging. *Marine Biology, 146*, 1015–1029. https://doi.org/10.1007/s00227-004-1488-2

Horodysky, A.Z., Brill, R.W., & Cooke, S.J. (2015). Physiology in the service of fisheries science: why thinking mechanistically matters. *Reviews in Fish Biology and Fisheries, 25*, 425–447. https://doi.org/10.1007/s11160-015-9393-y

Horodysky, A.J., Cooke, S.J., Graves, J.E., & Brill, R.W. (2016). Fisheries conservation on the high seas: linking conservation physiology and fisheries ecology for the management of pelagic fishes. *Conservation Physiology, 4*, 1–18. https://doi.org/10.1093/conphys/cov059

Horodysky, A.Z., Kerstetter, D.W., Latour, R.J., & Graves, J.E. (2007). Habitat utilization and vertical movements of white marlin (*Tetrapturus albidus*) released from commercial and recreational fishing gears in the western North Atlantic Ocean: inferences from short duration pop–up archival satellite

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tags. *Fisheries Oceanography, 16*, 240–256. https://doi.org/10.1111/j.1365-2419.2007.00419.x

Hulson, P.J.F., Quinn, T.J., Hanselman, D.H., & Ianelli, J.N. (2013). Spatial modeling of Bering Sea walleye pollock with integrated age–structured assessment models in a changing environment. *Canadian Journal of Fisheries and Aquatic Sciences, 70*, 1402–1416. https://doi.org/10.1139/cjfas-2013-0020

ICCAT. (2016). ICCAT Manual. International Commission for the Conservation of Atlantic Tuna. Available at: https://www.iccat.int/en/iccatmanual.html (Accessed: 19/12/2017).

IUCN. (2011). *Thunnus maccoyii, Katsuwonus pelamis, Thunnus alalunga, Thunnus obesus, Thunnus thynnus, Thunnus albacares, Thunnus atlanticus, Thunnus tonggol* spatial data, Version 2016-2. The IUCN Red List of Threatened Species. https://www.iucnredlist.org/

IUCN. (2014). *Thunnus orientalis* spatial data, Version 2016-2. The IUCN Red List of Threatened Species. https://www.iucnredlist.org/

Ilyina, T., Six, K.D., Segschneider, J., Maier–Reimer, E., Li, H., & Núñez–Riboni, I. (2013). Global ocean biogeochemistry model HAMOCC: Model architecture and performance as component of the MPI–Earth system model in different CMIP5 experimental realizations. *Journal of Advances in Modeling Earth Systems, 5*, 287–315. https://doi.org/10.1029/2012MS000178

Ito, T., Minobe, S., Long, M.C., & Deutsch, C. (2017). Upper ocean O_2 trends: 1958–2015. *Geophysical Research Letters, 44*, 4214–4223. https://doi.org/10.1002/2017GL073613

Jones, C.D., Hughes, J.K., Bellouin, N., Hardiman, S.C., Jones, G.S., Knight, J., … Zerroukat, M. (2011). The HadGEM2–ES implementation of CMIP5 centennial simulations. *Geoscientific Model Development, 4*, 543–570. https://doi.org/10.5194/gmd-4-543-2011

Jones, D.R., Brill, R.W., & Mense, D.C. (1986). The influence of blood gas properties on gas tensions and pH of ventral and dorsal aortic blood in free–swimming tuna, *Euthynnus affinis*. *Journal of Experimental Biology, 120*, 201–213.

Jones, M.C., Dye, S.R., Pinnegar, J.K., Warren, R., & Cheung, W.W.L. (2015). Using scenarios to project the changing probability of fisheries under climate change. *Fish and Fisheries, 16*, 603–622. https://doi.org/10.1111/faf.12081

Josse, E., Bach, P., & Dagorn, L. (1998). Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologicia, 371*, 61–69. https://doi.org/10.1023/A:1017065709190

Joseph, J., Klawe, W., & Murphy, P. (1980). Tuna and Billfish — fish without a country. Inter–American Tropical Tuna Commission, La Jolla, California.

Keeling, R.F., Körtzinger, A., & Gruber, N. (2010). Ocean Deoxygenation in a warming world. *Annual Review of Marine Science, 2*, 199–229. https://doi.org/10.1146/annurev.marine.010908.163855

Killen, S.S., Glazier, D.S., Rezende, E.L., Clark, T.D., Atkinson, D., Willener, A.S.T., & Halsey, L.G. (2016). Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. *The American Naturalist, 187*, 592–606. https://doi.org/10.1086/685893

King, J.E., & Ikehara, I.I. (1956). Comparative study of food of bigeye and yellowfin tuna in the central Pacific. *Fishery Bulletin US, 57*, 61–85.

Kitagawa, T., Kimura, S., Nakata, H., & Yamada, H. (2004). Diving behavior of immature, feeding Pacific bluefin tuna (*Thunnus thynnus orientalis*) in relation to season and area: the East China Sea and the Kuroshio–Oyashio transition region. *Fisheries Oceanography, 13*, 161–180. https://doi.org/10.1111/j.1365-2419.2004.00282.x

Kitagawa, T., Boustany, A.M., Farwell, C.J., Williams, T.D., Castleton, M.R., & Block, B.A. (2007a). Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus orientalis*) in relation to seasons and oceanographic conditions in the eastern Pacific Ocean. *Fisheries Oceanography, 16*, 409–421. https://doi.org/10.1111/j.1365-2419.2007.00441.x

Kitagawa, T., Kimura, S., Nakata, H., & Yamada, H. (2007b). Why do young Pacific bluefin tuna repeatedly dive to depths through the thermocline? *Fisheries Science, 73*, 98–106. https://doi.org/10.1111/j.1444-2906.2007.01307.x

Kitagawa, T., & Kimura, S. (2015). *Biology and ecology of bluefin tuna*. CRC Press, London. https://doi.org/10.1201/b18714

Komoroske, L.M., & Lewison, R.L. (2015). Addressing fisheries bycatch in a changing world. *Frontiers in Marine Science, 2*, 83. https://doi.org/10.3389/fmars.2015.00083

Kornilova, G.N. (1981). Feeding of yellowfin tuna, *Thunnus albacares*, bigeye tuna, *Thunnus obesus*, in the equatorial zone of the Indian Ocean. *Journal of Ichthyology, 20*, 111–119.

Korsmeyer, K., & Dewar, H. (2001). Tuna metabolism and energetics. In B.A. Block, & E.D. Stevens (Eds.). *Fish Physiology, Volume 19, Tuna — Physiology, Ecology and Evolution.* Academic Press, San Diego. pp. 35–78. https://doi.org/10.1016/S1546-5098(01)19003-5

Korsmeyer, K.E., Lai, N.C., Shadwick, R.E., & Graham, J.B. (1997a). Heart rate and stroke volume contributions to cardiac output in swimming yellowfin tuna: Response to exercise and temperature. *Journal of Experimental Biology, 200*, 1975–1986.

Korsmeyer, K.E., Lai, N.C., Shadwick, R.E., & Graham, J.B. (1997b). Oxygen transport and cardiovascular responses to exercise in the yellowfin tuna *Thunnus albacares*. *Journal of Experimental Biology, 200*, 1987–1997.

Koslow, J.A., Goericke, R., Lara–Lopez, A., & Watson, W. (2011). Impact of declining intermediate–water oxygen on deepwater fishes in the California Current. *Marine Ecology Progress Series, 436*, 207–218. https://doi.org/10.3354/meps09270

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

Lehodey, P., Andre, J.M., Bertignac, M., Hampton, J., Stoens, A., Menkès, C., … Grima, N. (1998). Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical bio-geochemical model. *Fisheries Oceanography, 7*, 317–325. https://doi.org/10.1046/j.1365-2419.1998.00063.x

Lehodey, P., Chai, F., & Hampton, J. (2003). Modelling climate-related variability of tuna populations from a coupled ocean–biogeochemical-populations dynamics model.

Fisheries Oceanography, *12*, 483–494. https://doi.org/10.1046/j.1365-2419.2003.00244.x

Lehodey, P., Hampton, J., Brill, R.W., Nicol, S., Senina, I., Calmettes, B., … Sibert, J. (2011). Vulnerability of oceanic fisheries in the tropical Pacific to climate change. In J. Bell, J.E. Johnson, & A.J. Hobday (Eds.). *Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change*. Secretariat of the Pacific Community. Noumea, New Caledonia, pp. 447–506.

Lehodey, P., Senina, I., Sibert, J., Bopp, L., Calmettes, B., Hampton, J., & Murtugudde, R. (2010). Preliminary forecasts of Pacific bigeye tuna population trends under the A2 IPCC scenario. *Progress in Oceanography*, *86*, 302–315. https://doi.org/10.1016/j.pocean.2010.04.021

Lehodey, P., Senina, I., Calmettes, B., Hampton, J., & Nicol, S. (2013). Modelling the impact of climate change on Pacific skipjack tuna population and fisheries. *Climatic Change, 119*, 95–109. https://doi.org/10.1007/s10584-012-0595-1

Lehodey, P., Senina, I., Nicol, S., & Hampton, J. (2015). Modelling the impact of climate change on South Pacific albacore tuna. *Deep Sea Research Part II: Topical Studies in Oceanography*, *113*, 246–259. https://doi.org/10.1016/j.dsr2.2014.10.028

Lennert–Cody, C.E., Roberts, J.J., & Stephenson, R.J. (2008). Effects of gear characteristics on the presence of bigeye tuna (*Thunnus obesus*) in the catches of the purse–seine fishery of the eastern Pacific Ocean. *ICES Journal of Marine Science*, *65*, 970–978. https://doi.org/10.1093/icesjms/fsn075

Lindsay, K., Bonan, G.B., Doney, S.C., Hoffman, F.M., Lawrence, D.M., Long, M.C., … Thornton, P.E. (2014). Preindustrial–control and twentieth–century carbon cycle experiments with the earth system model CESM1(BGC). *Journal of Climate*, *27*, 8981–9005. https://doi.org/10.1175/JCLI-D-12-00565.1

Link, J.S., Nye, J.A., & Hare, J.A. (2011). Guidelines for incorporating fish distribution shifts into a fisheries management context. *Fish and Fisheries, 12*, 461–469. https://doi.org/10.1111/j.1467-2979.2010.00398.x

Locarnini, R.A., Mishonov, A.V., Antonov, J.I., Boyer, T.P., Garcia, H.E., Baranova, O.K., … Seidov, D. (2013). World Ocean Atlas 2013, Volume 1: Temperature. S Levitus (Ed.), A Mishonov (Technical Ed.). NOAA Atlas NESDIS 73, 40 pp.

Longhurst, A.R. (1976). Vertical migration. In *The Ecology of the Seas*. Blackwell, London, pp. 116–137.

Lowe, T., Brill, R., & Cousins, K. (2000). Blood oxygen-binding characteristics of bigeye tuna (*Thunnus obesus*), a high-energy-demand teleost that is tolerant of low ambient oxygen. *Marine Biology, 136*, 1087–1098. https://doi.org/10.1007/s002270000255

Lynch, P.D., Shertzer, K.W., & Latour, R.J. (2012). Performance of methods used to estimate indices of abundance for highly migratory species. *Fisheries Research, 125*, 27–39. https://doi.org/10.1016/j.fishres.2012.02.005

Mandic, M., Todgham, A.E., & Richards, J.G. (2009). Mechanisms and evolution of hypoxia tolerance in fish. *Proceedings of the Royal Society B Biological Sciences, 276*, 735–744. https://doi.org/10.1098/rspb.2008.1235

Marchal, E., & Lebourges, A. (1996). Acoustic evidence for unusual diel behaviour of a mesopelagic fish (*Vinciguerria nimbaria*)

exploited by tuna. *ICES Journal of Marine Science*, *53*, 443–447. https://doi.org/10.1006/jmsc.1996.0062

Marchal, E., Gerlotto, F., & Stequert, B. (1993). On the relationship between scattering layer, thermal structure and tuna abundance in the Eastern Atlantic equatorial current system. *Oceanologia Acta, 16*, 261–272.

McKenzie, D.J., Axelsson, M., Chabot, D., Claireaux, G., Cooke, S.J., Corner, R.A., … Metcalfe, J.D. (2016). Conservation physiology of marine fishes: state of the art and prospects for policy. *Conservation Physiology, 4*, 1–20. https://doi.org/10.1093/conphys/cow046

Methot, R.D., & Wetzel, C.R. (2013). Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research, 142*, 86–99. https://doi.org/10.1016/j.fishres.2012.10.012

Mislan, K.A.S., Dunne, J.B., & Sarmiento, J.L. (2016). The fundamental niche of blood–oxygen binding in the pelagic ocean. *Oikos, 125*, 938–949. https://doi.org/10.1111/oik.02650

Mislan, K.A.S., Deutsch, C.A., Brill, R.W., Dunne, J.B., & Sarmiento, K.L. (2017). Projections of climate–driven changes in tuna vertical habitat based on species–specific differences in blood oxygen affinity. *Global Change Biology, 23*, 4019–4028. https://doi.org/10.1111/gcb.13799

Miyake, M.P., Guillotreau, P., Sun, C., & Ishimura, G. (2010). Recent developments in the tuna industry: stocks, fisheries, management, processing, trade and markets. FAO Fisheries and Aquaculture Technical Paper 543, 125 pp.

Muhling, B.A., Brill, R.W., Lamkin, J.T., Roffer, M.A., Lee, S.–K., Liu, Y., & Muller–Karger, F. (2017). Projections of future habitat use by Atlantic bluefin tuna: mechanistic versus correlative distribution models. *ICES Journal of Marine Science, 74*, 698–716. https://doi.org/10.1093/icesjms/fsw215

Muhling, B.A., Lamkin, J.T., Alemany, F., García, A., Farley, J., Ingram, G.W. Jr., … Carrion, R.L. (2017). Reproduction and larval biology in tunas, and the importance of restricted area spawning grounds. *Reviews in Fish Biology and Fisheries, 27*, 697–732. https://doi.org/10.1007/s11160-017-9471-4

Muhling, B.A., Liu, Y., Lee, S.–K., Lamkin, J.T., Roffer, M.A., Muller–Karger, F., & Walter, J.F. III. (2015). Potential impact of climate change on the Intra–Americas Sea: Part 2. Implications for Atlantic bluefin tuna and skipjack tuna adult and larval habitats. *Journal of Marine Systems, 146*, 1–13. https://doi.org/10.1016/j.jmarsys.2015.01.010

Murua, H., Rodriguez–Marin, E., Neilson, J.D., Farley, J.H., & Juan–Jord, M.J. (2017). Fast versus slow growing tuna species: age, growth, and implications for population dynamics and fisheries management. *Reviews in Fish Biology and Fisheries, 27*, 733–773. https://doi.org/10.1007/s11160-017-9474-1

Murphy, T.C., & Sakagawa, G.T.A. (1977). Review and evaluation of estimates of natural mortality rates in tunas. *International Commission for the Conservation of Atlantic Tunas, Collected Volume of Scientific Papers, 6*, 117–123.

Musyl, M.K., Brill, R.W., Boggs, C.H., Curran, D.S., Kazama, T.K., & Seki, M.P. (2003). Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts of the Hawaiian Archipelago from archival tagging

data. *Fisheries Oceanography, 12*, 152–169. https://doi.org/10.1046/j.1365-2419.2003.00229.x

Nakamura, Y. (1993). Vertical and horizontal movements of mature females of *Ommastrephes bartramii* observed by ultrasonic telemetry. In T. Okutani, R.K. O'Dor, & T. Kubodera (Eds.). *Recent Advances in Fisheries Biology*. Tokai University Press, Tokyo, pp. 331–336.

Nakano, H., Okazaki, M., & Okamoto, H. (1997). Analysis of catch depth by species for tuna longline fishery based on catch by branch lines. *Bulletin of the Natural Resources Institute of the Far Seas Fisheries, 34*, 43–62.

Nikolic, N., Morandeau, G., Hoarau, L., West, W., Arrizabalaga, A., Hoyle, A., … Fonteneau, A. (2017). Review of albacore tuna, *Thunnus alalunga*, biology, fisheries and management. *Reviews in Fish Biology and Fisheries, 27*, 775–810. https://doi.org/10.1007/s11160-016-9453-y

Ommer, R.E., Jarre, A.C., Perry, R.I., Barange, M., Cochrane, K., & Moloney, C. (2009). Human dimensions of the fisheries under global change. In D. Checkley, J. Alheit, Y. Oozeki, & C. Roy (Eds.). *Climate Change and Small Pelagic Fish*. Cambridge University Press. pp. 275–284. https://doi.org/10.1017/CBO9780511596681.013

Palmer, J.R., & Totterdell, I.J. (2001). Production and export in a global ocean ecosystem model. *Deep Sea Research Part I: Oceanographic Research Papers, 48*, 1169–1198. https://doi.org/10.1016/S0967-0637(00)00080-7

Patterson, T.P., Evans, K., Carter, T.I., & Gunn, J.S. (2008). Movement and behaviour of large southern bluefin tuna (*Thunnus maccoyii*) in the Australian region determined using pop–up satellite archival tags. *Fisheries Oceanography, 17*, 352–367. https://doi.org/10.1111/j.1365-2419.2008.00483.x

Peck, M.A., Arvanitidis, C., Butenschön, M., Canu, D.M., Chatzinikolaou, E., Cucco, A., … van de Wolfshaar, K.E. (2016). Projecting changes in the distribution and productivity of living marine resources: a critical review of the suite of modelling approaches used in the large European project VECTORS. *Estuarine, Coastal and Shelf Science, 201*, 40-55. https://doi.org/10.1016/j.ecss.2016.05.019

Pelczarski, W. (1988). Examination of food of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) from the open waters of the central Atlantic. *Collective Scientific Papers ICCAT, 28*, SCRS 87/55, 58–73.

Pepperell, J.G., & Davis, T.L.O. (1999). Post–release behaviour of black marlin, *Makaira indica*, caught off the Great Barrier Reef with sportfishing gear. *Marine Biology, 135*, 369–380. https://doi.org/10.1007/s002270050636

Pinsky, M.L., & Fogarty, M. (2012). Lagged social–ecological responses to climate and range shifts in fisheries. *Climatic Change, 115*, 883–891. https://doi.org/10.1007/s10584-012-0599-x

Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L., & Levin, S.A. (2013). Marine taxa track local climate velocities. *Science, 341*, 1239–1242. https://doi.org/10.1126/science.1239352

Pohlot, B.G., & Ehrhardt, N. (2018). An analysis of sailfish daily activity in the Eastern Pacific Ocean using satellite tagging and recreational fisheries data. *ICES Journal of Marine Science, 75*, 871-879. https://doi.org/10.1093/icesjms/fsx082

Polovina, J.J., Howell, E., Kobayashi, D.R., & Seki, M.P. (2001). The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography, 49*, 469–483. https://doi.org/10.1016/S0079-6611(01)00036-2

Potier, M., Marsac, F., Cherel, Y., & Lucas, V. (2007). Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. *Fisheries Research, 83*, 60–72. https://doi.org/10.1016/j.fishres.2006.08.020

Potier, M., Marsac, F., Lucas, V., Sabatié, R., Hallier, J.–P., & Ménard, F. (2004). Feeding partitioning among tuna taken in surface and mid–water layers: the case of yellowfin (*Thunnus albacares*) and bigeye tuna (*T. obesus*) in the western tropical Indian Ocean. *Journal of Marine Science, 3*, 51–62.

Prince, E.D., & Goodyear, C.P. (2006). Hypoxia–based habitat compression of tropical pelagic fishes. *Fisheries Oceanography, 15*, 451–464. https://doi.org/10.1111/j.1365-2419.2005.00393.x

Prince, E.D., & Goodyear, C.P. (2007). Consequences of ocean scale hypoxia constrained habitat for tropical pelagic fishes. *Gulf and Caribbean Research, 19*, 17–20. https://doi.org/10.18785/gcr.1902.04

Prince, E.D., Luo, J., Goodyear, C.P., Hoolihan, J.P., Snodgrass, D., Orbesen, E.S., … Schirripa, M.J. (2010). Ocean scale hypoxia–based habitat compression of Atlantic istiophorid billfishes. *Fisheries Oceanography, 19*, 448–462. https://doi.org/10.1111/j.1365-2419.2010.00556.x

Prince, E.D., & Pulos, L.M. (1983). Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks. NOAA Technical Report NMFS 8, Southeast Fisheries Center, Miami Laboratory National Marine Fisheries Service, NOAA Miami, Florida.

Roger, C.R., & Grandperrin, R. (1976). Pelagic food webs in the tropical Pacific. *Limnology and Oceanography, 21*, 731–735. https://doi.org/10.4319/lo.1976.21.5.0731

Rossi–Fanellai, A., & Antoninie, E. (1960). Oxygen equilibrium of hemoglobin from *Thunnus thynnus. Nature, 186*, 895–896. https://doi.org/10.1038/186895a0

Safina, C. (2001). Tuna conservation. In B.A. Block & E.D. Stevens (Eds.). *Fish Physiology, Volume 19, Tuna — Physiology, Ecology and Evolution.* Academic Press, San Diego. pp. 413–459. https://doi.org/10.1016/S1546-5098(01)19012-6

Sanders, N.K., & Childress, J.J. (1990). Adaptations of the deep–sea oxygen minimum layer: Oxygen binding by the hemocyanin of the bathypelagic mysid *Gnathopsausia ingens* Dohrn. *Biological Bulletin, 178*, 286–294. https://doi.org/10.2307/1541830

Schaefer, K.M. (2001). Reproductive biology of tunas. In B.A. Block & E.D. Stevens (Eds.). *Fish Physiology, Volume 19, Tuna — Physiology, Ecology and Evolution*. Academic Press, San Diego. pp. 225–271. https://doi.org/10.1016/S1546-5098(01)19007-2

Schaefer, K.M., & Fuller, D.W. (2002). Movements, behavior, and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags. *Fishery Bulletin, 100*, 765–788.

Schaefer, K.M., & Fuller, D.W. (2007). Vertical movement patterns of skipjack tuna (*Katsuwonus pelamis*) in the eastern equatorial

Pacific Ocean, as revealed with archival tags. *Fishery Bulletin, 105*, 379–389.

Schaefer, K.M., & Fuller, D.W. (2010). Vertical movements, behavior, and habitat of bigeye tuna (*Thunnus obesus*) in the equatorial eastern Pacific Ocean, ascertained from archival tag data. *Marine Biology, 157*, 2625–2642. https://doi.org/10.1007/s00227-010-1524-3

Schaefer, K.M., Fuller, D.W., & Aldana, G. (2014). Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in waters surrounding the Revillagigedo Islands Archipelago Biosphere Reserve, Mexico. *Fisheries Oceanography, 23*, 65–82. https://doi.org/10.1111/fog.12047

Schaefer, K.M., Fuller, D.W., & Block, B.A. (2007). Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. *Marine Biology, 152*, 503–525. https://doi.org/10.1007/s00227-007-0689-x

Schaefer, K.M., Fuller, D.W., & Block, B.A. (2009a). Vertical movements and habitat utilization of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), and bigeye (*Thunnus obesus*) tunas in the equatorial eastern pacific ocean, ascertained through archival tag data. In J.L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage, & J. Sibert (Eds.). *Tagging and Tracking of Marine Animals with Electronic Devices, Reviews: Methods and Technologies in Fish Biology and Fisheries* Springer Science + Business Media B.V. pp. 121–144. https://doi.org/10.1007/978-1-4020-9640-2_8

Schaefer, K.M., Fuller, D.W., & Block, B.A. (2009b). Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the Pacific Ocean off Baja California, Mexico, determined from archival tag data analyses, including unscented Kalman filtering. *Fisheries Research, 112*, 22–37. https://doi.org/10.1016/j.fishres.2011.08.006

Schmidtko, S., Stramma, L., & Visbeck, M. (2017). Decline in global oceanic oxygen content during the past five decades. *Nature, 542*, 335–339. https://doi.org/10.1038/nature21399

Sepulveda, C.A., Knight, A., Nasby–Lucas, N., & Domeier, M.L. (2010). Fine–scale movements of the swordfish *Xiphias gladius* in the Southern California Bight. *Fisheries Oceanography, 19*, 279–289. https://doi.org/10.1111/j.1365-2419.2010.00543.x

Seibel, B.A. (2011). Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *Journal of Experimental Biology, 214*, 326–336. https://doi.org/10.1242/jeb.049171

Seibel, B.A. (2013). The jumbo squid, *Dosidicus gigas* (Ommastrephidae), living in oxygen minimum zones. II. Blood–oxygen binding. *Deep Sea Research Part II: Topical Studies in Oceanography, 95*, 139–144. https://doi.org/10.1016/j.dsr2.2012.10.003

Sharp, G.D. (1975). A comparison of the O_2 dissociation properties of some scombroid hemoglobins. *Comparative Physiology and Biochemistr*y, *52A*, 683–691. https://doi.org/10.1016/0300-9629(75)90357-6

Sharp, G.D. (1978). Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. In G.D. Sharp & A.E. Dizon (Eds.). *The Physiological Ecology of Tunas*. Academic Press, New York pp. 397–449. https://doi.org/10.1016/B978-0-12-639180-0.50032-X

Sharp, G.D. (1983). Trends in respiratory work and ecological position in the marine ecosystems. *Comparative Biochemistry and Physiology, 76A*, 405–511. https://doi.org/10.1016/0300-9629(83)90440-1

Sharp, G.D. (1995). It's about time: new beginnings and old good ideas in fisheries science. *Fisheries Oceanography, 4*, 324–341. https://doi.org/10.1111/j.1365-2419.1995.tb00077.x

Sharp, G.D. (2001). Tuna oceanography – an applied science. In B.A. Block & E.D. Stevens (Eds.). *Fish Physiology, Volume 19, Tuna — Physiology, Ecology and Evolution*. Academic Press, San Diego. pp. 345–380. https://doi.org/10.1016/S1546-5098(01)19010-2

Shiels, H.A., Freund, E.V., Farrell, A.P., & Block, B.A. (1999). The sarcoplasmic reticulum plays a major role in isometric contraction in atrial muscle of yellowfin tuna. *Journal of Experimental Biology, 202*, 881–890.

Shiels, H.A., Galli, G.L.J., & Block, B.A. (2015). Cardiac function in an endothermic fish: cellular mechanisms for overcoming acute thermal challenges during diving. *Proceedings of the Royal Society B Biological Sciences, 282*, 20141989. https://doi.org/10.1098/rspb.2014.1989

Sibert, J., Hampton, J., Kleiber, P., & Maunder, M. (2006). Biomass, size, and tropic status of top predators in the Pacific Ocean. *Science, 314*, 1773–1776. https://doi.org/10.1126/science.1135347

Stock, C.A., Alexander, M.A., Bond, N.A., Brander, K.M., Cheung, W.W., Curchitser, E.N., … Werner, F.E. (2011). On the use of IPCC–class models to assess the impact of climate on living marine resources. *Progress in Oceanography, 88*, 1–27. https://doi.org/10.1016/j.pocean.2010.09.001

Stoffels, R.J. (2015). Physiological trade–offs along a fast–slow lifestyle continuum in fishes: what do they tell us about resistance and resilience to hypoxia? *PLoS ONE, 10*, e0130303. https://doi.org/10.1371/journal.pone.0130303

Stramma, L., Schmidtko, S., Levin, L.A., & Johnson, J.C. (2010a). Ocean oxygen minima expansions and their biological impacts. *Deep Sea Research Part I: Oceanographic Research Papers,* 57, 587–595. https://doi.org/10.1016/j.dsr.2010.01.005

Stramma, L., Johnson, G.C., Firing, E., & Schmidtko, S. (2010b). Eastern Pacific oxygen minimum zones: Supply paths and multidecadal changes. *Journal of Geophysical Research, 115*, C09011. https://doi.org/10.1029/2009JC005976

Stramma, L., Johnson, G.C., Sprintall, J., & Mohrholz, V. (2008). Expanding oxygen–minimum zones in the tropical oceans. *Science, 320*, 655–658. https://doi.org/10.1126/science.1153847

Stramma, L., Schmidtko, S., Levin, L.A., & Johnson, G.C. (2012). Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nature Climate Change, 2*, 33–37. https://doi.org/10.1038/nclimate1304

Stevens, E.D. (1972). Some aspects of gas exchange in tunas. *Journal of Experimental Biology, 56*, 809–823.

Stevens, E.D. (1982). The effect of temperature on facilitated oxygen diffusion and its relation to warm tuna muscle. *Canadian Journal of Zoology, 60*, 1148–I152. https://doi.org/10.1139/z82-160

Stevens, E.D., & Carey, F.G. (1981). One why of the warmth of warm–bodied fish. *American Journal of Physiology, 240*, RI51–R155. https://doi.org/10.1152/ajpregu.1981.240.3.R151

SECTION 8.2

Stevens, E.D., & Fry, F.E.J. (1972). The effect of changes in ambient temperature on spontaneous activity in skipjack tuna. *Comparative Biochemistry and Physiology, 42*, 803–805. https://doi.org/10.1016/0300-9629(72)90457-4

Sumaila, U.R., Zeller, D., Watson, R., Alder, J., & Pauly, D. (2007). Potential costs and benefits of marine reserves in the high seas. *Marine Ecology Progress Series, 345*, 305–310. https://doi.org/10.3354/meps07065

Sund, P., Blackburn, M., & Williams, F. (1981). Tunas and their environments in the Pacific Ocean: A review. *Oceanography and Marine Biology Annual Review, 19*, 443–512.

Takahashi, M., Okamura, H., Yokawa, K., & Okazaki, M. (2003). Swimming behaviour and migration of a swordfish recorded by an archival tag. *Marine and Freshwater Research*, *54*, 527–534. https://doi.org/10.1071/MF01245

Taylor, K.E., Stouffer, R.J., & Meehl, G.A. (2012). An overview of the CMIP5 and the experiment design. *Bulletin of the American Meteorological Society, 93*, 485–498. https://doi.org/10.1175/BAMS-D-11-00094.1

Teo, S.L.H., & Boustany, A.M. (2016). Movements and habitat use of Atlantic bluefin tuna. In T. Kitahawa & S. Kimura (Eds.). *Biology and Ecology of Bluefin Tuna*. CRC Press, Boca Raton, Florida. pp. 137–188. https://doi.org/10.1201/b18714-11

Teo, S.H.L., Boustany, A., Dewar, H., Stokesbury, M.J.W., Weng, K.C., Beemer, S., … Block, B.A. (2007). Annual migrations, diving behavior, and thermal biology of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. *Marine Biology, 151*, 1–18. https://doi.org/10.1007/s00227-006-0447-5

Ward, P., & Hindmarsh, S. (2007). An overview of historical changes in the fishing gear and practices of pelagic longliners, with particular reference to Japan's Pacific fleet. *Reviews in Fish Biology and Fisheries, 17*, 501–516. https://doi.org/10.1007/s11160-007-9051-0

Ward, P., & Myers, R.A. (2005). Inferring the depth distribution of catchability for pelagic fishes and correcting for variations in the depth of longline fishing gear. *Canadian Journal of Fisheries and Aquatic Sciences, 62*, 1130–1142. https://doi.org/10.1139/f05-021

Watters, G.M.W., Olson, R.J., Francis, R.C., Fiedler, P.C., Polovina, J.J., Reilly, S.B., … Kitchell, J.F. (2003). Physical forcing and the dynamics of the pelagic ecosystem in the eastern tropical Pacific: simulations with ENSO–scale and global–warming climate drivers. *Canadian Journal of Fisheries and Aquatic Sciences, 60*, 1161–1175. https://doi.org/10.1139/f03-100

Wegner, N.C., Sepulveda, C.A., Aalbers, S.A., & Graham, J.B. (2013). Structural adaptations for ram ventilation: gill fusions in Scombrids and billfishes. *Journal of Morphology, 274*, 108–120. https://doi.org/10.1002/jmor.20082

Wells, R.M.G. (2009). Blood–gas transport and hemoglobin function. In J.G. Richards, A.P. Farrell, & C.J. Brauner (Eds.). *Fish Physiology Volume 27, Hypoxia*. Elsevier, London pp. 255–299. https://doi.org/10.1016/S1546-5098(08)00006-X

Westberry, T., Behrenfeld, M.J., Siegel, D.A., & Boss, E. (2008). Carbon–based primary productivity modeling with vertically resolved photoacclimation. *Global Biogeochemical Cycles, 22*, GB2024. https://doi.org/10.1029/2007GB003078

Wilberg, M.J., Thorson, J.T., Linton, B.C., & Berkson, J. (2010). Incorporating time–varying catchability into population dynamic stock assessment models. *Reviews in Fisheries Science, 18*, 7–24. https://doi.org/10.1080/10641260903294647

Wild, A. (1986). Growth of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean based on otolith increments. *Inter–American Tropical Tuna Commission Bulletin, 18*, 421–482.

Williams, P., & Terawasi, P. (2011). Overview of tuna fisheries in the western and central Pacific Ocean, including economic conditions–2010. Western & Central Pacific Fisheries Commission. WCPFC–SC7–2011/GN WP–1. Available at: https://www.wcpfc.int/node/2810

Williams, A.J., Allain, V., Nicol, S.J., Evans, K.J., Hoyle, S.D., Dupoux, C., … Dubosc, J. (2015). Vertical behavior and diet of albacore tuna (*Thunnus alalunga*) vary with latitude in the South Pacific Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography, 113*, 154–169. https://doi.org/10.1016/j.dsr2.2014.03.010

Wilson, S.G., Lutcavage, M.E., Brill, R.W., Genovese, M.P., Cooper, A.B., & Everly, A.W. (2005). Movements of bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic Ocean recorded by pop-up satellite archival tags. *Marine Biology, 146*, 409-423. https://doi.org/10.1007/s00227-004-1445-0

Wilson, S.G., Jonsen, I.D., Schallert, R.J., Ganong, J.E., Castleton, M.R., Spares, A.D., … Block, B.A. (2015). Tracking the fidelity of Atlantic bluefin tuna released in Canadian waters to the Gulf of Mexico spawning grounds. *Canadian Journal of Fisheries and Aquatic Sciences, 72*, 1700–1717. https://doi.org/10.1139/cjfas-2015-0110

Xu, Y., Nieto, K., Teo, S.L., McClatchie, S., & Holmes, J. (2015). Influence of fronts on the spatial distribution of albacore tuna (*Thunnus alalunga*) in the Northeast Pacific over the past 30 years (1982–2011). *Progress in Oceanography, 150*, 72-78. https://doi.org/10.1016/j.pocean.2015.04.013

Yang, T.H., Lai, N.C., Graham, J.B., & Somero, G.N. (1992). Respiratory, blood, and heart enzymatic adaptations of *Sebastolobus alascanus* (Scorpaenidae; Teleostei) to the oxygen minimum zone: A comparative study. *Biological Bulletin*, *183*, 490–499. https://doi.org/10.2307/1542026

Yatsu, A., Yamanaka, K., & Yamashiro, C. (1999). Tracking experiments of the jumbo flying squid, *Dosidicus gigas*, with an ultrasonic telemetry system in the Eastern Pacific Ocean. *Oceanographic Bulletin of the National Research Institute Far Seas Fisheries, 36*, 55–60.