Sharing the water column: physiological mechanisms underlying species-specific habitat use in tunas

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Sharing the water column: Physiological mechanisms underlying species-specific habitat use in tunas --Manuscript Draft--

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Abstract:	<p>Tuna species support some of the world's largest commercial and recreational fisheries. Their extensive migratory patterns expose them to multiple national and international fisheries and fishery management regimes. Several prized species have become the focus of global conservation efforts and there is a growing worldwide interest in establishing optimal strategies for sustainable tuna fisheries. Although this task has proven to be very challenging, it has taken on a new sense of urgency in the face of the potential effects of global climate change. A better understanding of the interactions between environmental conditions and tuna physiology and how they affect tuna behavior will offer population and stock assessment modelers and fisheries biologists a more mechanistic understanding of tuna distribution patterns and may help predict changes in both geographic and depth-related movement patterns. Indeed, physiological data comprise a growing component of multi-trait analysis approaches to species conservation. Our review aims to summarize what is known about differences among tuna species in distribution patterns, tolerances to environmental conditions, and physiological characteristics that correlate with the capacity to inhabit cooler (deeper, higher latitude) and even hypoxic waters. To achieve this goal, we discuss how these physiological traits are associated with habitat partitioning within the three-dimensional oceanic environment and with niche expansion into cooler and hypoxic waters. We also point out areas where additional research is needed to predict more accurately how future changes in oceanographic conditions will affect the distributions and movement patterns of tunas and their availability to fisheries.</p>	
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- 1 **Sharing the water column: Physiological mechanisms underlying species-specific habitat**
- 2 **use in tunas**
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Abstract

Tuna species support some of the world's largest commercial and recreational fisheries. Their extensive migratory patterns expose them to multiple national and international fisheries and fishery management regimes. Several prized species have become the focus of global conservation efforts and there is a growing worldwide interest in establishing optimal strategies for sustainable tuna fisheries. Although this task has proven to be very challenging, it has taken on a new sense of urgency in the face of the potential effects of global climate change. A better understanding of the interactions between environmental conditions and tuna physiology and how they affect tuna behavior will offer population and stock assessment modelers and fisheries biologists a more mechanistic understanding of tuna distribution patterns and may help predict changes in both geographic and depth-related movement patterns. Indeed, physiological data comprise a growing component of multi-trait analysis approaches to species conservation. Our review aims to summarize what is known about differences among tuna species in distribution patterns, tolerances to environmental conditions, and physiological characteristics that correlate with the capacity to inhabit cooler (deeper, higher latitude) and even hypoxic waters. To achieve this goal, we discuss how these physiological traits are associated with habitat partitioning within the three-dimensional oceanic environment and with niche expansion into cooler and hypoxic waters. We also point out areas where additional research is needed to predict more accurately how future changes in oceanographic conditions will affect the distributions and movement patterns of tunas and their availability to fisheries.

Keywords Swimming, metabolism, endothermy, hypoxia, thermoregulation, cardiac physiology, vision, digestion, movement patterns, diving

Introduction

Tuna biogeography and evolution

The 15 extant species of tunas (five genera: *Allothunnus*, *Auxis*, *Euthynnus*, *Katsuwonus*, *Thunnus*) form a monophyletic group (Tribe Thunnini) that differs morphologically and physiologically from their closest relatives, the bonitos (Tribe Sardini), within the Family Scombridae (Collette 1978; Altringham and Block 1997; Graham and Dickson 2000; Collette et al. 2001; Westneat and Wainwright 2001; Dowis et al. 2003; Sepulveda et al. 2003; Cieczarek et al. 2016) (Figure 1a). Molecular phylogenies place *Auxis*, *Euthynnus*, and *Katsuwonus* in a group separate from the most derived and speciose genus, *Thunnus* (Block et al. 1993; Chow and Kishino 1995; Chow et al. 2006; Collette et al. 2001; Orrell et al. 2006; Miya et al. 2013). Overall, tunas have wide geographic distributions, ranging from the tropics to latitudes as high as 72° North and 58° South, and are found in coastal and pelagic waters. Several tuna species are limited to warm waters ($\geq 20^{\circ}\text{C}$) and either remain within a specific tropical ocean basin (e.g., blackfin tuna, *Thunnus atlanticus*, and longtail tuna, *T. tonggol*), or are circumtropical (e.g., skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *T. albacares*). Other tunas spend considerable time in colder waters (e.g., below 18°C) as they migrate to high latitudes (e.g., Atlantic bluefin, *T. thynnus*, and southern bluefin, *T. maccoyii*) or routinely dive below the thermocline (e.g., bigeye tuna, *T. obesus*). Only one tuna species, the basal slender tuna (*Allothunnus fallai*) occurs primarily within the temperate waters of the Southern Ocean (reviewed in Collette and Nauen 1983).

While fossil evidence suggests that the Thunnini and Sardini diverged approximately 60 million years ago (mya) in the early Tertiary (Bannikov 1985; Carroll 1988; Monsch 2000), a recent molecular phylogenetic study (Miya et al. 2013) estimated the divergence time at 6-17 mya and proposed 61.6 mya as the origin of the Scombridae. Nonetheless, paleoceanographic evidence suggests that these fishes evolved in a tropical environment that progressively cooled starting at approximately 35-50 mya, resulting in increased vertical thermal stratification at lower latitudes and upwelling at higher latitudes (Berger 1981; Macdougall 1996; Lyle et al. 2008). The warm and well-oxygenated surface layer of the tropical oceans inhabited by ancestral tunas became geographically compressed, and areas of higher primary productivity developed at high latitudes. As a result, there would have been strong selective pressure for ancestral tunas to expand their distribution into more temperate environments where they would encounter high

prey densities allowing high rates of somatic and gonadal growth (i.e., increased larval survival rates and fecundity). The need to swim long distances to reach those productive foraging areas is proposed to have been a factor in the evolution of a suite of morphological and physiological characteristics that allowed tunas to migrate long distances and exploit cooler waters (reviewed by Graham and Dickson 2001; Dickson and Graham 2004). These adaptations include regional endothermy, the ability to retain metabolic heat and maintain the temperature of certain tissues (slow-oxidative locomotor muscle or red muscle, visceral organs, and eye and brain) above water temperature (reviewed in Carey et al. 1971; Block 1991; Graham and Dickson 2004). Even though some tuna species have expanded their distributions into higher latitudes or deeper waters, their reproductive biology reflects a tropical origin in that all tunas (except *Allothunnus fallai*) spawn in warm waters, with a sea surface temperature of at least 24°C (Schaefer 2001). The warm-water species spawn throughout the year, and the subtropical or temperate-water species undergo seasonal migrations to warmer waters to spawn (Schaefer 2001; Muhling et al. 2017).

Although the geographic distributions of several extant tuna species overlap, there are several lines of evidence demonstrating at least some degree of habitat partitioning. For example, Japanese longline catch data for tunas in the tropical central Pacific Ocean from the 1970s show that catches of skipjack, yellowfin, albacore (*T. alalunga*), and bigeye tunas peaked at different depths – near the surface, at depths of 125 m, 200 m, and the deepest waters fished by the longlines, respectively (Hanamoto 1987; Sharp 2001) – suggesting habitat partitioning by depth in regions where these four tuna species co-occur. Furthermore, the most recent phylogenies based on mitochondrial and nuclear DNA sequence data (Miya et al. 2013; Díaz-Arce et al. 2016; Suzuki and Chow 2016) indicate that thermal niche expansion into cooler waters may have occurred more than once among the *Thunnus* species (Figure 1a). The main focus of our review is to summarize the physiological characteristics that have allowed some tuna species to inhabit cooler waters at higher latitudes or depth, thus contributing to niche expansion or habitat partitioning within the three-dimensional oceanic environment.

Because the oceans are thermally stratified, and other environmental characteristics such as dissolved oxygen (DO) concentration, pressure, light intensity and quality, and prey abundance vary with depth, latitude, as well as seasonally, it is essential to understand the spatial and temporal movement patterns of tunas and to measure the corresponding environmental

conditions they encounter (Deary et al. 2015). In addition, the physiological tolerance limits of different tuna species must be understood mechanistically, in order to associate behavior and distribution patterns with interspecific differences in physiological capacities (Horodysky et al. 2015, 2016). Obtaining the data needed to test such associations in multiple species has been challenging because they are large, active pelagic animals with a worldwide distribution. However, over the last few decades, studies with archival tags, at shoreside facilities, and with fish maintained in at-sea floating enclosures have made it possible to begin to address such questions. Establishing relationships between environmental conditions and tuna physiology and behavior will help population and stock assessment modelers and fisheries biologists to predict distributions more accurately, even as oceanographic conditions change due to climate change (e.g., Lehodey et al. 2011; McKenzie et al. 2016), and to implement optimal strategies for sustainable tuna fisheries.

Movement patterns of tunas

Species-specific movement patterns of tunas can be inferred by analyzing latitudinal, temporal, and vertical (i.e., depth) distributions based on conventional fisheries data and acoustic or archival tagging data (e.g., Collette and Nauen 1983; Block et al. 1998; Gunn and Block 2001; Musyl et al. 2003; Bestley et al. 2009; Schaefer et al. 2009). Although the distributions of some tunas do show clear interspecific seasonal latitudinal differences (e.g., skipjack tuna versus Atlantic bluefin tuna), some species co-occur throughout the entire year (e.g., skipjack and yellowfin tunas in the eastern Pacific Ocean) or seasonally during spawning (e.g., blackfin and Atlantic bluefin tunas in the Gulf of Mexico). There are also differences in day-night depth distributions. During the nighttime, most tunas remain within the well-mixed surface layer above the thermocline, which is warm and well-oxygenated, leading to substantial overlap in their vertical distributions (e.g., Carey and Robinson 1981; Holland et al. 1990b; Schaefer and Fuller 2002; Musyl et al. 2003). In contrast, during daylight hours different tuna species may occupy different parts of the water column, with some species able to move into deeper, colder, and often hypoxic waters and others remaining in the surface layer (Figure 2). These day-night differences are most likely associated with the daily nocturnal vertical migration of the prey associated with the deep sound-scattering layer (DSL; Dagorn et al. 2000), the importance of vision during prey capture (e.g., Fritsches et al. 2003, 2005; Brill et al. 2005), and interspecific

differences in physiological tolerances for conditions at depth. For this review, we have divided tuna species into three groups based on the extent of their vertical and latitudinal movements (Bernal et al. 2009; Bernal 2011):

Vertical movement behavior Group 1 -- tunas that spend the majority of their time in the well-mixed surface layer above the thermocline

Group 1 tunas are consistently found in the upper layers of the ocean where the water column is well oxygenated and forms a thermally homogenous layer above the thermocline, with water temperatures generally above 20°C (Figures 2, 3a). The vertical movements of these species are limited by the presence of the thermocline (Figure 3c), the depth of which varies and is influenced by ocean-basin-specific oceanography. Group 1 species remain both day and night within the warm surface layer and rarely descend to waters with temperatures below 20°C. Members of the genera *Auxis* and *Euthynnus* and small yellowfin and skipjack tunas best exemplify this group (Dizon et al. 1978; Collette and Nauen 1983). Interestingly, the vertical movement behaviors of some species (e.g., skipjack and yellowfin tunas) change as they grow, with smaller individuals (< 4 kg) usually remaining within the surface layer of the ocean (i.e., Group 1) and larger individuals undertaking brief sojourns below the thermocline (i.e., Group 2; Figures 2, 3b). This size-related difference implies that these species may become more tolerant of cooler, less-well oxygenated waters as they grow larger.

Vertical movement behavior Group 2 -- tunas that undergo short excursions below the thermocline

Group 2 tunas (larger yellowfin and skipjack tunas) move from the surface layer during infrequent (one to several per day), short-duration descents to depths below the thermocline (e.g., Block et al. 1997; Schaefer et al. 2007; Schaefer and Fuller 2007) (Figures 3b, 4a). In general, Group 2 species spend the majority of the daylight hours above the thermocline, occasionally diving to or below the thermocline, and do not occur in cooler surface waters at high latitudes. The greater vertical movements exhibited by members of this group compared with Group 1 tunas expose them to a much wider thermal range (i.e., water temperatures below 10°C), lower light levels, and, in some geographic areas, hypoxic waters – but only for brief periods. In addition, some Group 2 tunas show diurnal vertical movement patterns, descending to deeper

depths during daylight hours and returning to shallower depths at night. Thus, tuna species in Group 2 tolerate wider ranges of environmental conditions than do those in Group 1.

Vertical movement behavior 3 (Group 3) -- tunas that make frequent excursions below the thermocline or migrate to high latitudes

Tuna species in Group 3 have the widest thermal and latitudinal ranges, with some frequently descending below the thermocline to temperatures as low as 5°C and others being exposed to cold waters at high latitudes for prolonged periods of time during their seasonal migrations. Members of this group include the Atlantic and southern bluefin tunas, which remain for months in cold water as a result of their long-distance migrations to high latitudes (Block et al. 2001; Gunn and Block 2001) (Figure 4b), and the slender tuna which resides permanently in cold water in the Southern Ocean (Collette and Nauen 1983). Other Group 3 species (e.g., bigeye tuna; Holland et al. 1992; Schaefer and Fuller 2010) make regular and frequent deep descents during the day (Figure 4b), with incursions into the oxygen minimum zone where water DO concentration is below 2 mg O₂ L⁻¹; these species tolerate hypoxia for extended periods. Furthermore, deep-diving species are almost continuously (day and night) exposed to low light levels. Thus, Group 3 tunas experience a much wider range of environmental conditions than do the other tuna species.

Although we can divide tunas into the above three groups based on depth distributions and vertical movement patterns, there is no evidence for absolute depth preferences in any tuna species. Instead, movement patterns appear to depend more on prey availability, reproductive migrations, and physiological capacities than on depth per se. Tunas and their prey inhabit a dynamic environment in which oceanographic conditions affect light penetration, water clarity, water temperature, deep-water mixing, nutrient availability (i.e., primary productivity), and DO concentration. Thus, changes in local or basin-wide oceanographic conditions will have a marked effect on the depth distribution of both tunas and their prey (e.g., Prince and Goodyear 2007, Prince et al. 2010; Lehodey et al. 2011; Schirripa et al. 2016; Yen and Lu 2016), and all of these factors and their interactions must be taken into account in predicting tuna behavior. Some prey species (e.g., cephalopods, crustaceans, vertically migrating fishes) move to deeper, colder waters during the daylight hours where light penetration and DO are limited, thus offering some

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4 205 refuge from predation (e.g., Drazen and Seibel 2007). Consequently, if tunas seek to exploit
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6 206 those prey during the day, they must be able to meet the metabolic demands involved in
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8 207 descending to depth, searching for prey, and recovering from any bout of burst activity
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10 208 associated with prey capture, all while being exposed to a cold and often hypoxic environment.
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12 209 Moreover, the senses that tunas rely on for prey detection (e.g., sight, smell, and hearing) must
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14 210 remain functional under cold, hypoxic, and relatively low-light conditions. Thus, the tuna species
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16 211 in Group 3, which have the greatest depth and latitudinal ranges, are expected to have
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18 212 physiological adaptations and broader tolerances associated with their ability to move into
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20 213 colder, deeper, darker, and hypoxic waters in search of prey. We therefore focus the remainder of
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22 214 our review on what is currently known about these physiological characteristics and how they
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24 215 differ interspecifically.
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26 217 **Swimming, muscle endothermy and thermoregulation**

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28 218 Tunas rely on continuous forward swimming to generate hydrodynamic lift and to pass
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30 219 water over their gills to support ram ventilation (Magnuson 1973, 1978; Magnuson and
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32 220 Weininger 1978; Alexander 1993). Relative to closely related taxa, all tunas possess
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34 221 morphological specializations that increase body streamlining and decrease drag [i.e., the slow-
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36 222 oxidative locomotor red muscle (RM) is located centrally (closer to the vertebrae) and has a
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38 223 more anterior distribution; Figure 1b, c], reducing locomotor costs (reviewed in Bernal et al.
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40 224 2001, 2009), but some features related to swimming do vary interspecifically. For example, the
41
42 225 species of the genera *Auxis*, *Euthynnus*, and *Katsuwonus*, all of which are relatively small and
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44 226 lack a swim bladder as adults (Collette 1978), have smaller total lift surface areas and higher
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46 227 minimum hydrostatic speeds compared to the members of the genus *Thunnus* (Magnuson 1978).
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48 228 The potential increased cost of generating hydrodynamic lift in those species correlates with a
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50 229 greater relative amount of RM which powers continuous swimming (Magnuson 1978; Graham et
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52 230 al. 1983; Dickson 1996; Graham and Dickson 2000). It does not appear, however, that swimming
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54 231 capacity either correlates with, or poses a limitation for, vertical or horizontal movements of
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56 232 tunas except as related to fish size.

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58 233 Interspecific differences in the pattern of blood flow to and from the RM may be related
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60 234 to the ability of some tuna species to tolerate rapid changes in water temperature during dives
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62 235 below the thermocline or to remain longer in cool, deep waters (Graham and Dickson 2001). In
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tunas, as in other fishes, oxygenated blood from the gills flows via the dorsal aorta to the locomotor muscles and other tissues, and deoxygenated blood returns from the tissues to the heart via the posterior cardinal vein and then is pumped to the gills (Harder 1975). Tunas have evolved central and lateral vascular counter-current heat exchangers, or *retia mirabilia*, composed of numerous parallel arterioles and venules that perfuse the RM (Kishinouye 1923; Carey and Teal 1969; Sharp and Dizon 1978; Bushnell et al. 1992; Graham and Dickson 2001). As warmed, deoxygenated blood flows away from the muscle through the *rete* venules, heat is transferred to oxygenated blood in the adjacent *rete* arterioles, retaining metabolic heat produced within the RM during sustained swimming, which would otherwise be lost to the environment as blood passes through the gills. These vascular heat exchangers enable all tuna species to maintain RM temperatures (T_{RM}) that are elevated significantly above ambient water temperature (T_a) (Figure 5) (Carey and Teal 1966; Carey and Lawson 1973; Brill et al. 1994; Stevens et al. 2000; Bernal et al. 2001; Marcinek et al. 2001; Dickson and Graham 2004). The basal slender tuna has only a central circulation that supplies blood to the RM via the dorsal aorta and post cardinal vein through the central vascular heat exchanger (Graham and Dickson 2000). All other tunas have an additional lateral circulation (via lateral arteries and veins and the associated lateral vascular heat exchangers) that provides another route for blood flow to and from the RM (Kishinouye 1923; Carey and Teal 1969; Sharp and Dizon 1978, Bushnell et al. 1992, Bernal et al. 2001, Graham and Dickson 2000, 2001; Figure 1b). Some *Thunnus* species lack a central *rete* (Collette et al. 2001), and those species should have a greater capacity to thermoregulate physiologically by adjusting the relative amount of blood flow to the RM via the lateral vascular heat exchangers and the dorsal aorta.

The conservation of heat by the RM vascular heat exchangers allows tunas to maintain elevated and more stable locomotor muscle temperatures at both high latitudes and when swimming below the thermocline (Carey et al. 1971; Carey 1982b; Holland et al. 1992; Block et al. 1998; Brill et al. 1999; Marcinek et al. 2001). Based on effects of temperature on RM contractile properties (Johnston and Brill 1984; Altringham and Block 1997) and on aerobic enzyme activities (Dickson 1996), maintaining an elevated T_{RM} should enhance or at least stabilize RM aerobic performance and sustainable swimming when tunas are in cool water. Measurements in tunas and closely related ectothermic fishes using swimming-tunnel respirometers have failed to document significant interspecific differences in maximum

sustainable swimming speeds, but have shown that tunas have higher standard metabolic rates (Sepulveda and Dickson 2000; Sepulveda et al. 2003; Blank et al 2007a, b). By contrast, a recent compilation of tracking data from a wide range of endothermic and ectothermic vertebrates (Watanabe et al. 2015) showed that routine cruising speeds and maximum annual migration ranges in fishes with RM endothermy are two to three times greater than those of the ectothermic fishes included in the study, suggesting a benefit of RM endothermy. Watanabe et al. (2015) also found that the total cost of transport in the endothermic fishes is twice that of ectothermic fishes, which is in agreement with the higher metabolic rates in endothermic fishes measured under laboratory conditions and the previous characterization of tunas as “energy speculators” (Brill and Bushnell 1991a; Brill 1996).

The ability not only to elevate T_{RM} , but also to control rates of heat transfer with the environment, would be expected to be especially beneficial to Group 3 species that spend more time in cooler waters. Evidence for physiological thermoregulation, presumably by modulating blood flow patterns to the RM to adjust efficiency of heat exchange, and by varying aerobic swimming speed to alter rates of heat production, has been obtained for several tuna species (Holland et al. 1992; Dewar et al. 1994). Physiological control of heat transfer has been measured in juvenile skipjack, yellowfin, and albacore tunas held under conditions in which T_a could be altered (Stevens et al. 1974; Dizon and Brill 1979a, b; Graham and Dickson 1981; Brill et al. 1994; Dewar et al. 1994). Archival tag studies on free-swimming bigeye tuna (Group 3), recording both water temperature and muscle or peritoneal temperature, indicate that whole-body thermal balance is adjusted during vertical oscillations between the surface water and the water below the thermocline (Holland et al. 1992; Holland and Sibert 1994; Malte et al. 2007; Figure 4b, 6a). Bigeye tunas use physiological mechanisms to reduce heat loss to the environment as they descend to cool waters and absorb heat during ascents when water temperature exceeds tissue temperatures. In southern bluefin tuna, a potential behavioral mechanism to absorb heat was observed when individuals exposed both dorsal and ventral surfaces of their body to the warm ocean-air interface (Gunn and Block 2001). There is also evidence that tunas can use behavioral and physiological mechanisms to increase rates of heat loss. For example, when swimming yellowfin and skipjack tunas were exposed to unusually warm water (30-32°C), the physiological mechanisms involved in heat transfer apparently shifted modes, from heat retention to heat loss to the environment, presumably in an attempt to avoid overheating (Dizon

and Brill 1979a, b; Dewar et al. 1994). Similarly, the frequent, short-lived, non-feeding-related forays below the thermocline by free-swimming Pacific bluefin tuna (*Thunnus orientalis*) may be a mechanism to transfer more heat to the water and thus reduce T_{RM} (Kitagawa et al. 2006).

Bluefin, albacore, and bigeye tunas, the species that lack a central vascular heat exchanger (Collette et al. 2001), should have a greater ability than other tuna species to control T_{RM} physiologically. Their circulatory anatomy allows blood flow to the RM via two routes, one with lateral vascular heat exchangers (i.e., lateral circulation) and one without (i.e., dorsal aorta), thus providing a mechanism by which convective heat transfer between the RM and ambient water may be controlled (Graham and Dickson 2001). This potential capacity for physiological thermoregulation, along with regional endothermy, makes these tuna species less dependent upon environmental temperatures and behavioral thermoregulation to maintain locomotor muscle temperatures within functional ranges. It is possible that the upper and lower thermal limits of tuna distributions occur when the T_{RM} reaches a value that is above or below a threshold value at which muscle contractile mechanics are negatively affected. For example, tracking data for free-swimming bigeye tuna undergoing a series of repeated descents below the thermocline (to waters as cold as 7°C), showed that when the RM cooled to 17-18°C individuals quickly returned to the warm surface layer, presumably to re-warm the RM (Holland et al. 1992; Figure 6a). Effects of temperature on contraction mechanics of isolated RM fibers have been investigated in kawakawa (*Euthynnus affinis*), skipjack and yellowfin tunas (Johnston and Brill 1984; Altringham and Block 1997), but not in any Group 3 tunas. Thus, the idea that temperature effects on muscle function limit the latitudinal and depth distributions of tunas and determine interspecific differences in movement patterns cannot be adequately tested at this time. It may be that, when compared to tuna species in Groups 1 and 2, the red muscle of Group 3 tunas has a greater thermal range for optimal function as a result of acclimatization during migration to high latitudes (in species such as Atlantic bluefin tuna) or the alteration of intrinsic muscle properties such a calcium cycling, as has been investigated in the cardiac muscle (Shiels et al. 1999, 2011; Landeira-Fernandez et al. 2004; Galli et al. 2009a, b). Alternatively, Group 3 tunas may be able to maintain T_{RM} within the range for optimal muscle function over a wider range of environmental temperature using thermoregulatory mechanisms (Figure 6b) and because they can also elevate visceral temperatures (Carey and Lawson 1973; Carey et al. 1984; Fudge et al. 1997). A greater degree of regional endothermy may allow Group 3 tunas to increase the

frequency of vertical movements and reduce surface residency intervals, which may extend their absolute time at depth and thus increase the probability of encountering prey without compromising locomotor muscle function while in the deep and cold water. On the other hand, the effects of temperature on the heart (which is maintained at ambient temperature) may be more important in limiting time in cold waters (Brill 1987; Brill et al. 1999; Blank et al. 2004; Shiels et al. 2015). More information on interspecific differences in these physiological characteristics and how they are affected by temperature is needed.

The capacity for RM endothermy develops ontogenetically in tunas (Funakoshi et al. 1985; Dickson 1994; Dickson et al. 2000; Kubo et al. 2008). In most tuna species, small juveniles appear to be limited to warm waters and may avoid incursions into colder waters at depth or higher latitudes until they have developed sufficient capacity to maintain elevated tissue temperatures. For example, during the first year of life, southern bluefin tuna move with the Leeuwin Current from warm-water spawning grounds to more productive waters at higher latitudes off Western Australia, and analysis of otolith stable isotope composition indicates a reduction of 8-10°C in temperature during that period (Shiao et al. 2009; Muhling et al. 2017; Hobday et al. 2017). Pacific bluefin tuna remain in warm coastal waters near the main spawning grounds in the East China Sea and Sea of Japan until their first or second year when they move into cooler waters of the transition zone between the Kuroshio and Oyashio Currents and subsequently migrate to the eastern Pacific Ocean (reviewed in Fujioka et al. 2017). It was recently shown that Pacific bluefin juveniles experience a dietary shift to more active prey at a size of 25-35 cm fork length, which was hypothesized to be related to the development of better capacities for endothermy and swimming (Kitagawa and Fujioka 2017). Similarly, in Hawaii, juvenile yellowfin tuna larger than 1.5 kg shifted from surface-oriented prey to deep-water shrimp, implying that yellowfin tuna of that size or greater have a wider depth range as a result of having developed sufficient capacity to produce and retain metabolic heat (Graham et al. 2007). The ability of skipjack, as well as yellowfin tunas, when larger than ~1-2 kg, to undertake more extensive vertical excursions characteristic of Group 2 species (Schaefer and Fuller 2007; Schaefer et al. 2009) may be explained by several size-related effects: greater mass of RM to generate heat during swimming, the development of larger and more effective heat exchangers, greater thermal inertia, and greater absolute swimming velocity. Unfortunately little is known about the development of endothermy in the cold-water Group 3 tunas (i.e., *Thunnus* spp.) as

their distribution expands from either the tropics to higher latitudes (as in bluefin tunas) or into deeper water (bigeye tuna). It remains unknown whether such migrations are causally associated with the development of the capacity for endothermy, if short-duration excursions into cooler water may stimulate the development of heat production and heat conservation mechanisms in juvenile tunas, or if diet may somehow influence the development of endothermy.

Digestion and visceral endothermy

The presence of visceral vascular heat exchangers, and thus the capacity to elevate visceral temperatures (T_v) above ambient temperature, occurs only in tuna species that inhabit the coldest waters (i.e., Atlantic, Pacific and southern bluefin, albacore, and bigeye tunas; Carey and Lawson 1973; Carey et al. 1984; Fudge et al. 1997; Bernal et al. 2001) (Figure 7). These species possess variable numbers of visceral *retia* along the coeliac-mesenteric artery, allowing for conservation of heat produced post-feeding within the entire visceral mass, with the exception of the distal regions of the liver and the gonads that are not perfused via a *rete* (Kishinouye 1923; Gibbs and Collette 1967; Carey et al. 1984; Fudge and Stevens 2005; Whitlock et al. 2013). Digestive processes within the cecal mass are likely to be the primary heat source for visceral endothermy (Carey et al. 1984; Stevens and McLeese 1984). An elevated T_v is a potential mechanism to enhance rates of digestion and assimilation, which would reduce gut clearance times, decrease the interval between feeding events, and allow higher feeding rates, especially in areas of high productivity, and thus increase somatic and gonadal growth rates (Dickson 1995; Brill 1996; Whitlock et al. 2013). When compared to RM endothermy, visceral endothermy results in warming of a greater percentage of body mass and thus may allow tunas that have evolved this trait to spend more time in cold waters before tissue temperatures reach a critical value requiring behavioral thermoregulation (Holland et al. 1992; Dickson and Graham 2004) (see Figure 7).

Free-swimming Atlantic bluefin tuna have been observed to maintain a nearly constant difference (6°C) between T_v and T_a ($T_v - T_a = T_x$, or excess temperature) until a feeding event, after which T_x increased to as much as 20°C above T_a , followed by a steady decline back to the pre-feeding temperature over the next 20-30 h (Carey and Lawson 1973; Carey et al. 1984; Stevens and McLeese 1984). The onset and offset of this temperature increase suggest that heat production results from increased aerobic metabolism associated with digestion and assimilation

(the heat increment of feeding). In free-swimming southern bluefin tuna implanted with data loggers to record T_v , consuming a cold meal (sardines) reduced T_v by approximately 2°C during times when ambient temperature remained nearly constant (i.e., 18-19°C), and that decrease was promptly followed by an increase of 0.5-2.6°C h⁻¹ to a maximum T_v of 23.3°C as the meal was processed (Clark et al. 2008b). Similar increases in T_v have been measured in Pacific bluefin tuna (Clark et al. 2013; Whitlock et al. 2013). T_v “spikes” in archival tag data have been used to estimate mean feeding frequencies in free-ranging Pacific and southern bluefin tunas of between 0.89 and 1.8 feeding events per day (Gunn and Block 2001; Kitagawa et al. 2004; Bestley et al. 2008; Whitlock et al. 2013). The feeding frequencies of other tunas remain unknown. It is also unknown whether there is a direct link between vertical excursions and feeding for the larger skipjack and yellowfin tunas that are capable of descending below the thermocline, or for bigeye tuna which undergo regular vertical excursion below the thermocline when they are not associated with fish-aggregating devices (FADs). Nevertheless, in the *Thunnus* species with visceral *retia*, the measured feeding frequencies and durations of post-feeding elevation of T_v suggest that T_v is maintained above T_a most of the time (Figure 7), which may contribute to thermal niche expansion. It remains unknown, however, whether the ability to elevate T_v is a causative factor in broadening the thermal range of Group 3 tunas.

Cranial endothermy

All tuna genera have the capacity to elevate the temperature of the cranial region (eyes and brain) above T_a (reviewed in Bushnell et al. 1992; Dickson and Graham 2004; Sepulveda et al. 2007), but the degree of cranial endothermy (the T_x of the cranial region) varies among tuna species and with T_a (Figure 8). For example, within the surface layer of the tropical ocean, the eye and brain temperature of Atlantic bluefin tuna may exceed T_a only by several degrees, whereas at depth or at high latitudes it may be elevated by as much as 18°C above T_a (Linthicum and Carey 1972; Figure 8). Cranial endothermy has also been documented in billfishes, lamnid sharks, and the opah (*Lampris guttatus*), suggesting a similar selective pressure related to this trait among epipelagic fishes that make extensive vertical movements (reviewed in Runcie et al. 2009). The mechanisms for heat production and retention vary among the different fish groups that have evolved cranial endothermy. For example, in billfishes, one of the six extra-ocular muscles of each eye, the superior rectus, is modified into a thermogenic tissue (Carey 1982a;

Block 1991), and the proximal region of the lateral rectus muscle of the opah has an elevated capacity for heat generation (Runcie et al. 2009). In tunas, however, there are few anatomical studies on the metabolic heat source and heat retention mechanisms. In the basal slender tuna, the four pairs of rectus extra-ocular muscles are modified as a potential thermogenic tissue, but there is no evidence of modification of the extra-ocular muscles as a heat source for cranial endothermy in other tunas (Sepulveda et al. 2007; Figure 8). The ocular muscles of skipjack, yellowfin, and Pacific bluefin tunas have similar citrate synthase activities (i.e., capacity for aerobic heat production) and relative muscle masses (i.e., amount of tissue potentially involved in heat production) as do those of the ectothermic scombrids eastern Pacific bonito (*Sarda chiliensis*) and Pacific chub mackerel (*Scomber japonicus*) (Holtz 2013). A pair of orbital *retia* that arise from the internal carotid arteries has been described in several tuna species; this vascular modification would allow the arterial blood entering the orbital *retia* to be warmed on its way to the brain and eyes via counter-current heat exchange (Linthicum and Carey 1972; Bernal et al. 2001; Sepulveda et al. 2007).

To date, all eye and brain temperature measurements from tunas used to assess the degree of cranial endothermy (Figure 8) have been collected invasively by inserting a temperature sensor into the cranial region of individuals that have been captured and brought on board a vessel. Because there are no studies of cranial endothermy in free-swimming tunas, we do not know the exact capacity tunas may have to modulate cranial temperatures. Furthermore, we have only a partial picture of how the specializations and capacity for cranial endothermy vary interspecifically or affect the vertical and latitudinal distributions of tunas. Despite our limited knowledge, the potential physiological consequences of cranial endothermy for sensory perception and neural integration are profound. Warming of the brain and eyes should enhance the rate of physiological processes associated with vision and the central nervous system, and maintaining a stable cranial temperature as T_a changes during descents below the thermocline would be expected to buffer the central nervous system from rapid temperature changes, maintain sensory and integrative functions, and minimize temperature-induced decreases in cranial blood flow while tunas occupy cold, dark waters at depth (Konishi and Hickman 1964; Linthicum and Carey, 1972; Friedlander et al. 1976; Montgomery and MacDonald 1990; Block 1991; Fritsches et al. 2005; van den Burg et al. 2005; Sepulveda et al. 2007). The capacity for cranial endothermy is therefore expected to be the most developed in the Group 3 tuna species.

Sensory perception

Sensory studies generally require access to live animals in a controlled laboratory setting, usually with large and expensive holding systems (Nakamura 1972). The nature of tunas (i.e., large, pelagic, obligate ram-ventilating, highly aerobic) makes them inherently difficult to capture, transport, and maintain in good condition at shoreside tanks and requires large holding facilities. Because tunas are difficult and expensive to acquire and to maintain in captivity, they are routinely kept in only a few laboratories (Farwell 2001; Margulies et al. 2013). As a result, their sensory abilities are much less studied than those of freshwater or inshore species. During the last several decades, however, it has become more critical to understand the sensory biology of pelagic fishes due to the effects of environmental conditions on gear vulnerability and the resultant catch per unit effort data upon which population assessments are built (e.g., Mejuto et al. 2005); as well as the need to develop effective strategies to reduce the capture of non-target species or undersized individuals (e.g., Southwood et al. 2008). Here we focus on vision, because anatomical, functional, and behavioral studies show that vision is a critically important sense for tunas (Magnuson 1963; Nakamura 1968; Kawamura et al. 1981a, b; Somiya et al. 2000; Torisawa et al. 2015).

Vision

Tunas have large eyes which may, in the optically clear aquatic habitat of the open ocean, have horizontal detection ranges of up to 40 m in brightly-lit surface waters (Clarke and Denton 1962; Jerlov 1976; Morinaga et al. 1993a, b). Sight feeding at depth (~500 m) in tunas has also been confirmed by their capture on longlines using artificial lures that lack olfactory or gustatory cues (Kawamura et al. 1981b). In addition, there is evidence that tunas visually communicate the presence of prey to other members of the school by using skin chromatophores to effect subtle changes in banding patterns (Strasburg and Marr 1961; Nakamura 1972).

Visual pigments and spectral absorption

Early measurements of the electrical responses (i.e., electroretinograms, ERGs) to monochromatic light flashes in intact eyes or isolated retinas of tunas demonstrated their peak visual sensitivity to be centered at the blue-green color range (peak absorbancies ~480-505 nm),

where 481 nm is the wavelength that is transmitted the greatest distance in clear oceanic waters (Tamura et al. 1972; Hanyu et al. 1973; Niwa et al. 1975; Kawamura et al. 1981a, b; Morinaga et al. 1993b). More recent microspectrophotometry (MSP) data (i.e., direct measurement of the wavelengths absorbed by the visual pigments) from adult yellowfin tuna (Group 2 species) show that the predominant visual pigment in rods and cones (i.e., individual dim-light and bright-light retinal photoreceptor cells, respectively) has a maximal absorbance at 483 and 485 nm, respectively (Figure 9a, b) (Loew et al. 2002). Rare cones containing a visual pigment with maximal absorbance centered on a shorter violet wavelength (426 nm) were also found (Loew et al. 2002). The presence of three visual pigments (with peak absorbancies of 423-436, 473, and 512-515 nm) has also been documented using ERG in juvenile Pacific bluefin tuna (Group 3 species) (Matsumoto et al. 2011b). Three visual pigments (436, 488, and 531 nm) are also present in istiophorid billfishes (e.g., marlin; reviewed in Bernal et al. 2009), implying a commonality in visual function between tunas and istiophorid billfishes and the ability (albeit limited) to perceive color at least by those species known to spend the majority of their time in brightly-lit surface waters (Holland et al. 1990a, b; Brill et al. 1993; Fritsches et al. 2000, 2003; Kitagawa et al. 2007a; Schaefer et al. 2011; Figure 9a, b).

In contrast, MSP data for species that descend to depths below the brightly-lit surface waters imply that these fishes have visual systems sensitive to a narrower range of wavelengths. The wavelength of maximal absorbance by the visual pigment in cones of bigeye tuna (488-490 nm) and of swordfish (495-508 nm) suggests that these species have monochromatic vision (i.e., they are “color blind”; Fritsches and Warrant 2004). When not associated with FADs, bigeye tuna spend more time at greater depths (> 400 m) during the daytime than do skipjack or yellowfin tunas (Dagorn et al. 2000; Bernal et al. 2009; Schaefer and Fuller 2010; Schaefer et al. 2011; Figures 2, 3, 4), making only occasional forays up to the surface layer to rapidly warm their tissues by absorbing heat from the surrounding water (Holland et al. 1992; Musyl et al. 2003; Malte et al. 2007), but they return to the surface waters during the night. Likewise, swordfish predominantly spend daylight hours below 600 m and nighttime hours at the surface (Carey and Robinson 1981; Abascal et al. 2010; Sepulveda et al. 2010; Dewar et al. 2011; Evans et al. 2011). Because light is largely monochromatic during the nighttime hours in the surface layer and at depth (Morinaga et al. 1993a), there is no disadvantage to monochromatic vision in these Group 3 species.

The retinal cell density in the eyes of tunas and istiophorid billfishes is highest in the ventro-temporal region, indicating that the best visual axis in these fishes is up and forward (Tamura and Wisby 1963; Kawamura et al. 1981b; Somiya et al. 2000; Torisawa et al. 2015). This, in turn, suggests that, in brightly-lit surface waters, tunas and istiophorid billfishes attack their prey from below and that their visual systems are tuned to maximize visual contrast of prey silhouetted by down-welling light (i.e., prey are detected as dark objects against a bright background). These data are congruent with the “sensitivity hypothesis,” which predicts that to maximize visual perception there should be a match between the down-welling light (e.g., 481 nm) and the peak visual sensitivity (Lythgoe 1979; Douglas 2001). It is also plausible, however, that in dim-light conditions (i.e., at night or at depth) tunas and istiophorid billfishes also detect prey by silhouetting them against the moonlight or the bioluminescence produced by common planktonic organisms that is centered at 475 nm (Widder 2002). Alternatively, tunas may detect bioluminescent prey organisms as point-light sources contrasted against a dark background (Warrant and Locket 2004).

The visual situation is more complicated when additional species-specific movement patterns are taken into account. For example, Pacific and Atlantic bluefin tunas (Group 3 species) occupy both coastal and pelagic waters in which the maximal light transmission is centered at different wavelengths [green (~510 nm) versus blue (~480 nm) light, respectively; Figure 9a, b] (Jerlov 1976; Morinaga et al. 1993b; Lutcavage et al. 2000; Douglas 2001; Block et al. 2005; Wilson et al. 2005; Kitagawa et al. 2007a, b). For this reason, the presence of two visual pigments, one of which is offset from the predominant wavelength of light, should maximize visual perception (“contrast hypothesis”) under more turbid coastal conditions (Lythgoe 1979), and this effect may better explain the selective advantages conferred by the multiple visual pigments present in at least some Group 3 species (e.g., Pacific bluefin tuna). Clearly, there is much more to learn before we understand the link between interspecific differences in visual pigments and movement patterns in tunas.

Light sensitivity

Light intensity levels decrease rapidly with depth as spectral irradiance narrows simultaneously (i.e., available light becomes dim and monochromatic), even in clear oceanic waters (Morinaga et al. 1993a; Warrant 2004; Figure 9a, b). Dim-light conditions are well known

to reduce the ability of fishes, including tunas, to detect and capture prey and to maintain school integrity (e.g., Hunter 1968; Glass et al. 1986; Torisawa et al. 2007a).

To date there are few data on the light sensitivity of tunas, with most work having been conducted on Pacific bluefin tuna, an important aquaculture species (Sawada et al. 2005; Torisawa et al. 2015). This Group 3 species has been documented to make frequent (albeit brief) non-feeding-related forays below 300 m during the day (Kitagawa et al. 2006, 2007a, b). Based on light levels required for schooling behavior, the optomotor reaction (the ability for eye movements to follow moving strips), and the ERG responses to various light levels, Pacific bluefin tuna appear to have poorer low-light vision than do other marine fishes (Ishibashi et al. 2009; Matsumoto et al. 2009, 2011a; Torisawa et al. 2011, 2015). It is possible that the visual limitations of this species to low light precludes their vertical movements from being prey-driven, but rather their vertical movements may be a mechanism to avoid overheating (Kitagawa et al. 2006). Similarly, feeding in southern bluefin tuna mostly occurs throughout the day, with the highest feeding frequency occurring around dawn, with rare feeding events at night associated with a full moon (Bestley et al. 2008).

In contrast, the vertical movement patterns of bigeye tuna give an *a priori* reason to expect that this Group 3 species would have a visual system that can function well at low light levels. Although sparse, anatomical data support this prediction; for example, large eyes are commonly associated with enhanced vision in low light because they accommodate larger numbers of photoreceptor cells per solid angle of image space (Motani et al. 1999; Fritsches et al. 2003; Pope et al. 2010). The bigeye tuna has larger eyes than its sister species, yellowfin tuna (Godsil and Byers 1944; Itano 2004); relative to skipjack and yellowfin tunas of similar size, the diameter of the lens in bigeye tuna is two times larger than the former and 1.4 times larger than the latter, allowing more light to be collected (Warrant 2004; Warrant and Locket 2004; Kröger et al. 2009). Of the tuna species studied to date, moreover, only the bigeye tuna has a tapetum lucidum, a guanine layer located behind the retina that serves to increase low-light sensitivity (Somiya et al. 2000). Albacore tuna, another Group 3 species, also has larger eyes than species in Groups 1 and 2, but unfortunately the visual capacities (i.e., light sensitivity) of this species remain unmeasured. Nonetheless, Pacific albacore are usually associated with cooler (i.e., deeper, darker) waters and are known to frequent oceanic fronts (i.e., areas of high primary

productivity) that tend to have increased turbidity and decreased water clarity (Laurs et al. 1977, 1984).

Summation and speed of vision

In addition to the anatomical (i.e., optical) adaptations for enhancing low-light sensitivity, spatial and temporal summation may occur (Warrant 1999). In vertebrates, spatial summation is achieved by having a high number of photoreceptor cells (rods and cones) converge (through a network of bipolar cells) on ganglion cells, which eventually carry the visual information to the brain (Hughes 1977). There is, however, the inevitable tradeoff that increased low-light sensitivity achieved through convergence reduces visual acuity (i.e., the ability to distinguish two points as separate, or to distinguish the fine detail of an object) (Pettigrew et al. 1988). Measurements of retinal cell density in tunas suggest a relatively high visual acuity (Tamura and Wisby 1963; Kawamura et al. 1981b; Torisawa et al. 2007b, 2015), although initial behavioral trials did not support this hypothesis (Nakamura 1968). Using only retinal cell density as a measure would, however, overestimate visual acuity if tunas have high levels of spatial summation, and using behavioral responses may underestimate visual acuity if the test images were presented directly in front of the fish (i.e., projected on a part of the retina that does not have the highest retinal cell density). Understanding visual acuity and the extent of spatial summation in tunas is critical to understanding species-specific vertical movement patterns, feeding effectiveness, and gear vulnerability (Kawamura et al. 1981b), and additional research in this area is clearly needed.

Temporal summation provides a second mechanism for enhanced low-light sensitivity by extending the time over which photons are captured by the visual system (Lythgoe 1979; Warrant 1999). As with spatial summation, there is an inevitable tradeoff because temporal summation reduces the speed of vision. More specifically, eyes with long temporal summation times necessarily have a low flicker fusion frequency (FFF), the highest frequency at which a flashing light appears as individual flashes rather than as a continuous light source. In visual systems with long temporal summation times (i.e., low FFFs), fast moving objects appear blurred, if they are detectable at all – clearly a situation disadvantageous to species hunting fast moving prey (e.g., squid) in water with low light levels. While yellowfin tuna (at 25°C) have a FFF of 60 Hz (Bullock et al. 1991), which is similar to that of other fishes including other marine

piscivores (Ali and Muntz 1974; Horodysky et al. 2010), bigeye tuna have a lower FFF (40 Hz), but preliminary ERG data imply a greater low-light sensitivity (Brill et al. 2005). Both findings are congruent with bigeye tuna's anatomical adaptations (e.g., large lens, presence of a tapetum lucidum) and reflect the fact that bigeye tuna spend more time at depth during the day than do yellowfin tuna. Incongruously, juvenile Pacific bluefin tuna show both a low FFF (20 Hz) and poor low-light sensitivity (Matsumoto et al. 2009, 2011a; Torisawa et al. 2015), suggesting that they are restricted to feeding in brightly-lit surface waters (Kitagawa et al. 2006). This may mean that Pacific bluefin tuna are unable to track prey at depth (i.e., at low light levels) and must therefore hunt in well-lit surface waters, resulting in their need to migrate long distances to feed on surface-associated prey in highly productive waters (i.e., upwelling regions). By contrast, bigeye tuna can remain more geographically localized by exploiting the prey at depth by descending with the DSL during the day and following it to shallower waters at night (Musyl et al. 2003; Schaefer and Fuller 2005; Holland and Grubbs 2007). It remains unknown, however, whether the monochromatic tuna species lost color vision as a function of their feeding ecology or if color vision is a derived feature of the surface-associated tunas. MSP data for all tuna species, as well as their sister species, the bonitos, will be needed to address this question.

Thermal effects on speed of vision

The speed of vision (i.e., FFF) is significantly influenced by temperature (Ali and Muntz 1974), and work on isolated retinas from yellowfin and bigeye tunas shows that the fractional change in FFF per 10°C change in temperature (Q_{10}) is 2.3 and 2.5, respectively (i.e., for every 10°C decrease in temperature FFF decreases by more than half) (Fritsches et al. 2005; Figure 9c). Surprisingly, this thermal effect on FFF in both tunas is similar to that documented in ectothermic fishes (Hanyu and Ali 1964; Ali and Muntz 1974), whereas in swordfish it is much greater ($Q_{10} = 5.1$; Fritsches et al. 2005; Figure 9c). In swordfish, modifications of the superior rectus extra-ocular muscles allow for the generation of heat at significant rates (Carey 1982a; Block 1991), and cranial temperatures elevated 13°C above T_a were recorded by acoustic telemetry in one individual during deep descents (Carey, 1990). The swordfish can maintain relatively stable cranial temperatures and high FFF when descending into cold water, but it is not known whether this effect also occurs in tunas as a result of cranial endothermy. Because most tunas do not have extra-ocular muscles specialized for thermogenesis, cranial temperatures may

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4 638 vary considerably during descents to depths below the thermocline, and a lower Q_{10} would
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6 639 reduce the rate of change in FFF that occurs as cranial temperature decreases.

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8 640 We also note, however, that while elevated eye temperatures in tunas would improve
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10 641 FFF, there is an inevitable tradeoff due to the effect of temperature on low-light sensitivity.
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12 642 Minimal detectable light levels are set by the ability of the visual system to distinguish signals
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14 643 arising from light striking the retinal receptor cells (i.e., rods) from endogenous thermal noise.
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16 644 Because of this effect, a 10°C increase in temperature can reduce low-light sensitivity by as
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18 645 much as 10-fold (Reilly and Thompson 2007). It therefore appears that Group 3 species are, in
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20 646 some measure, maintaining low light sensitivity during descents at the expense of a reduced
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22 647 speed of vision (i.e., a reduced FFF). Additional research on the effects of temperature on low-
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24 648 light sensitivity and FFF in various tuna and other pelagic species is also clearly warranted.
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26 650 *Diurnal change in vision*

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28 651 In many vertebrates there are diel rhythms in visual function that mirror day-night cycles.
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30 652 These visual adaptations, termed “retinomotor movements,” refer to the contraction and
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32 653 expansion of the masking pigments in the retinal epithelial cells accompanied by the
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34 654 simultaneous movements of rods and cones (Ali 1974). Although this circadian rhythmicity is
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36 655 inherent to the retina itself, the timing (onset versus offset) may be entrained by rhythmic
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38 656 changes in light level at dawn and dusk (Kolbinger et al. 1996; Cahill and Hasegawa 1997). The
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40 657 changes in retinal anatomy are accompanied by functional changes (e.g., light sensitivity and
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42 658 FFF) that are easily demonstrated by ERG (Cameron et al. 2008). The rhythmic changes in
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44 659 retinal function are likewise reflected in circadian rhythms in behavior, including feeding activity
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46 660 (e.g., Olla and Marchioni 1968; Ali 1974). The extent of retinomotor movements, although
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48 661 important for understanding visual capabilities, has not been extensively studied across tuna
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50 662 species. Juvenile Pacific bluefin tuna (Group 3 species) do demonstrate rapid (15 min)
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52 663 retinomotor responses following a change in light level (Masuma et al. 2001), which correlates
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54 664 with the effects of changing light levels during school formation (Torisawa et al. 2007a, 2015).
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56 665 The light threshold for inducing retinomotor movements in Pacific bluefin tuna is higher than
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58 666 those in other fish species (Masuma et al. 2001; Torisawa et al. 2007a) and corresponds with the
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60 667 relatively poor low-light sensitivity in this species (Ishibashi et al. 2009; Torisawa et al. 2015).
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62 668 ERG data from yellowfin tuna (Group 2 species) held in constant darkness show that nighttime
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light sensitivity increases approximately 10 times relative to daylight hours (Brill et al. 2005; K. Fritsches and E. Warrant, unpublished results) and demonstrate a strong circadian clock inherent in tuna retinal tissue, as is common in other vertebrates (e.g., Cameron et al. 2008). Reflective of the changes in light sensitivity, the FFF of yellowfin tuna decreases from 60 Hz during daylight hours to below 30 Hz at night (Bullock et al. 1991; K. Fritsches and E. Warrant, unpublished). The relationships of retinomotor movement, circadian rhythms in light sensitivity, FFF, and fish behaviors clearly deserve more attention. Because bigeye tuna remain at depth (often below 400 m) when not associated with FADs or seamounts, they exist in almost constant darkness. In contrast to yellowfin tuna, visual function in bigeye tuna does not show a circadian rhythm, but rather their eyes remain in continuous “night-mode” (i.e., they exhibit high light sensitivity and low FFF) (Brill et al. 2005; K. Fritsches and E. Warrant, unpublished results).

It is unlikely, however, that these are genetically fixed (i.e., species-specific) differences. Rather, retinomotor movements in yellowfin tuna are probably entrained by the day-night light level changes they experience in surface waters, whereas those of bigeye tuna are unlikely to be because this species almost continuously occupies low-light environments. Bigeye tuna do, however, adopt vertical movement patterns similar to those of yellowfin tuna when associated with FADs or seamounts, but immediately revert to their typical repeated-diving behavior pattern when they move away (Holland et al. 1990b; Musyl et al. 2003; Schaefer and Fuller 2005). Thus, the retinomotor movements of bigeye tuna can be out of synchrony with the local light cycle when they first arrive at FADs, or immediately after they depart (assuming retinomotor movements become entrained to the day-night light cycle while the fish occupy surface waters). Knowing how quickly retinomotor movements of bigeye tuna entrain and de-entrain to daily light cycles and whether visual function is impaired immediately after bigeye tuna arrive at or depart from FADs is important to understand and predict behaviors, changes in gear vulnerability, and FAD attraction.

Lunar phase has been documented to influence nighttime depth distributions of various tuna species, with fish remaining deeper during the full moon than during the new moon (Schaefer and Fuller 2002; Musyl et al. 2003; Wilson et al. 2005; Bestley et al. 2009; Orbesen et al. 2017). The most probable explanation is that these behaviors mirror the movements of tuna prey organisms associated with the DSL (Josse et al. 1998; Schaefer and Fuller 2002), rather than being a function of the tunas’ visual abilities. The daily vertical movements of bigeye tuna are

well known to mirror those of the DSL (e.g., Josse et al. 1998; Dagorn et al. 2000); depending on temperature and light conditions, the DSL organisms descend to 250-500 m during the day (Dagorn et al. 2000; Domokos et al. 2007).

Cardiovascular function

The heart

Tuna hearts are generally larger (0.3-0.8% body mass) than those of other active teleosts (e.g., rainbow trout: 0.1% body mass, ectothermic scombrids: 0.1-0.4% body mass) (Basile et al. 1976; Farrell 1991). Tuna hearts also have high values of several indices of aerobic metabolic capacity, including citrate synthase activity (Dickson 1995; Blank et al. 2004, Swimmer et al. 2005), mitochondrial oxygen consumption rate (Moyes et al. 1992), and myoglobin content (Giovane et al. 1980). Some tunas also have a highly developed coronary circulation and a large proportion of the ventricle composed of compact myocardium compared with other active fishes (Tota 1978; Brill and Bushnell 1991a; Farrell et al. 1992). For example, the hearts of bigeye tuna (Group 3) have the largest percentage of compact myocardium of any fish species studied to date (~75%; Brill and Bushnell, 1991a) which correlates with strong force development (Galli et al., 2009b). Taken together, these cardiac characteristics allow tunas to achieve maximal heart rates above 120 beats per minute (bpm, at 25°C), peak (i.e., systolic) ventricular pressures that are ~50% greater than in other active teleosts, and maximum cardiac outputs of ~200 ml min⁻¹ kg⁻¹ in skipjack tuna (Group 1 species) and ~170 ml min⁻¹ kg⁻¹ in southern bluefin tuna (Group 3 species) (Basile et al. 1976; Tota 1978; Bushnell and Brill 1991a; Bushnell and Jones 1994; Brill and Bushnell 2001; Clark et al. 2008b). The high maximum cardiac output in tunas is driven by a large volume of blood pumped per beat (stroke volumes ~1-2 ml kg⁻¹) paired with high maximum heart rates (Bushnell and Brill 1991a; Farrell 1996; Blank et al. 2002, 2004). Despite these impressive maximum cardiac capabilities, recent work on free-swimming southern bluefin tunas in sea pens (Clark et al. 2008b) and Pacific bluefin tunas in large holding tanks (Clark et al. 2013) implanted with heart rate data-logging tags show that routine heart rates are much lower, ranging from 20 to 50 bpm at ~20°C. Thus, the cardiac performance specializations may be important for providing a wide scope for increasing maximum cardiac function in tunas, rather than to sustain an elevated routine cardiac performance (Brill and Bushnell 1991a).

Because limited information is available to correlate *in vivo* cardiac function with vertical distribution among tuna species, our current understanding relies primarily on data from isolated cardiac muscle strip preparations and isolated single atrial and ventricular muscle cells (cardiomyocytes). *In vivo* cardiac data from free-swimming fish exist only for juvenile Pacific and southern bluefin tunas (Clark et al. 2008b, 2013), and most *in situ* whole heart data and isolated muscle strip data are from juvenile skipjack, yellowfin, and Pacific bluefin tunas (Keen et al. 1992; Shiels et al. 1999; Blank et al. 2004). Because as tunas grow there appear to be changes in thermal preferences (e.g., juvenile skipjack and yellowfin tuna belonging to Group 1 and larger individuals belonging to Group 2), there is a need to study both a broader size range and the species in Group 3 that routinely occupy colder waters and maintain a greater T_{RM} elevation (Carey and Gibson 1983; Blank et al. 2007a, b; Clark et al. 2010; Figures 5). Furthermore, very little is known about the effects of hypoxia, or the combined effects of hypoxia and decreased temperature, on tuna hearts.

Heart function during temperature change

The tuna heart is located downstream from vascular heat exchangers and thus receives coronary arterial blood from the gills at ambient water temperature (Brill 1987; Brill et al. 1999). Thus, unlike the tissues served by heat exchangers (i.e., RM, eyes, brain, viscera), which are maintained at higher temperatures, the tuna heart is in thermal equilibrium with T_a and changes with T_a , yet must supply blood to warmer, metabolically active tissues. It is therefore probable that the thermal sensitivity of the tuna heart is a critical component limiting short-term vertical movements and long-term horizontal (i.e., latitudinal) migrations (Brill 1987; Brill et al. 1999; Blank et al. 2004; Shiels et al. 2015). Indeed, the short, rapid vertical movement behavior of Group 2 and 3 species has been hypothesized to involve cardiac rewarming (Shiels et al. 2015) (Figures 4, 6a) in addition to the rewarming of the RM and viscera discussed above. The myocardium of Pacific bluefin tuna has also been shown to remodel both morphologically and functionally following chronic temperature change [e.g., with thermal acclimation (Galli et al. 2009a; Shiels et al. 2011)], which may occur naturally during latitudinal migrations. These responses suggest that cardiac function is strongly impacted when tuna move between different thermal environments.

Studies with isolated tuna hearts show that, similar to other teleosts, acute cooling slows heart rate (i.e., results in bradycardia) (Blank et al. 2004; Clark et al. 2013). Although stroke volume in tunas is at the high end for teleosts, it may be relatively fixed (Farrell, 1996; Brill and Bushnell 2001). Thus, any cold-induced reductions in heart rate will also tend to reduce cardiac output (the volume of blood pumped by the ventricle per minute, or heart rate x stroke volume) because the heart has limited ability to counteract the reduced heart rate with an increase in stroke volume. Consequently, acute thermal effects on heart function during descents below the thermocline may limit the vertical movements of tunas. This is particularly noteworthy because adrenergic stimulation appears to be less effective when the hearts of tunas are rapidly cooled (Galli et al. 2009b; Shiels et al. 2015) suggesting adrenergic stimulation may be less cardio-protective in tunas when compared to other fishes (e.g., salmonids; Graham and Farrell 1989; Shiels et al. 2003). Interestingly, isolated hearts of small (less than 4 kg) yellowfin (Group 1), albacore and Pacific bluefin (Group 3) tunas show a similar degree of cold-induced bradycardia, with heart rate declining from ~110 bpm at 25°C to 10-15 bpm at 7°C (Blank et al. 2004). The hearts of Pacific bluefin differed, however, in that they were able to contract at temperatures as low as 2°C, a temperature at which the hearts of the other two species failed, suggesting a greater thermal tolerance for cardiac performance in that Group 3 species (Figure 10a). Although *ex vivo* (i.e., isolated heart) data strongly indicate that tunas may differ in cardiac thermal adaptations that reflect their distributions, there is little known about their *in vivo* cardiac performance. Moreover, *ex vivo* data must be interpreted with caution as, for example, a cardiac output of ~14 ml min⁻¹ kg⁻¹ at 2°C (recorded *ex vivo*) in Pacific bluefin (Figure 10a) would be too low to meet the estimated aerobic oxygen demand of active foraging in this species (Blank et al. 2007a, b), even if venous blood oxygen content was reduced to zero (i.e., 100% oxygen delivery to the working tissues). Nonetheless, the interspecific differences in cardiac thermal sensitivity measured *ex vivo* may directly affect the vertical and latitudinal range of tunas. Thus, physiological adjustments during acute cooling, and acclimatization of key heart characteristics during chronic cooling, may be necessary to maintain cardiac function in tunas that routinely dive below the thermocline or in those that undergo cold exposure for prolonged periods during migration to high latitudes.

Isolated cardiac tissue function during temperature change

The thermal sensitivity of the whole heart is mirrored by the temperature sensitivity of contraction in isolated myocardial tissue. In bigeye tuna (Group 3), when the heart is stimulated at a constant frequency at temperatures from 25°C to 5°C, contractile force is maximal at 15°C (Galli et al. 2009b). The positive inotropic effects (i.e., increase in force) of cooling from 25°C to 15°C (at 0.5 Hz) may allow cardiac function to be sustained in cooler waters in bigeye tuna, and correlates with the broader thermal range of this species (Brill et al. 1999). By contrast, cooling the isolated myocardial tissue from yellowfin tuna had a more detrimental effect on contractile performance (Galli et al. 2009b), which may reflect the more limited vertical movements of this species.

In many teleost species, adrenergic stimulation is known to ameliorate the depressive effect of reduced temperature on cardiac function (e.g., Graham and Farrell 1989; Keen et al. 1992). Independent of temperature, adrenergic stimulation (in the nM - μ M range) in atrial muscle preparations from skipjack and yellowfin tunas increases contractile force (Keen et al. 1992; Shiels et al. 1999), a similar scenario that has been documented in ventricle muscle preparations from yellowfin and bigeye tunas (Galli et al. 2009b), but has marginal effects on power output of whole hearts isolated from yellowfin tuna (Blank et al. 2002). When compared at any given temperature, the addition of 1 μ M adrenaline elevated ventricular contractile force more in bigeye tuna (~330% increase) than in yellowfin tuna (~190 % increase) (Galli et al. 2009b). This finding suggests that bigeye hearts are more sensitive to adrenaline and that adrenergic stimulation may be an important mechanism for maintaining cardiac force. As discussed above, the efficacy of adrenaline in stimulating contractile force was reduced at cooler temperatures (below 15°C) in both bigeye and yellowfin tunas (Shiels et al. 1999; Galli et al. 2009b), which is opposite to the effect in salmonids in which adrenergic sensitivity is greater at acutely cooler temperatures (Keen et al., 1993; Shiels et al. 2003). Thus, the utility of this mechanism for modulating cardiac function in Group 2 and 3 tunas when in cold, deep waters may be limited. The multitude of physiologically relevant changes that the tuna heart experiences during descent below the thermocline has not been investigated in a systematic way, although initial investigations on myocytes from Pacific bluefin tuna highlight the complexity of the situation at a subcellular, mechanistic level (Shiels et al. 2015). Clearly, future work measuring the contractile response of cardiac muscle to the interactive effects of temperature, adrenaline, and hypoxia, as well as measuring cardiac frequency in species with wide a versus narrow

vertical distribution, is needed to better understand the physiological adaptations and limitations of tunas.

Temperature and tuna cardiac myocyte function

Cardiac function is underpinned by the function of the atrial and ventricular cardiomyocytes that make up the contractile chambers of the heart. In general, the morphology of the cardiomyocytes of tunas is similar to that of other fishes, being long (100-150 μm) and thin (3-20 μm) (Shiels et al. 2004; Di Maio and Block 2008), and there do not appear to be differences in myocyte morphology between similarly sized tunas in Groups 1, 2, and 3 (Shiels, and Brill, unpublished observations).

Many studies have tried to identify cellular specializations in excitation-contraction (EC) coupling that allow for the robust maximal *in vivo* cardiac performance of tunas. EC coupling is the physiological process responsible for cellular contraction and relaxation and is achieved via the transient rise and fall in intracellular Ca^{2+} in response to membrane excitation (reviewed in Vornanen et al. 2002). Tunas possess cellular specializations that enhance both the rate and magnitude of Ca^{2+} cycling (Keen et al. 1992; Shiels et al. 1999; Landeira-Fernandez et al. 2004; Castilho et al. 2007; Di Maio and Block 2008; Galli et al. 2009a, b; Shiels et al., 2011), including increased reliance on the intracellular Ca^{2+} stores of the sarcoplasmic reticulum (SR) (Shiels and Sitsapesan 2015). Temperature affects all biochemical and biophysical processes in the myocyte, including the function of ion channels and pumps that are responsible for cycling Ca^{2+} during EC coupling. In teleosts, temperature effects are apparent for the L-type Ca^{2+} channel (Shiels et al. 2000, 2003), the ryanodine receptor (SR Ca^{2+} -release channel) (e.g., Hove-Madsen et al. 2001; Shiels et al. 2002), the SR Ca^{2+} ATPase (SERCA pump) (Shiels et al. 2002; Landeira-Fernandez et al. 2004; Castilho et al. 2007; Di Maio and Block 2008), and the Na^{+} - Ca^{2+} exchanger (NCX) (Hove-Madsen et al., 2000; Llach et al. 2001; Marshall et al. 2002).

The action potential (AP) that initiates EC coupling, measured from the surface of isolated yellowfin tuna hearts using monophasic action potential recordings (Patrick et al. 2011) and in single isolated Pacific bluefin tuna myocytes (Galli et al. 2009a; Shiels et al. 2015), was found to be broadly the same as that of other teleost species (Haverinen and Vornanen 2009). The AP duration in Pacific bluefin tuna is highly sensitive to acute temperature changes (Galli et al. 2009a; Shiels et al. 2015) and appears to be less affected by thermal acclimation than it is in

freshwater teleost hearts. Indeed, Galli et al. (2009a) hypothesized that the Pacific bluefin heart does not become refractory (i.e., it will still be responsive to a new AP stimulation) in the cold, despite prolongation of the AP, because the basal duration is shorter than that of other species. Although this hypothesis remains to be tested, it may explain how bluefin tunas (Group 3) are able to prevent cardiac refractoriness when cooling prolongs AP duration as they move into cold waters in search of prey.

There are two main sources of Ca^{2+} that power myocardial contraction in teleosts. The first is Ca^{2+} influx across the sarcolemmal membrane of cardiac myocytes through the L-type Ca^{2+} channel (Keen et al. 1992; Shiels and Farrell 1997; Vornanen et al. 2002; Shiels et al. 2006), and the second source for Ca^{2+} is the intracellular stores of the SR. There is no evidence to support differences in L-Type Ca^{2+} channel current underlying differences in vertical mobility among tunas, but data are limited. Work on the closely related ectothermic scombrids (*Scomber japonicus* and *Sarda chiliensis*) showed that the Ca^{2+} current amplitude is lower in these species compared to tunas (Shiels et al. 2004; Galli et al. 2011). In addition, while acute cooling decreased peak current amplitude in both yellowfin (larger than 4 kg; Group 2) and Pacific bluefin (Group 3) tunas, the total Ca^{2+} carried by the L-type Ca^{2+} channel was inhibited more significantly by the cold in the Pacific bluefin, due to differing kinetics. This could be explained if this species relies more on intracellular Ca^{2+} stores released from the SR. That hypothesized interspecific difference is supported by finding that the SR Ca^{2+} stores in Pacific bluefin tuna (Group 3) myocytes are significantly greater than those of the yellowfin tuna (Group 2) (Galli et al. 2011). Relatively little is known, however, about this aspect of EC coupling in the myocardium of other tuna species.

Role of the sarcoplasmic reticulum (SR)

In Group 3 tuna species, which tolerate cold temperatures, myocardial contraction appears to be more dependent on SR Ca^{2+} stores (Galli et al. 2011; Shiels et al. 2011). This is not surprising given that increased SR Ca^{2+} cycling is a hallmark of thermal tolerance in hibernating endotherms (Wang et al. 1997), suggesting a common mechanism for cold tolerance across vertebrates. Recent work has also demonstrated that Pacific bluefin tuna are able to increase the SR complement and SR Ca^{2+} utilization in response to chronic cold (Shiels et al. 2011). Although there are no similar cellular data for bigeye tuna, isolated ventricular myocardium from

bigeye tuna showed a greater reduction in developed force (30%) when Ca^{2+} contribution from the SR was inhibited than did ventricular myocardium from yellowfin tuna (6%) (Galli et al. 2009b). A potential mechanism to increase SR Ca^{2+} content in the cold is via upregulation of the Ca^{2+} -ATPase pump (SERCA), which moves cytosolic Ca^{2+} into the SR during relaxation. Biochemical studies with isolated SR vesicles clearly show that, at comparable temperatures, SERCA activity is greater in Pacific bluefin tuna myocardium compared with other tuna species and other scombrids (Landeira-Fernandez et al. 2012) (Figure 10b). In addition, the myocardium of Pacific bluefin tuna has both a more extensive SR and a higher amount of SERCA than that of yellowfin and albacore tunas and Pacific chub mackerel (Landeira-Fernandez et al. 2004; Castilho et al. 2007; Di Maio and Block 2008). The extensive SR development in the myocardium of Pacific bluefin tuna may allow this species to recruit additional SR-derived Ca^{2+} and maintain cardiac contractility in cold waters (Shiels and Sitsapesan, 2015). The SR complement can, moreover, be increased by remodeling processes that occur during cold acclimation (> 4 weeks) to provide stronger and faster contraction (Shiels et al. 2011), resembling the changes that occur in temperate freshwater perch (Bowler and Tiiri 1990) and hibernating mammals (Wang et al. 1997). The ability to recruit the intracellular SR Ca^{2+} stores when descending below the thermocline or migrating latitudinally into cold water, is probably an important factor in maintaining heart function.

The role of other cellular processes and components of Ca^{2+} cycling (including the sarcolemmal sodium-calcium exchanger (NCX), the ryanodine receptor, and Ca^{2+} buffering) have yet to be directly investigated in any tuna myocardium.

Integrative cardiac responses to a changing ambient environment

Due to the inherent difficulties in measuring cardiac function in free-swimming, unrestrained tunas, very little is known about the integrative cardiac response to changes in ambient water conditions. Recently, Clark and colleagues (Clark et al. 2008b, 2013) have employed archival tag technology to understand how heart rate is altered by decreases in temperature in swimming tuna. Their work shows routine heart rates of ~40 bpm at 30°C, and a cold-induced bradycardia (Q_{10} of ~2.7) as temperature decreases to 15°C. These findings support a direct effect of temperature on tuna cardiac function and suggest that bradycardia would occur during descents below the thermocline. It is, however, important to know the extent to which

stroke volume can change *in vivo* to understand the influence of cold-induced bradycardia on overall cardiac output. Indeed, a decrease in heart rate could be accompanied by an increase in stroke volume due to longer filling times, which would minimize the decrease in cardiac output, as has been demonstrated in isolated working hearts from Pacific bluefin and yellowfin tunas (Blank et al. 2002, 2004). This inverse relationship between heart rate and stroke volume is, however, observed only when the heart is not working maximally (Blank et al. 2002). At maximal filling pressures, the stroke volume in yellowfin tuna is invariant during a decrease in temperature; thus, a drop in temperature leads to decreased cardiac output (Blank et al. 2002). Clearly, there remain gaps in our understanding of the *in vivo* scope for stroke volume modulation in tuna, and data of this nature are necessary to reconcile tradeoffs between heart rate and stroke volume in regulating cardiac output.

Recently the interacting effects of temperature, contraction frequency, and adrenergic stimulation were investigated in isolated ventricular myocytes from the Pacific bluefin tuna in an attempt to understand how cardiac contractility could be maintained *in vivo* during a descent into cool waters when several variables change simultaneously (Shiels et al. 2015). The results showed that action potential duration is prolonged by adrenaline (500 nM) which helps to offset the direct effect of temperature and cardiac frequency on Ca^{2+} influx (Figure 10c), such that when these stressors were combined in a physiologically realistic way, intracellular Ca^{2+} levels were fairly consistent during a 20°C acute temperature change (Figure 10d). These interacting processes have not been systematically studied in other tuna species. Moreover, the extent to which adrenergic stimulation can rescue the fall in cardiac output at cold temperatures requires additional study because adrenaline is less effective at cooler temperatures in tunas than it is in other fishes (Blank et al. 2002; Galli et al. 2009b; Shiels et al. 2015).

In summary, we are a long way from understanding the interrelations among temperature, cardiac frequency, stroke volume, and inotropic agents, even in a single species of tuna. Work is needed across levels of biological organization, particularly *in vivo*, to understand the role that cardiac function plays in limiting the movements of tunas and explaining their distributions within the pelagic environment.

Hypoxia tolerance

There has been a long standing interest in the hypoxia tolerance of tunas because of its importance for defining suitable habitats, mechanistically explaining latitudinal distributions and vertical movement patterns, standardizing fishery catch and effort statistics, and predicting the effects of climate change on tuna fisheries (e.g., Barkley et al. 1978; Brill 1994; Brill and Lutcavage 2001; Kirby 2001; Bigelow et al. 2002; Bigelow and Maunder 2007; Bestley et al. 2009; Lehodey et al. 2011; Raye and Weng 2015). Initial laboratory work investigating the effects of reduced concentrations of dissolved oxygen (DO) in the ambient water (i.e., hypoxia) on skipjack and yellowfin tunas (at 25°C) showed that the former consistently increased swimming speeds at moderate levels of hypoxia (DO of ~3.5 mg L⁻¹), presumably to increase ventilation or move away from the hypoxic water, and survived relatively short exposures (less than 1 h) to more severe hypoxia (DO below 3 mg L⁻¹). In contrast, yellowfin tuna did not increase swimming speed until ambient DO reached lower levels (2.4 mg L⁻¹) and survived exposure to extreme hypoxia (DO ~1.3 mg L⁻¹) for over 3 h (Dizon 1977; Gooding et al. 1981). Taken together, these observations imply that skipjack tuna is less tolerant of hypoxia than yellowfin tuna. Albacore tuna (Group 3) also appear intolerant of hypoxia because their oxygen consumption rate (at 15°C) decreased as DO was reduced from 5.1 to 2.6 mg L⁻¹ (Graham et al. 1989), implying that oxygen delivery to the tissues could not be maintained at these levels of hypoxia. Subsequent laboratory work aimed at understanding the physiological responses of skipjack and yellowfin tunas to hypoxia showed that, in both species, even modest reductions in DO concentration (to ~5.5 mg L⁻¹ at 25°C) induce physiological responses, including increases in ventilation volume and bradycardia (Bushnell et al. 1990; Bushnell and Brill 1991, 1992; Brill 1994; Korsmeyer et al. 1996a). These responses to hypoxia are well documented in fishes and serve to maintain rates of oxygen uptake and delivery to tissues and to protect cardiac function (e.g., Gamperl and Driedzic 2009; Perry et al. 2009). Because tunas appear to have a limited ability to increase stroke volume during hypoxia-induced bradycardia, cardiac output fell with heart rate (Bushnell and Brill 1992; Farrell et al. 1992; Brill and Bushnell 2001; Blank et al. 2002, 2004). This may be because stroke volume was already maximal under the experimental conditions, although the ability of tunas to increase stroke volume to offset changes in heart rate *in vivo* remains unknown. Regardless of compensatory change in stroke volume during hypoxic bradycardia, impaired oxygen delivery by the cardio-respiratory system undoubtedly contributes to hypoxia sensitivity in tunas.

Models of tuna oxygen demand and delivery (based on the laboratory-derived data) were subsequently developed and used to investigate maximum rates of oxygen delivery, maximum sustainable swimming speeds, and times required to recover from exhaustive exercise at various levels of hypoxia (Bushnell and Brill 1991; Brill 1994; Korsmeyer et al. 1996a, b). Yellowfin tuna are predicted to be able to survive in DO concentrations of 3.7 mg L⁻¹, but only at their minimum swimming speeds (i.e., those needed to maintain hydrostatic equilibrium; Magnuson 1973), whereas skipjack tuna cannot survive oxygen levels this low. For skipjack and yellowfin tunas, reductions in DO concentrations to below 74% saturation (5 mg O₂ L⁻¹, at 25°C) and 66% saturation (4.5 mg O₂ L⁻¹, at 25°C), respectively, are predicted to significantly prolong the time required to recover from exhaustive exercise and to impair the ability to meet metabolic oxygen demands above those needed for swimming (Brill 1994; Bushnell and Jones 1994). These data agree with oxygen limitation on vertical movements of these species observed with acoustic telemetry (Holland et al. 1990b; Cayré and Marsac 1993), but are higher than the DO concentrations that induce a behavioral response in laboratory studies (Dizon 1977).

Acoustic telemetry studies, archival tag records, and depth of capture data from longline fisheries all indicate that bigeye tuna are much more tolerant of hypoxia than are skipjack and yellowfin tunas, and that they routinely occupy depths where DO concentration is below 21% saturation at 10°C (2 mg O₂ L⁻¹) (Hanamoto 1987; Holland et al. 1990b; Boggs 1992; Musyl et al. 2003; Evans et al. 2008; Schaefer et al. 2009; Howell et al. 2010; Schaefer and Fuller 2010). Direct laboratory measurements of physiological responses likewise demonstrate a greater tolerance to hypoxia in bigeye tuna compared to skipjack and yellowfin tunas (Bushnell et al. 1990). Larger skipjack and yellowfin tunas occasionally make rapid brief descents below 300 m in the eastern and central Pacific Ocean, but these species do not occupy those depths for extended periods of time as do bigeye tuna (Schaefer and Fuller 2007; Schaefer et al. 2009, 2011; Howell et al. 2010). Thus, we argue that skipjack and yellowfin tunas cannot survive this level of hypoxia (2 mg O₂ L⁻¹) for long periods of time, especially given the simultaneous reductions in temperature (to less than 10°C) which would result in reduced heart rate and thereby exacerbate the reduced oxygen delivery by the cardio-respiratory system caused by hypoxia (Korsmeyer et al. 1996a; Blank et al. 2002, 2004). There are, however, no published studies describing the effects of simultaneous reductions in temperature and DO concentration on the functioning of tunas' cardio-respiratory systems, and research to ascertain how and how well

various tuna species tolerate simultaneous acute reductions in temperature and oxygen are clearly warranted.

Temperature and hypoxia effects on blood hemoglobin-oxygen binding

As described above, tunas subject themselves to extensive changes in water temperature through their daily vertical and seasonal latitudinal movements (Gunn and Block 2001; Sharp 2001). The binding of oxygen to hemoglobin is an exothermic reaction (i.e., produces heat) and, because added heat (i.e., an increase in temperature) tends to reverse exothermic binding reactions, the tendency of hemoglobin to bind oxygen (i.e., hemoglobin oxygen-binding affinity) is reduced by an increase in temperature (Powers et al. 1979; Weber and Fargo 2004). Tuna blood must retain its functional properties (i.e., the ability extract oxygen from the ventilatory water stream passing over the gills and to deliver it to the tissues) in spite of being subjected to large temperature changes (up to 20°C) that occur over time scales ranging from seconds due to vertical movements, to months due to latitudinal migrations. Tuna blood also experiences rapid changes in temperature as it passes from the gills (which are at ambient temperature) to the tissues (swimming muscle, eyes and brain, and, in some species, the viscera), which are maintained at elevated temperatures. Rossi-Fanelli and Antonini (1960) were the first to describe the unusual temperature independence of oxygen-binding affinity in tuna hemoglobin preparations and ascribed this to the necessity for blood to retain its functional properties over a wide range of temperatures. Subsequent work involving whole blood from several tuna species confirmed this general idea, but also showed the effects of temperature on whole tuna blood oxygen-binding affinity to be species-specific, and reflective of hypoxia tolerance and vertical movement patterns (Cech et al. 1984; Jones et al. 1985; Brill and Bushnell 1991b, 2006; Lowe et al. 2000; Clark et al. 2008a). A recent study (Lilly et al. 2015) demonstrated how blood oxygen-binding affinity is affected by temperature acclimation as would occur during latitudinal migrations in Group 3 tunas.

The effects of temperature on tuna blood oxygen binding and release are complicated by the fact that tuna blood is subjected to both “open-system” and “closed-system” temperature changes. The former refers to the situation occurring in the gills where blood is free to exchange gases and proton equivalents with another medium (in this case, the water passing over the gills) and temperature changes are rapid due to vertical ascents or descents. The latter refers to the

situation occurring as blood passes through the vascular counter-current heat exchangers and arterial blood temperature increases from that in the gills (i.e., ambient temperature) to that of the warmed tissues but is not able to exchange gases or proton equivalents with another medium (Stevens et al. 1974). During open-system temperature change, blood O₂ content remains constant, whereas the partial pressures of oxygen and carbon dioxide (pO₂ and pCO₂, respectively) vary and are thus accompanied by relatively minor changes in plasma pH (pHe) (~0.004 ΔpHe Δ°C⁻¹). By contrast, closed-system temperature changes are accompanied by greater change in pHe (~0.016 ΔpHe Δ°C⁻¹) and substantial alterations in pCO₂ due to changes in CO₂ solubility in the plasma and the reciprocal titration of plasma proteins and plasma bicarbonate (Perry et al. 1985; Truchot 1987; Brill et al. 1992).

Fish species that are hypoxia-tolerant have blood with a high oxygen-binding affinity, meaning that the blood has the ability to remove oxygen from the ventilatory water stream even at low ambient oxygen levels (Jensen et al. 1993; Mislán et al. 2016). Not surprisingly, bigeye tuna (Group 3) blood has a higher oxygen-binding affinity than does blood of skipjack (Group 1) and yellowfin (Group 2) tunas (Brill and Bushnell 1991b; Lowe et al. 2000), reflecting the greater tolerance of environmental hypoxia of bigeye tuna. Blood with high oxygen-binding affinity may, however, release less oxygen at active tissues, thereby limiting aerobic metabolic rates, especially in the tissues maintained at elevated temperatures (Yang et al. 1992). Bigeye tuna have surmounted this limitation by having unique blood oxygen-binding characteristics that simultaneously enable this species to be both hypoxia-tolerant and able to maintain high tissue O₂ consumption rates (Brill 1996; Lowe et al. 2000). In brief, when the blood of yellowfin, skipjack, and bigeye tunas is compared during similar temperature changes, the latter shows a larger decrease in oxygen-binding affinity when subjected to closed system increases in temperature. As a result, oxygen off-loading in the swimming muscles is not compromised, even though bigeye tuna blood has a high oxygen-binding affinity under the conditions occurring during its passage through the gills. The high oxygen-binding affinity and enhanced response to closed-system temperature changes in bigeye tuna blood thus provides an effective system for extracting oxygen at high rates from the ventilatory water stream even during conditions of low ambient oxygen, while simultaneously ensuring high rates of oxygen delivery and offloading in the muscle capillaries.

The characteristic of bigeye tuna blood with respect to the effects of closed-system temperature change on oxygen-binding affinity that provide hypoxia tolerance requires sustained elevated tissue temperatures and may explain bigeye tuna's well documented regular upward excursions into warm surface layers (e.g., Holland et al. 1992; Musyl et al. 2003, 2004; Schaefer and Fuller 2010; Figures 4b, 6a). Because maintenance of a significant difference between ambient temperature and the endothermic tissue temperatures is obligatory for blood oxygen delivery, when tissue temperatures reach 17-18°C at depth, bigeye tuna return to warm surface layers to get a “gulp” of heat in a way roughly analogous to the way marine mammals return to the surface to get a “gulp” of air (Holland et al. 1992; Brill et al. 2005; Malte et al. 2007).

Not all Group 3 tunas share with bigeye tuna a higher blood oxygen binding affinity, because they may not be routinely exposed to environmental hypoxia. For example, the blood oxygen-binding affinity of the Atlantic bluefin tuna is similar to that of skipjack, yellowfin, and kawakawa tunas (Jones et al. 1985; Brill and Bushnell 2006), suggesting that this species is as intolerant of hypoxia as are Group 1 and 2 species. This similarity is not unexpected, given the movement patterns of juvenile and adult Atlantic bluefin tunas (Block et al. 2001, 2005; Wilson et al. 2005; Lawson et al. 2010). With the possible exception of spawning areas in the Gulf of Mexico (Teo et al. 2007a, b), this species does not frequent coastal areas with relatively shallow oxygen minimum zones (Garcia et al. 2009; Prince et al. 2010) and would not be expected to encounter hypoxic water to the same extent that bigeye tuna do during their daily vertical movements. By contrast, the blood oxygen affinity of southern bluefin tuna is similar to that of the bigeye tuna (Jones et al. 1985; Lowe et al. 2000; Brill and Bushnell 2006; Clark et al. 2008a), implying that bigeye and southern bluefin tunas share similar tolerances of environmental hypoxia. Southern bluefin tuna can maintain aerobic metabolism at DO concentrations below ~2.5 mg O₂ L⁻¹ (Fitzgibbon et al. 2007, 2010), but it is not known whether southern bluefin are normally exposed to hypoxia. Like Atlantic bluefin tuna, southern bluefin tuna make brief forays to depths below 600 m (Bestley et al. 2009), but in areas devoid of shallow coastal oxygen-minimum zones (Garcia et al. 2009). The presumed hypoxia tolerance of southern bluefin tuna thus lacks an obvious explanation. Pacific bluefin tuna, in contrast, frequent coastal areas of the eastern Pacific (Boustany et al. 2010) with shallow oxygen-minimum zones (Garcia et al. 2009), and the vertical movement patterns of this species most likely exposes individuals to severe

hypoxia during their dives (Domeier et al. 2004). Unfortunately, the hypoxia tolerance and blood oxygen-binding affinity of Pacific bluefin tuna have not been measured.

Summary

In this review, we attempt to summarize what is currently known about the physiological characteristics of tunas that we contend are related to tuna distribution, niche expansion, and habitat partitioning within the heterogeneous, three-dimensional oceanic environment. Many characteristics of the pelagic environment, including temperature, dissolved oxygen, pressure, light, and prey abundance, vary with depth and/or latitude, as well as seasonally. Interspecific differences in the physiological tolerance ranges for these environmental variables, alone and in combinations experienced in the field, are associated with the behavior and distribution of the various tuna species. We have focused the discussion on interspecific differences in swimming muscle physiology, visual physiology, and cardiovascular physiology, and on how regional endothermy affects the function of these systems. Tunas share adaptations for continuous and rapid swimming, regional endothermy, and the ability to meet multiple metabolic demands simultaneously (e.g., swim continuously, recover rapidly from exhaustive exercise, and meet the increase in metabolic demand following feeding). The Group 3 tuna species, with the widest ranges both in latitude and depth, are also the species that have evolved visceral endothermy in addition to muscle and cranial endothermy, and thus can maintain more of the core body tissues at temperatures elevated significantly above ambient temperature. These species also have a greater capacity for physiological thermoregulation of muscle temperatures. Although the greater extent of regional endothermy and thermoregulation may be causally related to thermal niche expansion in these tunas, many other factors are involved in the ability of Group 3 tunas to migrate to higher latitudes and especially to descend repeatedly to depths below the thermocline which simultaneously exposes fish to rapid changes in several environmental conditions (temperature, pressure, light level, DO, and prey availability). Although only a limited number of species from each group have been studied in detail, cardiac Ca^{2+} cycling and cardiac contractility are elevated in the hearts of Group 3 species, which may allow heart function during acute or prolonged forays into cold and sometimes hypoxic waters. The bigeye tuna's hemoglobin has the unusual ability to simultaneously allow oxygen uptake in hypoxic waters and effective delivery of oxygen to warm, active tissues. Thus, adaptations in cardiac characteristics,

as well as in hemoglobin function, may be critical for niche expansion in these tuna species. As tunas are visual predators, low light sensitivity and increased temporal summation are characteristics associated with vision in Group 3 tunas. Together with cranial endothermy, these features may be important for effective predation in cool, dark and deep waters. Much more remains to be learned, especially in regard to simultaneous changes in multiple environmental variables and whether interspecific differences in integrated physiological performance are causally associated with distribution limits. Future research to understand how and how well different tuna species deal with thermal challenges and hypoxia exposure is needed to understand species-specific movements and distributions, as well as how those may change in the face of changing oceanic conditions, with obvious implications for future tuna fisheries management and resource conservation.

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Fig. 1 a Phylogeny of the tunas (Tribe Thunnini) based on morphological and molecular characters. Modified from Graham and Dickson 2000; Miya et al. 2013; Diaz-Arce et al. 2016. **b** Transverse sections for the indicated species showing position of red muscle (RM) and the approximate location of vascular counter-current heat exchangers. Modified from Sepulveda et al. 2008. **c** Representative RM longitudinal distribution in albacore tuna (*Thunnus alalunga*) and the eastern Pacific bonito (*Sarda chiliensis*). The amount of RM at each position along the body (% of fork length, FL) is expressed as a proportion of the amount of RM at 50% of fork length. The grey shaded areas represent the position where the relative amount of RM is maximal. Modified from Graham et al. 1983; Bernal et al. 2009.

Fig. 2 Representative vertical movement distribution patterns for tunas. Color fish images represent the average depth (combined night and day) for each species. Gray-filled fish outlines represent the depth at which each species spent 95% of the time during the night. Open outlines represent the depth at which each species spent 95% of the time during the day. Grey shaded bar represents the thermocline, defined as the depth range in which water temperature changes rapidly, separating the water column into the upper well-mixed surface layer (i.e., water above 20°C, well oxygenated) and the cooler, deeper waters (i.e., below 15°C). Group 1: Tunas that spend the majority of their time in the upper uniform-temperature surface layer (e.g., *Auxis* spp., *Euthynnus* spp., *K. pelamis* juveniles, *T. albacares* juveniles). Group 2: Tunas that undertake short excursions below the thermocline (e.g., adults of *K. pelamis* and *T. albacares*). Group 3: Tunas that spend significant periods in cool water at high latitudes (e.g., *T. thynnus*, *T. alalunga*) or below the thermocline (e.g., *T. obesus*). Modified from Musyl et al. 2004; Bernal et al. 2009.

Fig. 3 Representative vertical movement patterns for an adult skipjack tuna (70 cm fork length) implanted with an archival tag swimming in the eastern equatorial Pacific Ocean. **a** On April 11, 2004, the tuna was in the vicinity of a floating object and showed surface oriented diving behavior characteristic of tunas in Group 1. **b** On April 18, 2004, the same individual showed repeated diving behavior to deeper water when in the open ocean. Grey shaded areas indicate nighttime. **c** Vertical thermal profile of the water column and (horizontal bars) the relative time spent at depth (15 m intervals) for five skipjack tuna swimming in the open ocean. Grey bars are relative time spent at depth during the night and white bars are relative time spent at depth during the day. Modified from Schaefer and Fuller 2007.

Fig. 4 Representative vertical movement patterns (left) and temperature-depth profiles (right) for **a** Group 2 yellowfin tuna and **b** Group 3 bigeye tuna. Inserts in **b** show an expanded 7-day time period and a detailed 48-h time period. Date-marks indicate midnight of that day. Modified from Musyl et al. 2004; Bernal et al. 2009; M. Musyl and R. Brill, unpublished (data collected near the main Hawaiian Islands)

Fig. 5 Red muscle temperature (T_{RM}) as a function of sea surface temperature (SST) in tunas and the Atlantic mackerel. Grey shaded area represents a T_{RM} below SST. Data are shown as mean $\pm$ s.e.m. for slender tuna (*Allothunnus fallai*, n=30), frigate tuna (*Auxis thazard*, n=7), little tunny (*Euthynnus alletteratus*, n=16), and bigeye tuna (*Thunnus obesus*, n=17). Individual data shown for Atlantic mackerel (*Scomber scombrus*, n=1) and albacore tuna (*Thunnus alalunga*, n=1); linear regressions are shown for Atlantic bluefin tuna (*Thunnus thynnus*, n=162; $T_{RM} = 25.84 + 0.206 \text{ SST}$), skipjack tuna (*Katsuwonus pelamis*, n=53, $T_{RM} = 13.7 + 0.68 \text{ SST}$), and yellowfin tuna (*Thunnus albacares*, n=62, $T_{RM} = 7.47 + 0.81 \text{ SST}$). Transverse section for each species showing medial position of RM and the approximate location of vascular counter-current heat exchangers. Modified from Sepulveda et al. 2008; Bernal et al. 2009.

Fig. 6 a Daily archival tag record of free-swimming bigeye tuna (131 cm fork length, 44.5 kg) off the Hawaiian coast, showing depth (black line) and internal body temperature (red line). Grey shaded areas indicate approximate light levels at sunrise and sunset. Internal temperature taken from a thermistor inserted several centimeters below the skin in the epaxial swimming muscles in close proximity to the first dorsal fin. Red shaded area shows the time during the day at which the fish repeatedly dove below the thermocline. Note that the muscle temperature does not decrease below 17°C. Modified from Musyl et al. 2003. **b** Telemetry record for deep body (i.e., red muscle) temperature from four Atlantic bluefin tuna swimming in a sea-pen (maximum pen depth 17-20 m) off the coast of Nova Scotia. **c** Thermal profile of the water column during the four telemetry experiments (Roman numerals in **b**). Note that the deep body temperature of the tuna remains significantly above ambient temperature during the multiday experiment. All tuna were in excess of 400 kg dressed. Modified from Stevens et al. 2001.

Fig. 7 Archival tag record of free swimming juvenile Pacific bluefin tuna off the California coast, showing depth (blue) and ambient and peritoneal (red line) temperatures. Juvenile bluefin tuna demonstrate rapid bouts of diving associated with foraging behavior that occur prior to a visceral heat increment of feeding event (peritoneal warming). This “bounce diving,” where time at depth is short and interspersed regularly with time at the surface, may be related to cold-induced cardiac bradycardia and subsequent oxygen delivery limitations at depth. Modified from Shiels et al. 2015.

Fig. 8 Cranial temperature as a function of sea surface temperature (SST) or white myotomal (WM) temperature in tunas. Grey shaded area represents a cranial temperature below SST or WM temperature. Insert shows potential heater tissue in the slender tuna. Species-specific data are identified by number: 1=*Auxis thazard* (n=5); 2=*Katsuwonus pelamis* (n=29); 3=*Euthynnus lineatus* (n=4); 4=small *Thunnus thynnus* (n=6); 5=*T. obesus* (triangles); 6=*E. alletteratus* (n=16); 7=*T. alalunga*; 8=*Allothunnus fallai*; 9=giant *T. thynnus*; 10=*T. albacares* (squares). Values are individual data points or mean $\pm$ SD,

linear regressions shown for giant *T. thynnus* [cranial temperature = $21.1 + 0.3 \text{ SST}$]. Data from Stevens and Fry 1971; Linthicum and Carey 1972; Schaefer 1984, 1985; Sepulveda et al. 2007; Runcie et al. 2009; C. Sepulveda unpublished.

Fig. 9 a Relative spectral sensitivity in the eyes of four tuna species (*Thunnus* spp.). Raw data shown, shaded bars indicate range and solid line approximates the mean response; values for bluefin tuna (n=6) are mean $\pm$ S.D. **b** Representative color, intensity and visible light spectral penetration in oceanic and coastal waters. **c** Daytime speed of vision (i.e., flicker fusion frequency, FFF) in the eyes of bigeye and yellowfin tunas and swordfish at ambient temperature and at *in vivo* temperatures (i.e., cranial endothermy; red shaded images). Ambient and *in vivo* temperature (black values) shown next to images and the approximate fold-increase in FFF due to elevated cranial temperatures are shown in red. Modified from Kawamura et al. 1981a; Fritsches et al. 2005; Matsumoto et al. 2009; Horodysky et al. 2016.

Fig. 10 Comparison of *in situ* cardiac performance in albacore tuna (red), bluefin tuna (blue) and yellowfin tuna (yellow). **a** Cardiac output, recorded in isolated perfused spontaneously beating hearts. **a1** Maximal values of heart rate and stroke volume. **b** Rate of Ca^{2+} uptake catalyzed by SERCA2 in ventricular homogenates from different fish species at 25°C. **c** Effect of acute temperature changes, contraction frequency, and adrenergic stimulation (500 nM) on the action potential and **d** on the peak intracellular Ca^{2+} transient ($[\text{Ca}^{2+}]_i$) in Pacific bluefin tuna ventricular myocytes. Slowing of contraction frequency (as indicated by Hz in the legend) and adrenergic stimulation (500 nM) both prolong action potential duration, which together normalize the $[\text{Ca}^{2+}]_i$. Values in **a** are means $\pm$ s.e.m. [bluefin tuna, n=3 (2°C), n=4 (10, 20, 25°C), n=5 (5°C), n=6 (15°C); yellowfin tuna, n=4 (10, 25°C), n=5 (15°, 20°C); albacore tuna, n=1]. Values in **b** represent the average $\pm$ s.e.m. of at least three experiments performed with preparations from three individual fish and **c** are means $\pm$ s.e.m. for 8-11 myocytes. Dissimilar letters in **b** and **d** show significant differences; ANOVA, $P < 0.05$. Effects of adrenaline in **c** are significant (not shown). Modified from Blank et al. 2004; Landeira-Fernandez et al. 2004; Shiels et al. 2015.