BIGEYE TUNA (*THUNNUS OBESUS*) BEHAVIOR
AND PHYSIOLOGY AND THEIR RELEVANCE TO STOCK
ASSESSMENTS AND FISHERY BIOLOGY

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SUMMARY

*Bigeye tuna (*Thunnus obesus*) have distinctive depth distributions and vertical movement patterns. They remain in the uniformed temperature surface layer at night and can descend to greater than 500 m depth at dawn. They thus mirror the vertical migrations of the small nektonic organisms of the deep sound scattering layer and extensively exploit these as a food resource. At their maximum depths, bigeye tuna frequently experience prolonged exposure to ambient temperatures (≈5 ℃) that are up to 20 ℃ colder than surface layer temperature, and oxygen concentrations less than 1.5 ml O_2 l^{-1}. In contrast, skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*T. albacares*) generally limit their forays to depths where water temperatures are no more than 8 ℃ below surface layer temperatures, and ambient oxygen levels are above 3.5 ml O_2 l^{-1}. Understanding the vertical movements and depth distribution of bigeye tuna, as well as the physiological abilities/tolerances and oceanographic conditions controlling them, has been shown key for improving longline catch-per-unit effort analysis and long-term populations assessments in the Pacific. Similar work is needed in the Atlantic.*

RÉSUMÉ

*Le thon obèse (*Thunnus obesus*) présente des distributions en profondeur et des schémas de déplacements verticaux particuliers. Il reste dans la couche superficielle qui a une température constante la nuit et peut descendre à des profondeurs de plus de 500 m à l'aube. Il reflète donc les déplacements verticaux des petits organismes nectoniques de la couche dispersante profonde et les exploite extensivement comme ressource alimentaire. Aux profondeurs maximales atteintes, le thon obèse est fréquemment confronté à une exposition prolongée à des températures ambiantes (≈5 ℃) qui sont jusqu'à 20 ℃ plus froides que la température de la couche superficielle et à des concentrations d'oxygène inférieures à 1,5 ml O_2 l^{-1}. En revanche, le listao (*Katsuwonus pelamis*) et l'albacore (*T. albacares*) limitent généralement leurs incursions à des profondeurs où la température de l'eau ne descend pas de plus de 8 ℃ par rapport à la température de la couche superficielle et où les niveaux d'oxygène ambiants sont supérieurs à 3.5 ml O_2 l^{-1}. La compréhension des déplacements verticaux et la distribution en profondeur du thon obèse, ainsi que les capacités/tolérances physiologiques et les conditions océanographiques les contrôlant, a été considérée comme fondamentale pour l'amélioration des analyses de capture par unité d'effort de la pêcherie palangrière et des évaluations des populations à long terme dans le Pacifique. Des travaux similaires sont nécessaires dans l'Atlantique.*

RESUMEN

*El patudo (*Thunnus obesus*) presenta distribuciones de profundidad y patrones de movimiento vertical característicos. Permanece en la capa superficial de temperatura uniforme por la noche y puede descender hasta profundidades de más de 500 metros al amanecer. De este modo refleja las migraciones verticales de los pequeños organismos nectónicos de la capa de reflexión profunda y explota extensivamente éstos como recurso alimentario. En sus profundidades máximas, el patudo experimenta frecuentemente una exposición prolongada a temperaturas ambientes (≈5 ℃) que son hasta 20 ℃, más frías que la temperatura de la capa de superficie y concentraciones de oxígeno inferiores a 1,5 ml O_2 l^{-1}. Por el contrario, el listado (*Katsuwonus pelamis*) y el rabil (*T. albacares*) limitan generalmente sus incursiones a profundidades en las que las temperaturas del agua no descienden más de 8 ℃ con respecto a*

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las temperaturas de la capa superficial y con niveles de oxígeno en el ambiente que se sitúan por encima de 3,5 ml O_2 l^{-1}. La interpretación de los movimientos verticales y la distribución en profundidad del patudo, así como las tolerancias/capacidades fisiológicas y las condiciones oceanográficas que lo controlan han demostrado ser un elemento clave para mejorar el análisis de la captura por unidad de esfuerzo del palangre y las evaluaciones de poblaciones a largo plazo en el Pacífico. Es necesario desarrollar un trabajo similar en el Atlántico.

1 Phylogenetic position of bigeye tuna

The exact phylogenetic relationship of bigeye (*Thunnus obesus*) tunas to other members of the genus *Thunnus* remains controversial and depends on which anatomical, allozyme, or DNA characters are considered (Gibbs and Collette 1967, Collette 1978, Sharp and Pirages 1978, Block *et al*. 1993, Chow and Kishino 1995, Elliott and Ward 1995, Finnerty and Block 1995, Alvarado Bremer *et al*. 1997, Collette *et al*. 2001). Based on anatomical characters, Collette (1978) originally divided the genus *Thunnus* into two subgenera, the "temperate" subgenus *Thunnus* containing bigeye tuna, bluefin tunas (*T. thynnus*, *T. orientalis*, *T. maccoyii*) and albacore *(T. alalunga)*; and the "tropical" subgenus *Neothunnus*, containing yellowfin tuna (*T. albacares*), blackfin tuna (*T. atlanticus*) and longtail tuna (*T. tonggol*). Subsequent allozyme (Elliott and Ward 1995) and mtDNA sequence data (Block *et al*. 1993, Chow and Kishino 1995) have failed to support this division. Some authors (e.g., Chow and Kishino 1995) have declared bigeye tuna to be an early offshoot of the genus *Thunnus*. Whereas others (e.g., Alvarado Bremer *et al*. 1997) continue to use Collette's (1978) original subgenera nomenclature, but consider bigeye tuna to be more closely related to the "tropical" subgenus *Neothunnus* than the "temperate" subgenus *Thunnus*.

We argue that classification of tunas into categories labeled "tropical" and "temperate" should be abandoned. These terms are generally used to refer to sea surface conditions which are largely irrelevant to tunas, as these species do not live exclusively at the sea surface. Moreover, although yellowfin tuna are caught in "tropical" areas, so are bigeye tuna (e.g., Holland *et al*. 1999, Itano *et al*. 2000). Yet the latter is often classified as "temperate." For the purposes of this review, therefore, we are following the phylogeny proposed by Sharp and Pirages (1978) and Alvarado Bremer *et al*. (1997). Specifically, we assume that bigeye tuna are derived from a tropical tuna ancestor that expanded its vertical range by the evolution of suite of unique characteristics which we will attempt to describe briefly. We are certain, however, that many of physiological and biochemical adaptations of bigeye tuna remain to be discovered.

2 Influence of temperature on vertical movements of tunas and other pelagic fishes

Several authors have attempted to explain distributions of various fishes based on preferences for specific water temperatures (e.g., Magnuson *et al*. 1979, Neill 1979), including those of tunas (e.g., Grundinin 1989, Sund *et al*. 1981, Roffer 1987). But we contend that the concept of "temperature preference" is not generally applicable to tunas (nor as we argue below to billfishes).

Extensive data sets on the vertical movement patterns and depth distributions of juvenile and adult bigeye and yellowfin tuna have been gathered with both acoustic telemetry (Carey and Olson 1982, Yonemori 1982, Holland *et al*. 1990b, Cayré 1991, Block *et al*. 1997, Brill *et al*. 1999) and archival tags (Schaefer and Fuller 2002, Musyl *et al*. 2003). In brief, both adult and juvenile yellowfin tuna spend the vast majority of their time in the uniform temperature surface layer, and generally show only minor day-night differences in depth distributions (**Figure 1**). The vertical movements of yellowfin tuna are nearly body size invariant. Moreover, in areas where the decrease of oxygen content with depth is not limiting, yellowfin tuna depth distributions are set not by a specific depth or water temperature, but by the relative change in water temperature with depth (Block *et al*. 1997, Brill *et al*. 1999). Although making occasional forays down to greater depths and colder water temperatures, yellowfin tuna spend upwards of 90% of the time at depths where the water temperature is no more than 8°C colder than surface layer temperature. The concept that the change in water temperature sets depth distribution has also been shown to be applicable to at least three Istiophorid billfish species: blue marlin *(Makaira nigracans)* (Holland *et al*. 1990a, Block *et al*. 1992, Graves *et al*. 2002, M. Muysl and R. Brill

unpublished observtions), striped marlin (*Tetrapturus audax*) (Holts and Bedford 1990, Brill *et al.* 1993), and black marlin (*Makaira indica*) (Pepperell and Davis 1999, Gunn *et al.* 2002). Like yellowfin tuna, the marlins do occasionally make forays down to colder water temperatures, but spend upwards of 90% of the time at depths where the water temperature is no more than 8°C colder than surface layer temperature. This occurs even though marlins lack counter-current heat exchangers in the vascular system supplying blood to the swimming muscles and, therefore, do not have the ability to sustain swimming muscle temperature significantly above ambient water temperature as do tunas (Lindsay 1968, Brill *et al.* 1994, Graham and Dickson 2001).

In contrast, bigeye tuna regularly expose themselves to temperature changes of up 20°C (from ≈25°C surface layer temperature to ≈5°C at ≈500 m depth) during their daily vertical movements (**Figure 1**). Moreover, there is a group of phylogeneticlly distant species that all behave similarly. Although data are still relatively sparse, studies employing acoustic telemetry (Carey 1990, Carey and Robison 1981, Nakano *et al.* 2003), archival tags (Takahashi *et al.* 2003), and pop-up satellite archival tags (PSATs) (Weng and Block 2004, R. Brill and M. Musyl unpublished observations) have confirmed that the daily vertical movements of swordfish (*Xiphias gladius*) and bigeye thresher sharks (*Alopias superciliosus*) are both closer to those of bigeye tuna than to either yellowfin tuna or the billfish species cited above (**Figure 2**). Swordfish and bigeye thresher sharks, like bigeye tuna, remain near the surface at night but descend during the day, routinely to depths where water temperatures are ≈5°C. Swordfish do occasionally make upward excursions into the mixed layer to warm their muscles (Carey and Robison 1981, Carey 1990), as do bigeye tuna.

3 Ecological implications of vertical movement patterns

Josse *et al.* (1998) recorded the movements of a bigeye tuna in French Polynesia carrying a depth-sensitive ultrasonic transmitter while simultaneously using an echosounder to follow the movements organisms (squid, euphausids, and mesopelagic fish) which comprise the sound scattering layer (SSL). The organisms of the SSL undertake extensive diurnal vertical migrations (Longhurst 1976, Nakamura, 1993, Yatsu *et al.* 1999, Marchal and Lebourges 1996), and Josse *et al.* (1998) found the excursions of bigeye to tuna mirror their movements. Bigeye tuna's ability to access great depths thus allows them to effectively exploit this deeper-living prey even after they descend at dawn (Roger and Grandperrin 1976, Grudinin 1989, Marchal *et al.* 1993, Marchal and Lebourges 1996, Josse *et al.* 1998, Bertrand *et al.* 1999, 2002a, 2002b, Dagorn *et al.* 2000a, 2000b, 2000c).

Certainly the ability to be able to mirror the movements of a vertically migrating prey confers selective advantages. Yet yellowfin tuna do not make as extensive vertical excursions as do bigeye tuna. Studies of the stomach contents of bigeye and yellowfin tunas landed in the central Pacific, equatorial Indian, and central Atlantic oceans show dietary overlap (King and Ikehara 1956, Kornilova 1981, Pelczarski 1988). But the differences led the latter two authors to conclude that bigeye tuna fed at deeper depths than yellowfin tuna. Recent studies of tunas' trophic ecology near the main Hawaiian Islands have (via gut samples) confirmed that bigeye tuna generally select mesopelagic prey from the SSL, while yellowfin tuna feed primarily on epipelagic prey from the mixed layer even when the fish are caught in the same areas (Grubbs and Holland 2003). Carey (1990), using similar technologies to Josse *et al.* (1998), found that the daily vertical movements of swordfish also to mirror the movements of the SSL. It should be noted, however, that the swordfish are most likely following the vertical movements of larger cephalopods (e.g., the neon flying squid, *Ommastrephes bartramii*), which they exploit as a primary food resource (Nakamura 1985). The larger squid are, in turn, following the movements of the SSL (Nakamura 1993, Smale 1996).

Based on the foregoing discussion, we have therefore organized our brief review around two central hypotheses. The first, as suggested by Childress and Nygaard (1974), is that the fishes and crustaceans of the SSL migrate downward during the day into the cold, oxygen minimum layer as a refuge against predation. The second, as suggested by Josse *et al.* (1998), is that the vertical movements of large pelagic predators (i.e., tunas, billfishes, and squids) mirror the movements of their prey to the extent allowed by each species' physiology. Studies of crustaceans living in the cold oxygen minimum zone have shown that they are able to do so due to a suite of morphological, physiological, and biochemical adaptations (e.g., Childress 1971, Belman and Childress 1975, Sanders and Childress 1990). We assume the selection pressure to evolve these unique abilities to have been predator avoidance. But certain pelagic species (e.g., bigeye tuna, swordfish, bigeye thresher sharks, neon flying squid) have likewise evolved physiological abilities to invade the SSL organisms' predator refuge. We view this situation as a sort of "physiological arms race."

4 Fisheries assessment implications of tuna vertical movement behaviors

The limitations of employing nominal catch-per-unit effort (CPUE) data for population assessments have long been recognized (e.g., Ricker 1940), because equating nominal CPUE with abundance requires the assumption that three situations are occurring over the time and space for which population assessments are being made:

1 Vulnerability to fishing gear is equal.
2 Fishing effort is randomly distributed.
3 The target species is randomly distributed.

As extensively discussed by Hilborn and Walters (1992) and Fréon and Misund (1999), the above requirements are only rarely met. The terms "apparent abundance" or "relative apparent abundance" (e.g., Marr 1953) are therefore generally used in recognition that variations in CPUE may not be associated with changes in abundance, but rather to changes in "availability" or "gear vulnerability" due commonly to variations in environmental conditions and the fishes' responses to them.

The problems are especially acute when trying to estimate abundance of highly mobile pelagic fishes, such as tunas, from CPUE data. We argue, as have others (e.g., Blackburn 1965, Brill and Lutcavage 2001, Sharp 1978, 2001) that because tunas are so highly mobile, robust population assessments depend on a thorough understanding of both short- and long-term movement patterns. Barkley *et al.* (1978), Sharp (1978), Sund *et al.* (1981), Brill (1994), Fréon and Misund (1999), and Holland *et al.* (2001) all describe how the effectiveness of specific fishing gears are influenced by oceanographic conditions and the horizontal movements and vertical distributions of various tuna species. In longline fishing, gear is deployed such that hooks target specific depths. Longline CPUE data are, therefore, as likely to be a function of effective gear targeting (e.g., placing longline hooks at depths where fish are aggregated), as they are to reflect true fish abundance (Boggs 1992, Hinton and Nakano 1996, Hinton and Deriso 1998, Bigelow *et al.* 2002, Bertrand *et al.* 2002a, Bach *et al.* 2003).

There are currently two generally approaches for CPUE standardization utilized in pelagic fisheries. In the first (more traditional) method, catch and effort data are fitted by employing generalized linear models (GLMs). This statistical approach attempts to account for the variation in CPUE based on nominal effort by fitting a predicted CPUE to observed CPUE. GLMs are general in scope. They usually do not, however, include what we consider to be an important model input – variations in environmental conditions and the fishes' responses to them. These effects can be very difficult to quantify and critical values that are of interest to population modelers are not well described. The second method employs habitat-based models to predict fish distributions and builds on concepts presented by Barkley *et al.* (1978) and Sharp (1978). In the deterministic "habitat based standardization" (HBS), effective effort is modeled as the joint probability of the effectiveness of the gear (e.g., the depths of longline hooks) and the distribution of the species in the water column. The vertical distribution of particular tuna or billfish species is, in turn, based on habitat preferences and physiological tolerances in combination with environmental data (e.g., changes in temperature and/or oxygen conditions with depth) (**Figure 3**). HBS has been successfully used to estimate effective longline effort for both bigeye and yellowfin tunas (Bigelow *et al.* 1999, 2003) and several billfishes (Hinton and Nakano 1996, Hinton and Deriso 1998) captured in the Pacific. To the best of our knowledge, with the exception of Graves *et al.* (2002), this method is yet to be routinely applied to pelagic species in other than the Atlantic.

HBS methods may have a greater intuitive appeal than GLMs, but concerns have been raised regarding various assumptions inherent in the HBS method (e.g., Goodyear 2003a). These include:

1 the unquantified effect of inaccurate habitat preferences and associated vertical distributions for correcting CPUE,
2 the inapplicability of transferring habitat preferences of particular species to another species or to other oceans (**Figure 3**),
3 difficulties inherent in predicting actual longline hook depth and gear behavior while deployed,
4 differential catchability of various fishes while the gear is sinking, settled, or rising.

Unlike a GLM, a deterministic HBS does not estimate parameters by fitting to the catch data. Effective effort estimates may therefore not predict catch better than nominal effort if the above assumptions are not met, and especially if habitat preferences are structured incorrectly (**Figure 3**).

The question is how to determine the effects of environmental conditions on the depth distributions, travel speeds, residency times, propensity to aggregate, and eventually the vulnerability of highly mobile pelagic fishes to specific fishing gears? Numerous investigators have tried to delineate the habitat requirements of various tuna species by correlating catch statistics with oceanographic conditions averaged over time and space (e.g.,

Grudinin 1989, Hanamoto 1987). As we and other investigators have previously argued (Sharp 1978, 1995, Brill 1994), such correlations do not necessarily elucidate the requisite relationships because the data are often not gathered simultaneously, and because broad error terms associated with both make it difficult to demonstrate meaningful relationships (e.g., Podestá *et al.* 1993, Goodyear 2003b). Moreover, using catch statistics to determine the effects of environmental conditions on catch statistics (i.e., calculate a measure of gear vulnerability), without an independent estimate of abundance, can easily result in tautology (Brill 1994). The resulting conclusions have limited predictive value.

We contend, as have others (e.g., Hunter *et al.* 1986, Hampton *et al.* 1998, Bach *et al.* 2003), that measuring and ultimately predicting the effects of oceanographic conditions on the behaviors of tunas and other pelagic species requires direct observation. This can be done by equipping fish with either acoustic telemetry transmitters or archival (i.e., electronic data recording) tags[2]. These techniques allow detailed records of both the horizontal and vertical movements of pelagic fishes to be obtained and correlated with environmental conditions, (e.g., Dizon *et al.* 1978, Carey and Robison 1981, Carey and Olson 1982, Holland *et al.* 1990a, 1990b, Carey 1990, Brill *et al.* 1993, 1999, Dagorn *et al.* 2000a, 2000b, Arnold and Dewar 2001, Gunn and Block 2001, Graves *et al.* 2002, Musyl *et al.* 2003). Models capable of accurately predicting the movements and depth distributions of tunas and billfishes can subsequently be developed when detailed records of fish behavior are combined with data on changes in temperature or oxygen levels with depth, and/or forage abundance (i.e., movements of the organisms associated with the deep scattering layer, etc.) (Cayré and Marsac 1993, Josse *et al.* 1998, Bertraund *et al.* 2002). Furthermore, although this concept will not be extensively discussed here, we believe that behavioral studies can benefit significantly when they exist in a reciprocal relationship with laboratory research on physiological abilities and tolerances (Bushnell *et al.* 1990, Bushnell and Brill 1991, 1992, Lowe *et al.* 2000). By using this approach, each technique generates hypotheses that can be subsequently tested with the other (Brill 1994, Brill and Bushnell 2001).

In the Pacific, when applying HBS models, vertical distribution of blue marlin, striped marlin and swordfish has been assumed to be limited to the mixed layer and the change in temperature relative to the mixed layer (Hinton and Nakano 1996, Hinton and Deriso 1998). In contrast, the vertical distribution of bigeye tuna was related to ambient temperature (Bigelow *et al.* 2002), although future modeling efforts may consider additional factors that influence behavior and vertical distribution, such as ambient light levels or the depth of the deep scattering layer (Dagorn et. al. 2000a, Bertrand *et al.* 2002a, 2002b, Schaefer and Fuller 2002). Acoustic tracking and archival tagging studies have also shown, however, that bigeye tuna can remain in the surface layer both day and night when associated with floating objects or seamounts (Schaefer and Fuller 2002, Musyl *et al.* 2003). These specific behaviors are important for resource assessment issues as the behaviors of bigeye tuna around seamounts, and especially floating objects, make them significantly more vulnerable to a variety of fishing methods (Deriso *et al.* 1998, Itano and Holland 2000, Sibert *et al.* 2000, Holland *et al.* 2001).

5 Specific physiological adaptations of bigeye tuna

"Physiology" is generally defined as processes by which organisms maintain a relatively constant internal milieu and normal cellular function. Physiology is, therefore, the collection of internal cellular and organ-scale processes permitting (amongst other things) the conversion of ingested food to expendable energy for maintenance, growth, locomotion and reproduction, the detection and capture of prey, etc. For the purposes of fisheries science, however, physiology might best be thought of as the "transfer function" that relates the physical environment to species-specific behaviors and distributions. As such, we argue that a thorough understanding of the physiology and physiological abilities and tolerances of highly mobile pelagic species (i.e., tunas and billfishes) is essential in order to understand (and eventually predict) changes in behavior, distribution, and changes in gear vulnerability occurring in time and space.

Understanding of the sensory biology of tunas (and obviously other top pelagic predators) is likewise important. Sensory mechanisms (vision, olfaction, hearing, electro-, mechano-, and magnetic field detection) allow tunas to sample their environment in the search for food and mates, and to stay within physiologically tolerable ambient temperature and oxygen conditions. Yet we know relatively little of these mechanisms or the sensory biology of tunas and other large pelagic fishes in general. As a result, we will only discuss the sensory biology of bigeye tuna briefly. Clearly we need a better understanding of the sensory systems of pelagic fishes (e.g., detection thresholds and sensitivities), as well as the properties of the stimulus being detected (e.g., dispersion of odors,

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[2] Instrumented longlines have also been shown to be suitable for studying the vertical distribution of pelagic fishes (Boggs 1992; Bach *et al.* 2003).

propagation of sound, deterioration of visual images). This, in turn, will permit better modeling of physical processes influencing the distribution and movement of oceanic top predators at different spatio-temporal scales.

5.1 Ambient temperature and behavioral/physiological thermoregulation

Neill *et al*. (1976) and Stevens and Neill (1978) hypothesized that the main selective advantage of tunas' vascular counter-current heat exchangers (described by Kishinouye 1923, Carey and Teal 1966, Carey 1973, Graham and Dickson 2001) is that they slow rates of deep red muscle temperature change following abrupt reductions in ambient temperature. Vascular counter-current heat exchangers therefore provide tunas an enhanced thermal inertia compared to other similarly sized fishes. Neill *et al*. (1976) and Stevens and Neill (1978) further argue that enhanced thermal inertia allows tunas to maintain higher activity levels for longer periods when diving below the thermocline, and thus to escape predators or exploit deep food resources more effectively. Because the rate of change of deep red muscle temperatures following an acute ambient temperature change is also inversely proportional to body size (i.e., larger individuals have a larger thermal inertia and slower rates of muscle temperature change than smaller fish), a natural extension of Neill and Stevens' hypothesis is that large adult tunas should make more extensive vertical movements than juvenile fish. Large adult tunas should have the ability to spend more time below the thermocline, and thus exploit food resources not available to smaller individuals. This hypothesis, of course, assumes muscle temperature is indeed the factor limiting vertical movements below the thermocline. But, as described above, this is not the case.

The vertical movement patterns of tunas and billfishes appear to be species-specific and generally size independent. How bigeye tuna are apparently able to exploit deeper food resources than yellowfin tuna (and blue, black, or striped marlin) cannot be explained based on hypotheses about the limiting effects of temperature on swimming activity, nor the selective advantages afforded to tunas by the presence of vascular counter-current heat exchangers. Why do large adult yellowfin tuna (or large marlin) apparently not take advantage of their greater thermal inertia to exploit the vertically migrating organisms of the SSL, a food resource that even sub-adult bigeye tuna apparently follow down into ≈5°C water during daylight hours (Musyl *et al*. 2003)? It is possible that species differences in the anatomy of vascular counter-current heat exchangers in bigeye and yellowfin tunas [described in Godsil and Bayers (1944)], or differences in the physiological thermoregulatory abilities of yellowfin and bigeye tunas (i.e., differences in the ability to control the efficacy of vascular counter-current exchangers) explain the difference in behaviors. Available physiological evidence, however, indicates that bigeye and yellowfin tunas have roughly equivalent physiological thermoregulatory abilities (Dizon and Brill 1979, Holland *et al*. 1992, Brill *et al*. 1994, Holland and Sibert 1994, Dewar *et al*. 1994, Graham and Dickson 2001).

5.2 Ambient temperature and cardiac function

Although there are clear instances where the depth distribution of tunas are set by the depth distribution of their prey (e.g., Block *et al*. 1997, Marcinek *et al*. 2001), the dichotomous depth distributions of yellowfin and bigeye tunas in the same areas in the central Pacific implies that one or more abiotic factors are having an impact on their vertical movements. It is possible that changes in oxygen levels in the water column may be limiting, but in the central Pacific significant decreases in ambient oxygen do not occur in the portion of the water column occupied by yellowfin tuna (Brill *et al*. 1999). Rather, we argue that it is the effect of acute reductions in ambient temperature on cardiac function that limits the depth distribution of yellowfin tuna. We further argue that the same mechanism explains the apparent limiting effects of temperature change on the depth distribution of yellowfin tuna and marlins throughout their range in those areas where the decrease in oxygen with depth is not limiting.

In spite of the presence of vascular counter-current heat exchangers, tunas lack the ability to maintain cardiac muscle temperature significantly above ambient regardless of body size or regional endothermy. This occurs because the heart is near the ventral body wall and on the "downstream" side of the vascular heat exchangers. Because tunas' hearts are outside the area warmed by metabolic heat production, and because the blood supply to the coronary circulation arises directly from the gills, cardiac tissue remains within 1°C of ambient temperature and reflects almost immediately changes in ambient temperature (Carey and Gibson 1983, Carey *et al*. 1984).

More important, acute reductions in ambient temperature result in parallel decreases in heart rate and cardiac output in tunas (Brill 1987, Korsmeyer *et al*. 1997a, Blank *et al*. 2002, R. Brill, K. Cousins, and T. Lowe, unpublished observations). This occurs because, unlike most teleosts, tunas depend more on increases in heart rate than increases in stroke volume (i.e., the volume of blood pumped per heart beat) when elevated levels of cardiac output are needed such as during elevated activity or when recovering from exhaustive exercise (Brill and Bushnell 1991b, Farrell 1991, Farrell *et al*. 1992, Bushnell and Jones 1994, Farrell 1996, Korsmeyer *et al*.

1997b, Brill and Bushnell 2001). Moreover, tunas increase heart rate primarily by reducing activity in the vagus (X cranial) nerve (Keen *et al*. 1995), a situation which can be mimicked by the injection of vagolytic drugs such as atropine. But in yellowfin tuna, reductions in heart rate in response to acute 10°C reductions in ambient temperature are not reversible with the injection of atropine (**Figure 4**). This means that yellowfin tuna (and by implication other tuna and billfish species) have no ability to effect an increased heart rate and cardiac output following acute reductions in ambient temperature.

The question remains as to how bigeye tuna (as well as swordfish and bigeye thresher sharks) are able to apparently maintain cardiac function in the face of the up to 20°C ambient temperature reductions (**Figures 1** and **2**) to which they regularly subject themselves during their rapid vertical movements (i.e., to achieve their extensive vertical mobility and their apparent ability to exploit food resources well below the thermocline). There are several possible answers. Cardiac function could be far less impaired by acute reductions in ambient temperature. Heart rate may be less affected by temperature or, like other teleosts (e.g., Azuma *et al*. 1998), bigeye tuna may be able to compensate for reductions in heart rate by increasing stroke volume. But in the only *in vivo* study of bigeye tuna cardio-respiratory physiology, fish exposed to acute reductions in ambient oxygen responded with a decrease in heart rate that was unaccompanied by increases in stroke volume, and cardiac output fell with heart rate (Bushnell *et al*. 1990). Recent biochemical studies (Swimmer *et al*., submitted) have also failed to find any explanatory differences between yellowfin and bigeye tuna. Unfortunately, the requisite *in vivo* experiments monitoring cardiac function in the face of acute reductions of ambient temperature in bigeye tuna are yet to be conducted, as bigeye tuna are generally not available in captivity. Recent studies on bluefin tuna hearts have shown, however, some unique physiological characteristics suggestive of mechanisms allowing cardiac output to be maintained in the face of acute temperature change (Blank *et al*. 2004, Landeira-Fernandez *et al*. 2004). Adult Atlantic bluefin tuna, like bigeye tuna, tolerate acute ambient temperature changes of 16°C or more during their daily vertical movements (Wilson *et al*., in press).

5.3 Tolerance of acute reductions in ambient oxygen

Bigeye tuna are also apparently more tolerant of the reduced ambient oxygen levels (hypoxia) occurring with depth than are other tunas. Bigeye tuna routinely reach depths where ambient oxygen content is below 1.5 ml l^{-1} (Hanamoto 1987, Musyl *et al*. 2003). In contrast, a reduction of oxygen content to only 3.5 ml l^{-1} limits the depth distribution of skipjack and yellowfin tunas (Barkely *et al*. 1978, Gooding *et al*. 1981, Bushnell and Brill 1991, Cayré 1991, Cayré and Marsac 1993, Brill 1994, Korsmeyer *et al*. 1996). In laboratory studies, the onset of cardio-respiratory adjustments seen during acute hypoxia occurs at lower ambient oxygen in bigeye tuna, than in skipjack or yellowfin tunas (Bushnell *et al*. 1990).

But the extreme tolerance of low ambient oxygen in bigeye tuna seems incongruous in light of tunas' elevated metabolic rates (Dewar and Graham 1994, Korsmeyer and Dewar 2001). There is generally a direct relationship between a fish species' tolerance of low ambient oxygen and their blood oxygen affinity. Marine and freshwater fishes tolerant of hypoxia typically have blood and/or hemoglobin with a higher oxygen affinity than less tolerant species (Wood *et al*. 1975, Weber *et al*. 1976, Weber and Lykkeboe 1978, Powers 1980, 1985, Yang *et al*. 1992, Jensen *et al*. 1993). Simply stated, fish that are able to tolerate low ambient oxygen conditions have blood with the ability to remove oxygen from the water passing over the gills that does not have much oxygen in it. This modified blood functionality, and resultant increased tolerance of low ambient oxygen, comes at a cost however. Fishes tolerant of hypoxia are generally sluggish and have lower maximum metabolic rates. This occurs because blood with high oxygen affinity can not readily offload the oxygen it's carrying at the tissues, thereby compromising rates of maximum oxygen delivery. Fish with reduced maximum metabolic rates forgo all accompanying selective disadvantages conferred by high maximum metabolic rates (e.g., high growth rates, fast recovery from exhaustive exercise, etc.) (Brill 1996).

A specific example can be found in the scorpaenid fishes *Sebastolobus alascanus* and *S. guttata* studied by Yang *et al*. (1992). The former occurs predominantly within the oxygen minimum zone on the upper continental slope (400-1200m), and can regulate oxygen uptake rates down to down to ambient oxygen levels of 0.3 ml O2 l^{-1}. In contrast, the latter lives in shallow water (< 180 m) and shows decreases in oxygen uptake rates when ambient O$_2$ concentrations fall below 1 ml O$_2$ l^{-1}. The oxygen affinity of *S. guttata* blood is significantly above that of *S. alascanus* blood. In other words, the species more tolerant of low ambient oxygen has blood with a higher oxygen affinity. But the metabolic rate of the *S. alascanus* is approximately one half that of *S. guttata*, when measured at the at the same temperature, clearly demonstrating that blood with a high oxygen affinity necessary for tolerating low ambient oxygen conditions can compromise rates of oxygen delivery to the tissues.

Given their greater tolerance of hypoxic conditions, it would be predicted that bigeye tuna would have blood with a higher oxygen affinity than yellowfin tuna. Indeed this is the case (Brill and Bushnell 1991a, Lowe *et al*.

2000). Bigeye tuna have evolved blood with an unusual characteristic that enables them to be both tolerant of low ambient oxygen, and simultaneously able to maintain elevated metabolic rates characteristics of tunas (Lowe *et al*. 2000). In brief, bigeye tuna blood shows a large decrease in oxygen affinity as it is warmed during passage through the vascular counter current heat exchangers. As a result, oxygen off-loading in the swimming muscles is not compromised even though bigeye tuna blood has a high oxygen affinity under the conditions occurring during the blood's passage through the gills. As shown in **Figure 5**, bigeye tuna blood operates on oxygen dissociation curve "#1" during its passage through the gills, and on the right shifted (lower oxygen affinity) curve "#2" during passage through capillaries of the warmed deep red muscle. The high oxygen affinity seen in bigeye tuna blood thus provide 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 unusual characteristic of bigeye tuna blood (where oxygen affinity is reduced as it is warmed during passage through the vascular counter-current heat exchangers) requires maintenance of elevated muscle temperatures and may explain bigeye tuna's regular upward excursions into the warm surface layer (**Figure 1**). After spending time in conditions where ambient temperatures are considerably less than body temperature, bigeye tuna must return to the warm surface layer to increase muscle temperature (**Figure 6**). Bigeye tuna thus return to the warm surface layer to get a "gulp" of heat in a way roughly analogous to the way marine mammal return to the surface to get a "gulp" of air. More important, for bigeye tuna, maintenance of warm muscles (**Figure 6**) is more than advantageous. It is obligatory.

5.4 Visual function in bigeye tuna

It is plausible that different species of tuna may also be limited in their vertical movement patterns based on visual acuity and the ability to see in dim light (Somiya *et al*. 2000). The large eyes of tunas and billfishes, their clear-water habitat, and well developed visual centers in the brain, all suggest that vision is an important sense for feeding and other behaviors (Kawamura *et al*. 1981). The open ocean provides the optically clearest aquatic habitat (Jerlov 1976), allowing horizontal visibilities of up to 40m in brightly-lit surface waters (Clarke & Denton 1962), which makes the visual sense particularly useful for the detection and capture of prey.

The eyes of the bigeye tuna are well developed and with a large spherical lens (**Figure 7**). As in other fish species, the shape of the tuna lens is an adaptation to the aquatic environment. Studies of the accommodative movements of the lens and retinal photoreceptor topography indicate that the visual axis of the bigeye tuna is directed forwards and upwards, as it is in other tuna species, (Tamura and Wisby 1963, Somiya *et al*. 2000). Nothing is known of the visual acuity of bigeye tuna, but it is likely to be as equally well developed as in other tunas (Nakamura 1968). It may well be capable of distinguishing an object of ca. 80 mm in length at a distance of 30 m, which is thought to be typical for pelagic animals (Fritsches 2003a).

The ability to distinguish the different spectral information inherent in the environment (i.e., to see color) has a number of advantages (e.g., detecting and capturing prey, mate recognition, etc.), especially in the clear pelagic habitat. It was surprising, therefore, that earlier work did not find evidence for the presence of color vision in tunas (Kawamura *et al*. 1981, Munz and McFarland 1975). More recent studies on yellowfin tuna (Loew *et al*. 2002) and striped marlin (Fritsches *et al*. 2000, 2003b) have shown that these animals do possess several different visual pigments in their retinal cone cells, which is a prerequisite for color vision. Marlin also show an interesting adaptation to the different spectral bands within their habitat. The three different visual pigments are only found in the area of the eye which is directed towards the brightly-lit and colorful areas above the fish. The part of the eye that views the primarily blue (ca. 475nm) dark water below the fish contains predominately one visual pigment, and its spectral characteristics closely matched to the blue of the water (Fritsches *et al*. 2000, 2003b).

With increasing depths, spectral information is quickly attenuated to a narrow band of wavelengths; therefore color vision based on reflected light is only useful in the surface layers of the water column (Lythgoe 1988). When feeding at depths, bigeye tuna necessarily operate in an environment where the spectral band of the surrounding light is very narrow. Recently acquired anatomical evidence has shown the existence of two types of photoreceptors (**Figure 7**) suggesting that bigeye tuna might have two visual pigments, allowing them to detect spectral differences in their environment. However, the second photoreceptor type is only found sporadically in the retina. Moreover, a preliminary study of visual pigments in bigeye tuna using microspectrophotometry revealed only one visual pigment with an absorbency maximum closely matched to the surrounding ambient light at depth (max = 488nm, K. Fritsches, unpublished results). These observations suggest that bigeye tuna have more limited color vision than yellowfin tuna. In the vicinity of FADs and seamounts, however, bigeye tuna adopt a lifestyle exposing them to bright light during the day while feeding in

the spectrally diverse top layer of the water column (Itano *et al*. 2000, Schaefer and Fuller 2002, Musyl *et al*. 2003). It is also possible that bigeye tuna are searching for bioluminescent organisms at depth. Clearly, the "if, when, and how" questions concerning tunas' use of their ability for color vision will need to be studied further using behavioral methods, a considerable challenge given the remote habitat of these species.

All fishes adapt their eyes to daytime and nighttime light conditions through physical rearrangement of the position of their cone and rod cells (the bright-light and dim-light photoreceptors, respectively; Ali and Wagner 1974, Masuma *et al*. 2001). At dawn, rods contract away from the light-facing surface of the retina, and become surrounded by a dark pigment. Simultaneously, the cone cells do the opposite. At dusk these processes are reversed. The cone cells elongate away from the light, allowing the rods to physically move closer to the surface of the retina. These positional changes of the photoreceptor cells within the retina have a number of physiological effects. In yellowfin tuna for example, light sensitivity increases approximately 10 times between daytime and nighttime (**Figure 8**). Surprisingly, these changes are also observed in isolated retina, suggesting a strong circadian clock inherent in retinal tissue (**Figure 8**, K. Fritsches and E. Warrant, unpublished results).

The attenuating properties of even the clearest ocean water quickly reduce surface daylight intensities. By 600m, ambient light intensity is roughly equivalent to that at night at sea level provided by starlight alone (Warrant 2000). Therefore, as bigeye tuna descend at dawn (**Figure 1**), their visual systems are presented with a considerable challenge to adapt their light-gathering abilities to very low light levels. Bigeye tuna have eyeshine which is caused by a tapetum lining the back of the eye (Kawamura *et al*. 1981, Somiya *et al*. 2000). This reflective surface improves photon (light) catch and is commonly found in animals inhabiting a low-light environments (Nicol 1989). The large photoreceptors seen of bigeye tuna (**Figure 7**) also improve photon catch, increasing the sensitivity of the eye and therefore its ability to detect objects such as prey in dim light (Fritsches *et al*. 2003a).

As part of the adaptation to dim light, visual systems tend to slow down the speed of light-gathering in the photoreceptors (Lythgoe 1979), which is analogous to reducing a camera's shutter speed to gather sufficient light in dim light conditions. This process is crucial for maintaining optimal visual abilities in low light levels (Warrant 1999). Using a measure of response speed, the Flicker Fusion Frequency (FFF), yellowfin tuna have been found to have a FFF of over 60 Hz during the day, but a slower (FFF > 30 Hz) and more light sensitive eye during the night (**Figure 8**; Bullock 1991, K. Fritsches & E. Warrant, unpublished results). The FFF of bigeye tuna, however, does not change and remains at 40Hz both day and night (**Figure 8**; K. Fritsches & E. Warrant, unpublished results). In other words, the eyes of bigeye tuna are continuously in the "night mode." This is not surprising as bigeye tuna (like swordfish and bigeye thresher sharks, **Figure 2**) generally live in almost constant dim-light conditions, again suggesting an adaptation to their extensive vertical movements. In summary, bigeye tuna show specific adaptations for vision in dim light, strongly suggesting that vision plays an important role for feeding at depth.

Our knowledge of the visual capabilities of pelagic fish is increasing, but it is still relatively limited and fragmentary. Acquisition of more information on anatomy, optics, and physiology will allow us eventually to model the depth range for visually guided feeding (Warrant 1999). This will, in turn, permit effective modeling of physical processes taking place that influence the distribution and movement of oceanic top predators at different spatio-temporal scales. This information could then be integrated in stock assessment models that currently lack such information.

6 Summary and conclusions

We contend that the vertical movements of tunas and billfishes mirror the movements of their prey to the extent allowed by each species' physiology, and that bigeye tuna have evolved a suite of physiological adaptations (only a few of which are understood) that permit extensive vertical mobility. For example, bigeye tuna regularly expose themselves to temperature changes of up 20°C (from ≈25°C surface layer temperature to ≈5°C at ≈500 m depth) and routinely reach depths where ambient oxygen content is less than 1.5 ml l^{-1}. In contrast, an 8°C decrease in water temperature, or a reduction of oxygen content to only 3.5 ml l^{-1}, appears to limit the depth distributions of yellowfin tunas (and at least three Istiophorid billfishes: blue, striped and black marlin). We also contend (as have others) that, because tunas are so highly mobile, CPUE data are as likely to reflect effective gear targeting as they are to reflect true fish abundance; and that the incorporation of information on the effects of oceanographic conditions on movement patterns can significantly improve stock assessments. The usefulness of habitat-based standardization (HBS) methods are, however, dependent on a thorough understanding of all environmental and physiological factors influencing depth distributions and vertical movement patterns. The continued acquisition of data on the physiological capabilities of bigeye tuna (through laboratory experiments)

and their habitat (through ultrasonic telemetry and archival tags) in different oceanographic areas is therefore crucial. We further argue that such models and standardization procedures should eventually also include the effectiveness of visual function under various ambient light conditions, as well as the environmental factors controlling vertical movements of prey species.

Acknowledgments

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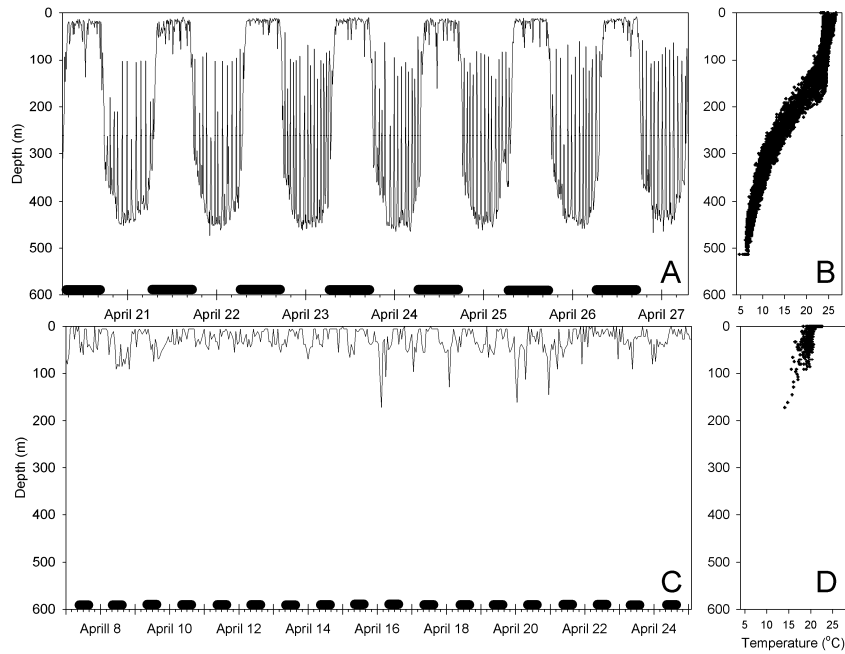
Figure 1. Depth records of adult bigeye and yellowfin tunas. The former was equipped with an archival tag, and the latter with a popup satellite archival tag. The fish were captured and released near the main Hawaiian Islands. Panel A shows a 7-day segment from the bigeye tuna that was at liberty for 84 days and exemplifies the characteristic "W" daytime vertical movement patterns and the dawn and dusk transitions. (The dark bars indicate nighttime.) Panel B shows the simultaneously recorded depth-temperature relationship. Note that the bigeye tuna occupied water temperatures of ≈25 °C during the night, but routinely descends to depths where the water temperatures (≈5 °C) are generally ≈20 °C colder than the surface layer temperatures occupied during the day. Panel C shows an 18-day depth record for a yellowfin tuna, and panel D the depth-temperature relationship. Note that the yellowfin tuna, unlike the bigeye tuna, remained primarily in the uniform temperature surface layer and generally experienced less than ≈8 °C temperature change during vertical movements.
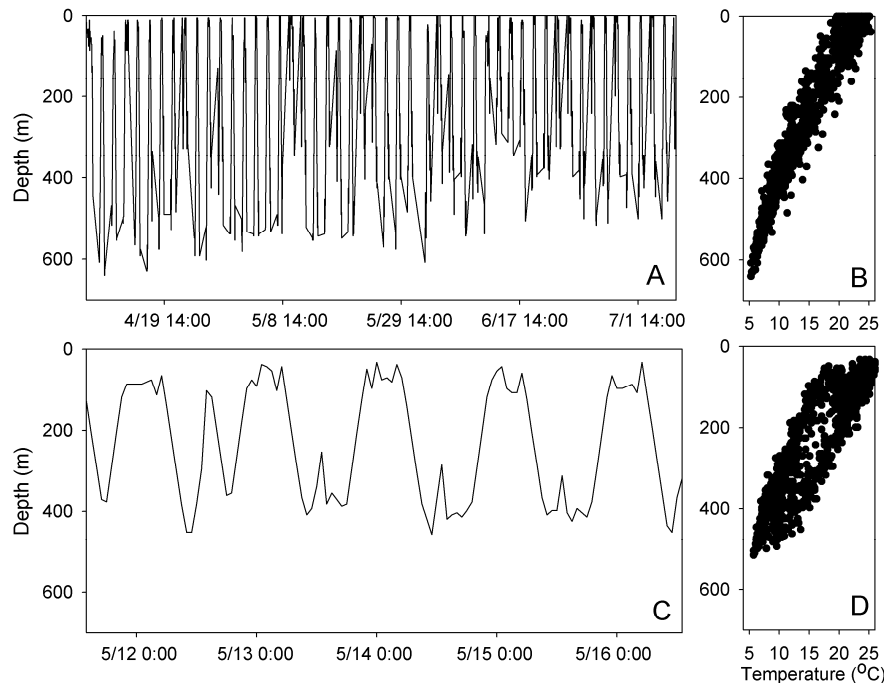
Figure 2. The daily vertical movement patterns of a swordfish (Panel A) and a bigeye thresher shark (Panel C) recorded with a pop-up satellite archival tags in the central north Pacific. Note that in both cases (Panel B and D), the fish occupy water temperatures of ≈25 °C during the night. But both species routinely descend to depths where the water temperatures (≈5 °C) are generally ≈20 °C colder than the surface layer temperatures occupied during the day.

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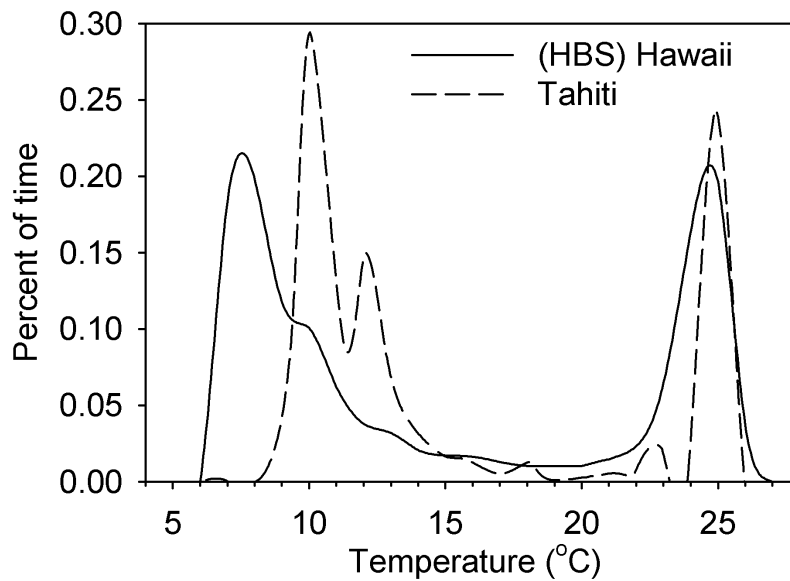
Figure 3. Observed bigeye tuna time-at-temperature data from Hawaii (Musyl et al. 2003) and Tahiti (Dagorn et al. 2000a). Each distribution is bimodal which reflects time spent in cooler, deeper waters during the day and warmer, shallower water at night. These data have been used to correct bigeye tuna CPUE in the deterministic "habitat based standardization" (HBS) method where effort is modeled as the joint probability of the effectiveness of the gear (the depths of longline hooks) and the distribution of the species in the water column. This method, however, may not predict catch better than nominal effort if habitat preferences are structured incorrectly. These techniques necessarily have to take into account differences occurring over time and space, or use a statistical procedure capable of estimating species preferences over appropriate spatial scales.
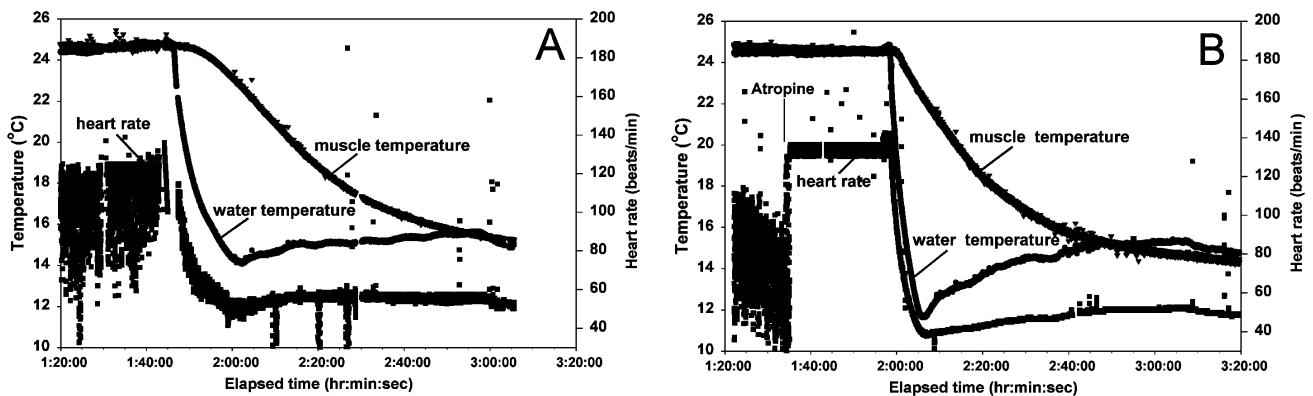
Figure 4. *In vivo* recordings of heart rate, muscle temperature and water temperature during laboratory experiments to measure the effects of an abrupt change in water temperature (from $\approx 25°C$ to $\approx 15°C$) on yellowfin tuna (R. Brill, K. Cousins, and T. Lowe, unpublished observations). Cardiac output (data not shown) follows heart rate because of tunas' limited ability to increase stroke volume (volume of blood pumped per heart beat). When the fish was injected with atropine (Panel B) to remove the vagus nerve's control of heart rate, normal beat-to-beat variability in heart rate disappears and heart rate increases. Note, however, the effects of temperature on heart rate with and without atropine are the same. These results show that yellowfin tuna at 15°C have no ability to increase heart rate and cardiac output to meet increased metabolic oxygen demand when feeding, escaping predators, etc. and imply that it is the effects of ambient temperature on cardiac function that limits the vertical movements of yellowfin tuna. Equivalent experiments on bigeye tuna are yet to be performed, as this species is not generally available in captivity for laboratory studies.
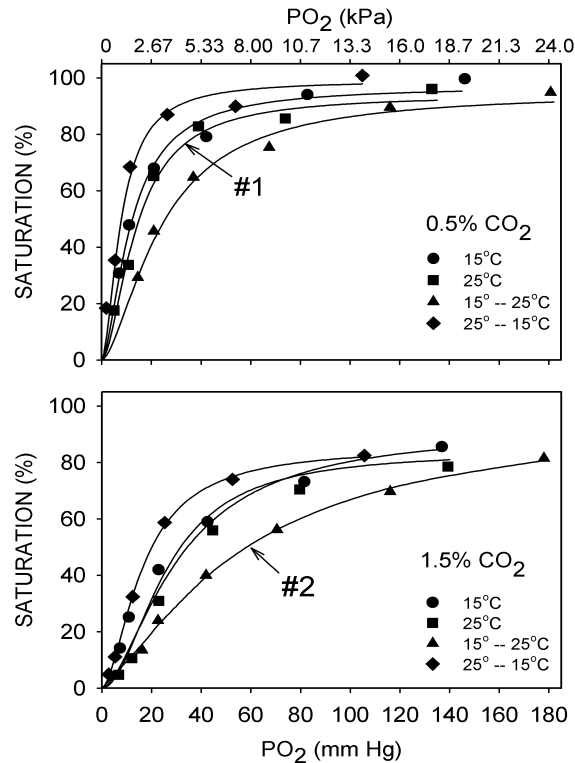
Figure 5. Bigeye tuna blood normally operates on oxygen dissociation curve #1 during its passage through the gills, and on the right shifted curve #2 during passage through capillaries of the warmed deep red muscle. The high oxygen affinity seen in bigeye tuna blood (curve #1) thus provides an effective system for extracting oxygen at high rates from the ventilatory water stream even during periods of low ambient oxygen. The reduction in blood oxygen affinity occurring as the blood is warmed during passage through the vascular counter-current heat exchangers (curve #2), however, ensures high rates of oxygen delivery and off-loading in the capillaries. (Figure is from Lowe et al. 2000.)
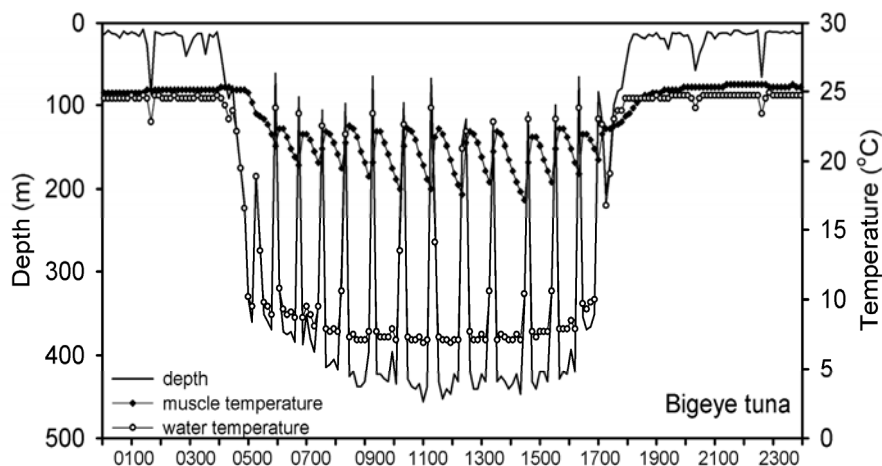
Figure 6. Twenty-hour record of depth, body temperature, and water temperature for 45 kg bigeye tuna carrying an archival tag. Note that after the fish descends at sunrise, it makes regular upward excursions into the warm ($\approx 25°$ C) surface layer. In essence, the fish is returning to near the surface to get a "gulp" of heat in a way analogous to marine mammals returning to the surface to get a "gulp" of air. By this behavior, the fish was able to maintain muscle temperature between ≈ 17-$22°$C, in spite of remaining for up to ≈ 45 minutes in water of ≈ 5-$7°$C. (Figure is from Brill and Bushnell 2001).

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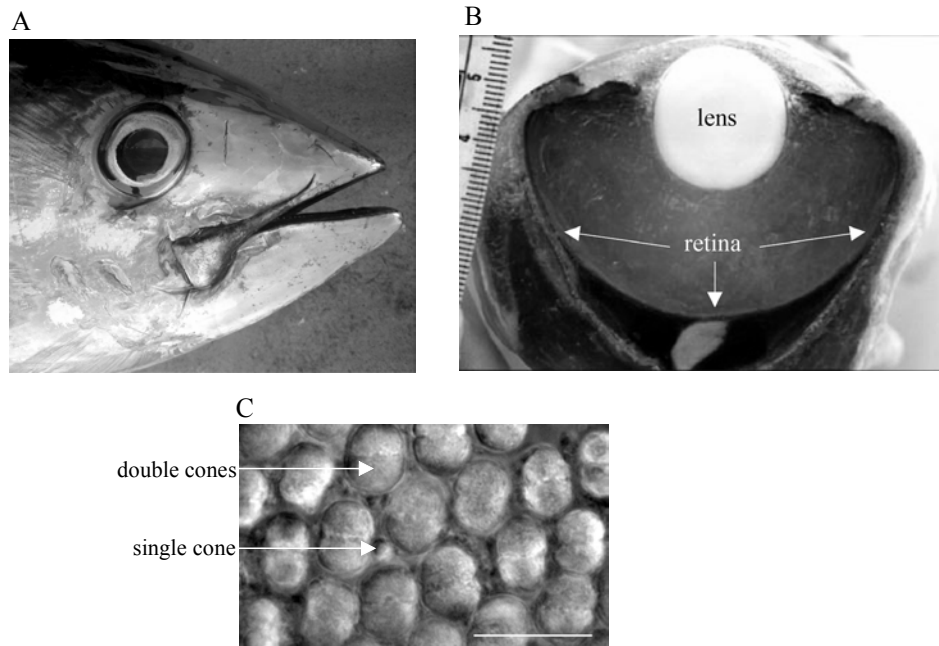
Figure 7. A close-up of a bigeye tuna head, showing the prominent eyes. B. Frozen section of the eye of a bigeye tuna, illustrating ocular components such as the lens and the retina; scale in cm. C. Photograph of cone photoreceptors as seen in a retinal wholemount. Double cones are prevalent while small single cones are found in much lower numbers; scale 25μm.
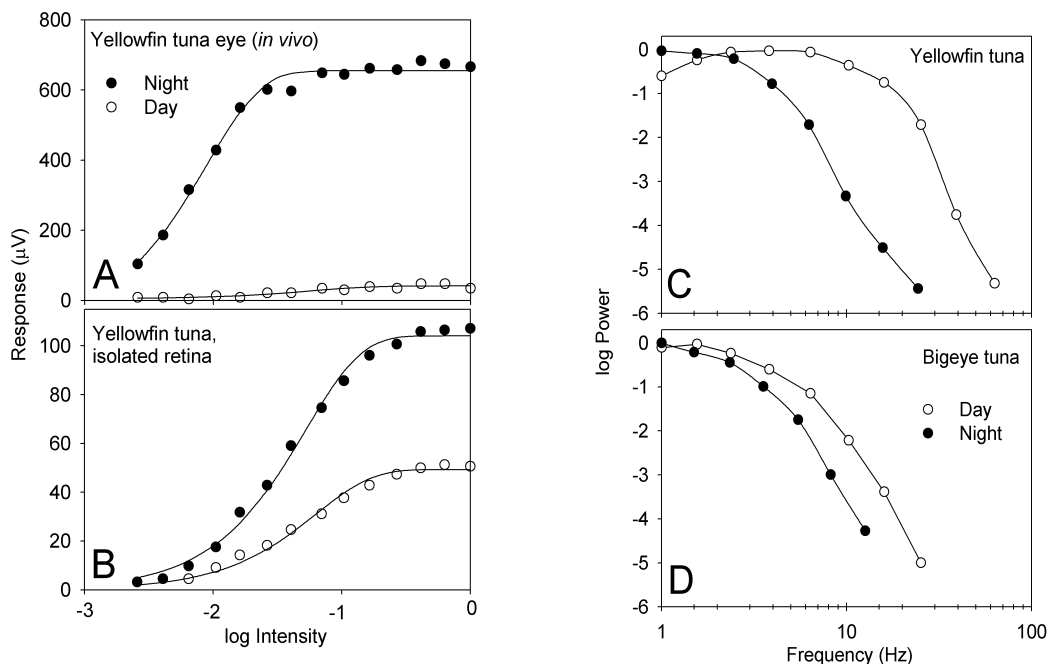
Figure 8. Yellowfin tuna eyes (*in vivo*) show dramatic (≈10x increase) increases in light sensitivity (response to brief single white light flashes) from day to night (Panel A). The change is also seen in isolated retinas (*in vitro*) (Panel B), indicating that the circadian rhythm is inherent in the retinal tissue. Accompanying the changes in light sensitivity are changes in speed (Panels C and D), herein expressed as amplitude of the retinal response to brief streams of repetitive light flashed at various frequencies. Retinas isolated from yellowfin tuna (Panel C) show dramatic day-night differences; the retinas are "faster' (i.e., have a higher flicker fusion frequency) during the day than during the night. Retinas isolated from bigeye tuna (Panel D), in contrast, do not show any day-night changes in function. Rather they appear to remain permanently in the "slower" night-mode.