A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments

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ABSTRACT

Detailed data on the physiological abilities and habitat requirements of some tuna species have now been collected. Laboratory and field studies show tunas are not strictly prisoners of their own thermoconserving mechanisms, but have rapid and extensive control over the efficacy of their vascular countercurrent heat exchangers. Skipjack tuna (*Katsuwonus pelamis*) are, therefore, probably not forced out of formerly suitable habitats as they grow because of the potential for overheating, as formerly thought. Because of their thermoregulatory abilities, bigeye tuna (*Thunnus obesus*) apparently can exploit food resources well below the thermocline by minimizing rates of heat loss when in cold water, and then maximizing rates of heat gain from the environment during brief upward excursions into the warmer mixed layer.

Widely cited estimates of limiting oxygen levels, based on estimated metabolic rates at minimum hydrostatic equilibrium swimming speeds, are not accurate because tunas have exceptionally high oxygen demands even at slow speeds. High metabolic rates, even at slow swimming speeds, most likely result from the high osmoregulatory costs engendered by tunas' large thin gills and/or their other adaptations for achieving exceptionally high maximum metabolic rates. Recent laboratory research and modelling efforts suggest the capacity of tunas' cardiorespiratory systems to deliver oxygen at extraordinarily high rates was evolved to allow rapid recovery from strenuous exercise, rapid digestion, and high rates of gonadal and somatic growth, not high sustained cruising speeds. The rate at which reduced ambient oxygen levels prolong the time required for tunas to recover from strenuous exercise appears to be a good index of habitat suitability, with respect to oxygen.

INTRODUCTION

Significant amounts of biological information (age and growth, reproduction, dispersal, etc.) are involved in population assessments and fisheries management of tunas (e.g. Forsbergh, 1989). Because of a lack of data and integrative models, however, abundances, distributions and movements are often inferred from catch per unit effort (i.e. fisheries data) assuming a constant catchability (i.e. constant gear vulnerability) and random distribution of fishing effort. Factors modifying catchability, such as changes in fishing technology, variations in fishing tactics, and (probably most important) non-random distributions of tunas, are simply 'swept under the rug'. Sharp (1978), however, has clearly shown the assumptions of random and uniform distribution of tunas and fishing effort must be relaxed in a meaningful way (i.e. based on solid biological and environmental information) to derive better indices of abundance and better management decisions. [1]

Various studies have attempted to delineate the habitat requirements of tuna species by employing catch statistics and oceanographic conditions averaged over time and space (e.g. Laevastu and Rosa, 1963; Broadhead and Barrett, 1964; Forsbergh, 1969; Williams, 1970; Blackburn and Williams, 1975). Averaged catch statistics and environmental data do not necessarily elucidate relationships. The data usually were not gathered simultaneously and (as demonstrated by Sharp and Francis, 1976, and Sharp, 1978) error terms associated with both averages are usually too broad to show meaningful relationships. More important, correlations of environmental conditions and catch rates do not prove causation and result in tautology. In other words, we 'know' that tunas are rarely or never caught under a

particular set of environmental conditions because the conditions are unsuitable. How do we 'know' that the environmental conditions are unsuitable? Because tunas are rarely or never caught when and where they occur. Correlations based on such circular logic eventually break down (Sharp *et al.*, 1983; Hunter *et al.*, 1986).

There is consensus that temperature and oxygen conditions drastically alter movements, distributions, and gear vulnerability of tunas (Blackburn, 1965; Green, 1967; Ingham *et al.*, 1977; Barkley *et al.*, 1978; Evans *et al.*,1981; Sund *et al.*, 1981; Hanamoto, 1987). Previously published models have shown that catch per unit effort data could be corrected to provide truer measures of abundance (i.e. more accurate stock assessments) when information about the physiological abilities and tolerances of tunas is combined with oceanographic data (Barkley *et al.*, 1978; Sharp, 1978, 1979; Hanamoto, 1987). Unfortunately, the data on tolerable ambient temperature and oxygen conditions used in these studies were either 'best guesses' or based on laboratory observations of overt behavioural changes caused by extreme conditions.

Only recently has detailed information on the physiological abilities and tolerences of tunas become available. Techniques to capture and maintain tunas in shoreside tanks were first developed at the National Marine Fisheries Service's Kewalo Research Facility in the early 1960s (described by Magnuson, 1965; Nakamura, 1972; Brill, 1992). Pioneering efforts at this laboratory subsequently made it possible to study the behavioural reactions of tunas to extreme conditions of temperature and oxygen (Dizon, 1977; Dizon *et al.*, 1977; Gooding *et al.*, 1981) and to predict habitat requirements of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), bigeye tuna (*T. obesus*) and kawakawa (*Euthynnus affinis*) (Sharp, 1978, 1979; Sund *et al.*, 1981). Due to development of improved handling, anaesthesia, surgical and experimental procedures (Jones *et al.*, 1986, 1990; Bushnell and Brill, 1991, 1992), much more detailed data on tuna physiology have now been collected. Good data are today available on the physiological thermoregulatory abilities and low ambient oxygen tolerances of skipjack, yellowfin, and bigeye tunas (Dizon and Brill, 1979a,b; Bushnell *et al.*, 1990; Bushnell and Brill, 1991, 1992; Holland *et al.*, 1992; Brill *et al.*, 1994; Dewar *et al.*, 1994).

Sund *et al.* (1981) have summarized the older literature on the effects of environmental conditions on tuna distribution, movements and gear vulnerability. The present review summarizes applicable research on the physiological abilities and tolerences of tunas, shows how physiological data might be used to predict distribution, and identifies key research areas.

AMBIENT TEMPERATURE LIMITS AND THERMOREGULATION IN TUNAS

That tunas maintain significantly elevated muscle temperatures and the anatomical basis for this ability (the presence of vascular countercurrent heat exchangers and internalized red muscle) have been agreed upon for many years (Kishinouye, 1923; Carey *et al.*, 1971; Carey, 1973; Stevens *et al.*, 1974; Stevens and Neill, 1978). The advantages conferred by elevated muscle temperatures and the ability of tunas to thermoregulate physiologically have, in contrast, been a matter of some debate (Neill and Stevens, 1974; Graham, 1975; Neill *et al.*, 1976; Brill and Dizon, 1979; Block *et al.*, 1993). In the late 1970s, moreover, Neill *et al.* (1976), Sharp and Vlymen (1978) and Barkley *et al.* (1978) published papers that radically altered thinking about the ability of tunas to maintain elevated muscle temperatures. Whereas previous workers discussed the advantages of this ability, Neill *et al.* (1976) postulated that skipjack tuna may face an overheating problem and may be activity limited in warmer waters. In other words, the ability to maintain elevated muscle temperatures could, under certain circumstances, be a disadvantage because it limits habitat volume. Sharp and Vlymen (1978) subsequently created a mathematical model, based on first principles, that predicts maximum muscle temperatures of yellowfin tuna at various body sizes and swimming speeds. As shown in Fig. 1, the model forecasts that unless yellowfin tuna have some physiological control over the efficacy of their vascular heat-retaining mechanisms, they would face a severe overheating problem even at sustainable swimming speeds. Barkley *et al.* (1978) assumed that skipjack tuna are indeed prisoners of their own thermoconserving mechanisms and are forced out of formerly favourable habitats as they grow because overheating becomes a more severe problem in larger fish. As shown in Fig. 2, in certain areas of the eastern tropical Pacific, water above the thermocline was considered too warm and water below it too deficient in oxygen for large skipjack tuna. Sharp (1978, 1979) subsequently presented similar arguments about environmental limitations on the distributions of other tuna species.

In response to these publications, laboratory studies were undertaken to measure the physiological thermoregulatory abilities of skipjack and yellowfin tunas (Brill *et al.*, 1978; Dizon *et al.*, 1978; Dizon and Brill, 1979a,b). The initial research entailed simultaneous, long-term (more than 12 h) recording of swimming

Figure 1. Output of a model, developed by Sharp and Vlymen (1978), predicting the steady-state maximum muscle temperatures of a yellowfin tuna (6.035 kg, 66.4 cm fork length) at various swimming speeds and levels of vascular countercurrent heat exchanger efficiency. When vascular heat exchangers are 100% efficient, 0% of metabolically produced heat is assumed to be lost via the gills and 100% is lost via the body surface. The model predicts lethal muscle temperatures (more than 10°C above ambient) at sustainable swimming speeds (about 180 cm s^{-1}) unless the efficacy of vascular countercurrent heat exchangers can be reduced. (Redrawn from data presented by Dizon and Brill, 1979a.)
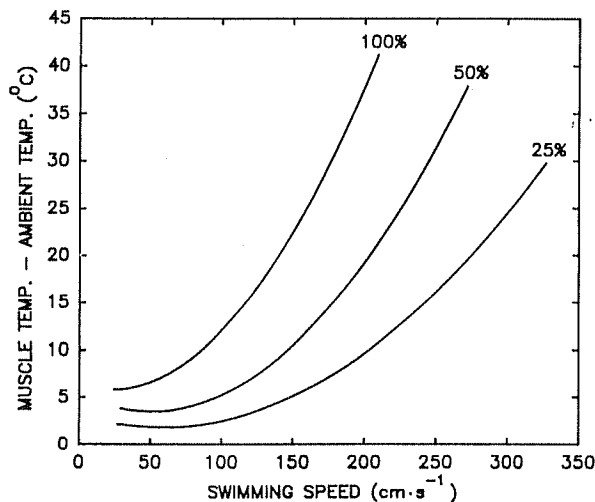

speeds and muscle temperatures, while water temperature was controlled at 20°C, 25°C or 30°C. The resultant data clearly showed that both tuna species could physiologically thermoregulate (i.e. tunas are not strictly prisoners of their own thermoconserving mechanisms). Because the experiments involved steady-state temperature measurements made on slowly swimming fish, neither the speed nor extent of thermoregulatory control could be strictly quantified.[2] Graham and Dickson (1981) were subsequently able to show that albacore (*Thunnus alalunga*) also have physiological thermoregulatory abilities.

More recently, by employing a large swimming tunnel, Dewar et al. (1994) could use non-steady-state techniques (i.e. measurement of rates of muscle temperature change) to gauge the physiological thermoregulatory abilities of yellowfin tuna. They found that this species can control the efficacy of their thermoconserving mechanisms enough to alter rates of muscle temperature change by more than an order of magnitude (Fig. 3). Their data also clearly showed that yellowfin tuna can adjust vascular countercurrent heat exchanger function within minutes.

The pioneering work by Neill et al. (1976), measuring rates of temperature change of skipjack tuna, formed the basis for the Barkley et al. (1978) model of skipjack tuna habitat. Neill et al. (1976) did not specifically investigate the effects of starting ambient temperature on rates of body temperature change. They failed, therefore, to measure the extent to which tunas may physiologically alter their rates of temperature change, later discovered by Dewar et al. (1994). More important, Neill et al. (1976) hypothesized that one main advantage of vascular countercurrent heat exchangers is the large thermal inertia they impart to tunas. They estimated rates of body temperature change in skipjack tuna to be only about 60% of those of other similar-sized teleosts. This would presumably be advantageous when skipjack tuna descend below the thermocline. Because their muscle temperatures decrease slowly, a 1°C or 2°C steady-state excess muscle temperature is rapidly magnified (Fig. 4). Neill et al. (1976), however, apparently did not appreciate a potential disadvantage of large thermal inertia. Tuna species normally occupying waters below the thermocline would warm relatively slowly if they adopted the strategy of regular upward excursions into the mixed layer. When a tuna dives below the thermocline, vascular heat exchangers retard the rate of cooling. In contrast, when a tuna's body temperature is below ambient (i.e. when a fish swims up into the mixed layer), vascular heat exchangers would be equally good at retarding heat gain from the environment and thus reducing the rate of muscle temperature increase.

Using ultrasonic transmitters to measure swimming depth and muscle temperature simultaneously in bigeye tuna, Holland et al. (1990, 1992) found the behaviour of this species to be almost the mirror image of that of skipjack and yellowfin tunas. The latter two species spend most of their time either in the mixed layer or at the top of the thermocline. They only occasionally make forays into deeper, colder waters (Dizon et al., 1978; Holland et al., 1990). Bigeye tuna, in contrast, spend most daylight hours well below the thermocline (in 15°C water) but make regular, brief upward excursions into the mixed layer. Holland et al. (1992) found rates of increase in muscle temperature (measured during upward excursions) to exceed rates of muscle temperature decrease (during the return to 15°C water) by two orders of magnitude (Fig. 5). These observations can only be explained if bigeye tuna reduce the efficacy of their vascular countercurrent heat exchangers while gaining heat from the environment, then increase it again when they return to depths below the thermocline. In other words, bigeye tuna swim up to the mixed layer to get a 'gulp' of heat in a way roughly analogous to

Figure 2. Temperature and dissolved oxygen isopleths along 119°W (eastern Pacific, Barkley *et al.*, 1978). The upper panel shows that in some areas water at less than 18°C forms the floor of the skipjack habitat and in other areas ambient oxygen levels less than 3.5 ml l^{-1} do so. Barkley *et al.* (1978) assumed skipjack tuna are prisoners of their own thermoconserving mechanisms, face an overheating problem in warmer waters, and must occupy cooler waters as they grow. In the lower panel, their model is shown to predict that fish larger than 4 kg have habitable water anywhere above the minimum ambient temperature–dissolved oxygen layers. Habitable water (i.e. at less than 26°C) for fish heavier than 4 kg but lighter than 9 kg is shown by the light cross-hatch. In large areas, this size range of skipjack tuna is predicted to have no access to the surface and to be essentially invulnerable to gear types (live bait fishing, purse seining) that depend on sighting surface schools. Habitable water (i.e. at less than 22°C) for skipjack tuna larger than 9 kg is shown by the heavy cross-hatch. In sizeable areas, large skipjack tuna are predicted to have no habitable water at all because water which is cool enough is too deficient in oxygen. (Reprinted from *Fishery Bulletin*, Vol. 78.)
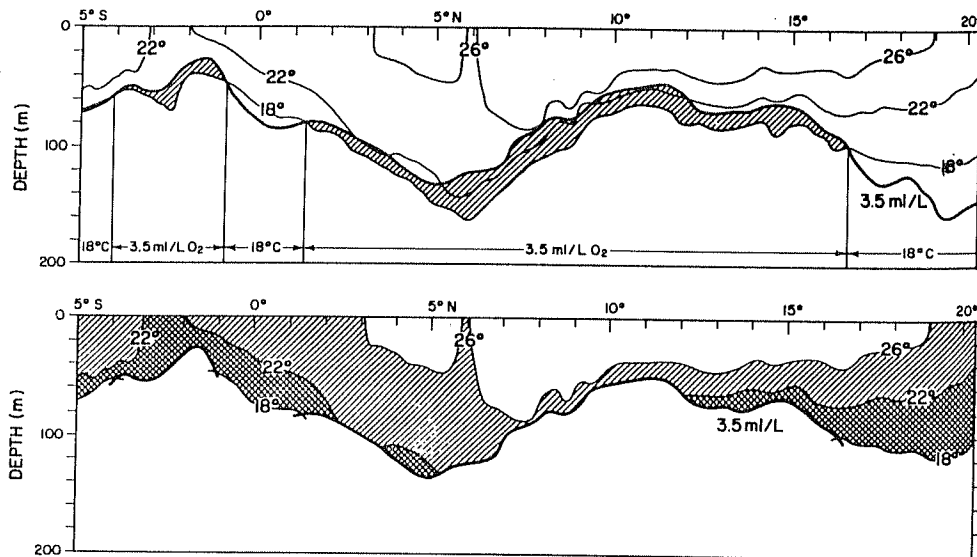
the way marine mammals return to the surface to get a 'gulp' of air. This ability presumably allows bigeye tuna to exploit deep food resources not available to other species. It is yet unclear why skipjack and yellowfin tunas do not display similar behaviour. Differences in movement patterns may reflect differences in counter-current vascular heat exchanger anatomy and perhaps differences in thermoregulatory abilities (Graham, 1975; Holland *et al.*, 1992).

There have been no laboratory studies on the cold temperature tolerance of tunas since the original work of Dizon *et al.* (1977). Their studies suggested that 15°C is the lower temperature limit for skipjack tuna captured near Hawaii. Recent ultrasonic telemetry of the swimming depths of striped marlin (*Tetrapturus audax*) near California (Holts and Bedford, 1990) and Hawaii (Brill *et al.*, 1993) have shown that these fish do not have a fixed temperature preference, but occupy the warmest water available (i.e. the mixed layer). More important, their lower temperature limit appears set by water 8°C colder than the mixed layer, not by a specific temperature. In other 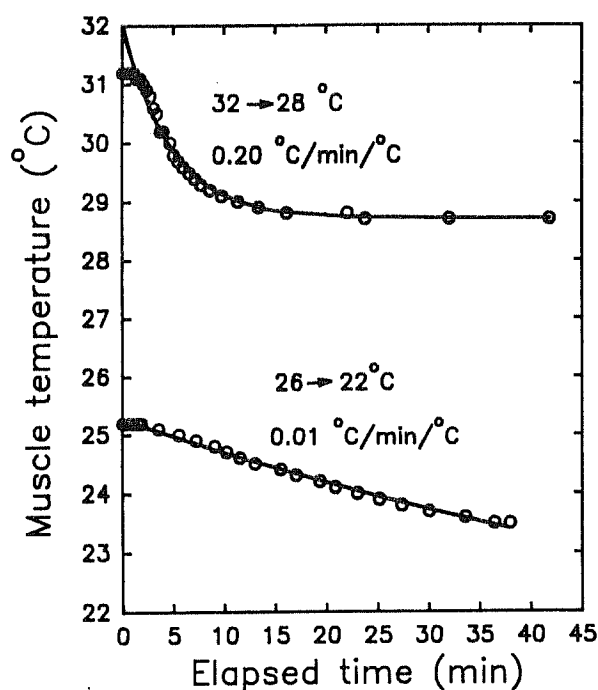words, it is the change in water temperature that is limiting. It remains to be learned if this idea is also applicable to any tuna species.

In summary, there is now abundant evidence that tunas are not strictly prisoners of their own thermoconserving mechanisms, and are not activity limited in warmer waters because they face an overheating problem. Rapid control of the efficacy of vascular countercurrent heat exchangers, in bigeye tuna at least, allows habitat expansion. The exact physiological mechanism tunas employ to control the efficacy of their vascular countercurrent heat exchangers, the amount of control various tuna species possess, and minimum tolerable temperatures should all clearly become active areas of investigation.

AMBIENT OXYGEN LEVELS LIMITING VERTICAL DISTRIBUTIONS

Although some authors believe pelagic fish do not encounter low ambient oxygen (Butler and Metcalfe, 1983; Heath, 1987), this is unquestionably not so. Reduced levels of ambient oxygen do occur at depths
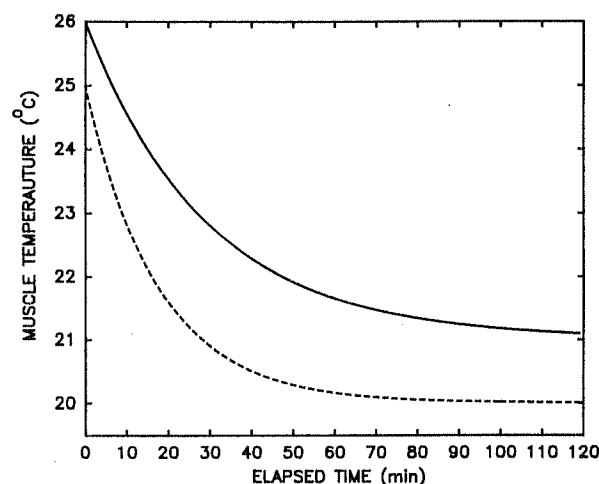
Figure 3. Rates of muscle temperature change in a single yellowfin tuna, swimming at constant speed in a water tunnel, subjected to step changes in water temperature from 26°C to 22°C and from 32°C to 28°C. At the higher starting temperature, the fish presumably has its vascular countercurrent heat exchangers operating at minimal efficacy in order to minimize steady-state excess muscle temperature. The fish therefore cools very rapidly. When subjected to an equivalent ambient temperature change starting at a lower temperature, where vascular countercurrent heat exchangers are presumably operating at a higher efficacy, the rate of cooling is more than an order of magnitude less. (Redrawn from data presented by Dewar et al., 1994.)

Figure 4. Simulated muscle temperatures of a 1.6 kg (sedated) skipjack tuna subjected to a step change in ambient temperature from 25°C to 20°C (solid line), assuming a coefficient of temperature change of $0.034°C \ min^{-1} \ °C^{-1}$ (Neill et al., 1976). The dashed line shows simulated muscle temperatures of an equal-sized teleost without vascular countercurrent heat exchangers that has a coefficient of temperature change 60% greater $(0.057°C \ min^{-1} \ °C^{-1})$. The sustained 1°C body temperature–ambient temperature difference of the skipjack tuna is greatly exaggerated during cooling because of reduced heat loss imparted by vascular countercurrent heat exchangers.

reached by tunas. More important, ambient oxygen levels plainly influence vertical distribution and gear vulnerability (Ingham et al., 1977; Hanamoto, 1987; Forsbergh, 1989). Most studies, however, relied on correlations of apparent gear vulnerability and average depth of reduced ambient oxygen layers to deduce the low ambient oxygen tolerance of various tuna species. The first direct measurements of the low ambient oxygen tolerance of skipjack tuna were not published until 1981 (Gooding et al., 1981).

Tunas use lift generated primarily by their pectoral fins to counteract negative buoyancy. As explained by Magnuson (1973) and Magnuson and Weininger (1978), species with large pectoral fin areas (e.g. yellowfin tuna, bigeye tuna, albacore) can fully counteract negative buoyancies at slower speeds

than those with smaller pectoral fin areas (e.g. skipjack tuna, kawakawa). Tunas, therefore, have size- and species-specific minimum hydrostatic equilibrium speeds (usually abbreviated as U_{100}). Sharp (1978) used these data to predict minimum tolerable oxygen levels of five tuna species at two body sizes (Table 1). He assumed that tunas that could swim slower than the 50 cm (fork length) skipjack tuna studied by Gooding et al. (1981) have proportionally lower oxygen demands and, therefore, tolerate proportionally lower ambient oxygen levels. In other words:

$$\frac{U_{100} \text{ skipjack tuna}}{U_{100} \text{ of other tunas}}$$

$$= \frac{\text{minimum tolerable } O_2 \text{ level of 50 cm skipjack tuna}}{\text{minimum tolerable } O_2 \text{ level of other tunas}}. \quad (1)$$

Although this idea is intuitively appealing, it is based on a misconception. Sharp's extrapolations assume that at low swimming speeds, metabolic oxygen demands are linearly proportional to speed, and at zero

Figure 5. Swimming depth, water temperature, and telemetered deep (red) muscle temperature of a free-swimming bigeye tuna. The fish apparently reduces the efficacy of its vascular countercurrent heat exchangers when returning to the mixed layer in order to maximize heat gain from the environment (i.e. maximize rates of muscle temperature increase). It increases the efficacy of its heat exchangers when diving below the thermocline to minimize rates of muscle temperature decrease. Rates of muscle temperature increase exceed rates of decrease by about two orders of magnitude. (Redrawn from data presented by Holland *et al.*, 1992.)
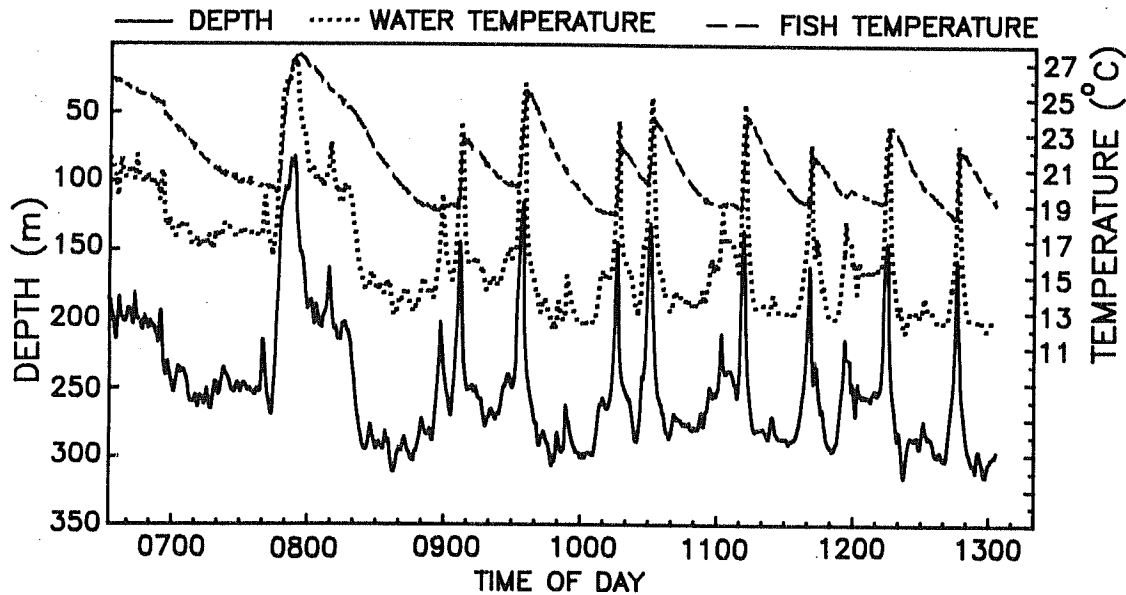
Table 1. Lower lethal oxygen levels for tunas as estimated by Sharp (1978). Data are based on the ratio of the minimum hydrostatic equilibrium speeds of a 50 cm (fork length) skipjack tuna to those of other tuna species and other body sizes. The lower lethal oxygen level for a 50 cm skipjack tuna is from Gooding *et al.* (1981). Conversion of mg O_2 l^{-1} to ml O_2 l^{-1} assumes a temperature of 25°C for skipjack, yellowfin and bigeye tunas, and 15°C for albacore.

Species	Fork length (cm)	Lower lethal O_2 level			
		mg l^{-1}	ml l^{-1}	mm Hg	% Saturation
Skipjack tuna	50	2.45	1.87	57	37
Skipjack tuna	75	2.83	2.16	66	43
Yellowfin tuna	50	1.49	1.14	35	23
Yellowfin tuna	75	2.32	1.77	54	35
Bigeye tuna	50	0.52	0.40	12	8
Bigeye tuna	75	0.65	0.50	15	10
Albacore	50	1.67	1.23	33	21
Albacore	75	1.39	1.03	27	18

swimming speed tunas have zero oxygen demand. No animal at zero activity has zero metabolic rate. The metabolic rate at zero overt muscular activity is substantial and is called 'basal metabolic rate' in mammals and 'standard metabolic rate' (SMR) in fishes.

Brill (1979, 1987) directly measured in the SMR of skipjack tuna, yellowfin tuna and kawakawa, and found it to be at least approximately five to seven times higher than that of other active teleosts. Although yet unconfirmed, the high SMR of tunas appears to result (at least in part) from the high energetic cost of maintaining salt and water balance (Bushnell and Brill, 1992). High osmoregulatory costs are, in turn, a result of tunas having gill surface areas approximately an

order of magnitude larger and blood–water barriers (i.e. secondary lamella thickness) within the gills up to an order of magnitude thinner than other teleosts (Hughes, 1984a, b; Perry, 1992). The large, thin gills of tunas permit extraordinarily high rates of O_2 and CO_2 exchange (Bushnell and Brill, 1992; Perry, 1992), and maximum aerobic metabolic rates of skipjack tuna are at least 2.5 times those of other teleosts (Brett, 1972; Gooding et al., 1981). This ability, however, apparently comes with a price – a high energetic cost for maintaining salt and water balance.

As in other fishes (e.g. Bushnell et al., 1994), SMR of skipjack and yellowfin tunas accounts for approximately 70% and 90% (respectively) of the total metabolic rate at U_{100} (Olson and Boggs, 1986; Brill, 1987). At slow speeds relatively little oxygen demand is, therefore, due to the energetic cost of swimming, and reductions in activity have little effect on metabolic rate. The predicted low ambient oxygen tolerences listed in Table 1 (based on equation 1) are, therefore, unrealistic. This conclusion is further supported by the observation that swimming albacore tuna show reduced rates of oxygen uptake in water containing less than 5 mg l^{-1} (about 3.7 ml l^{-1}, pO_2 about 98 mm Hg, about 64% saturation at 15°C [3] (Graham et al., 1989). This implies that the cardiorespiratory system of albacore is unable to deliver sufficient oxygen to the tissues under these conditions. Reviews of ambient oxygen levels causing either a reduced swimming ability or reduced metabolic rates in freshwater fishes also imply that tolerable oxygen levels of 1 mg l^{-1} or less (Table 1) are untenable (Doudoroff and Shumway, 1970; Heath, 1987).

Hanamoto (1987) analysed longline tuna catch statistics where oceanographic data were simultaneously gathered. From his analyses, it appears that 1.3 mg l^{-1} (1 ml l^{-1}, 26 mm Hg, 17% saturation at 15°C) is the lower oxygen boundary for bigeye tuna. Hanamoto (1987) calculated hook depths because these were not measured. Recent work by Boggs (1993), employing electronic depth–time recorders attached directly to longline fishing gear, shows horizontal current shear often causes longline hooks to be shallower than anticipated. In areas where the thermocline–oxycline is steep, small errors in calculated hook depths can result in large errors in estimated oxygen levels at the depths assumed to have been occupied by fish immediately before capture.

Dizon (1977) was the first to measure behavioural responses of skipjack and yellowfin tunas to reduced oxygen levels (at 25°C). The former species showed an increase in swimming speed at ambient oxygen levels below 4 mg l^{-1} (3.1 ml l^{-1}, 93 mm Hg, 61% satu-

ration). In contrast, yellowfin tuna showed no changes in swimming speed at oxygen levels as low as 2.5 mg l^{-1} (1.9 ml l^{-1}, 58 mm Hg, 38% saturation), implying either that yellowfin tuna are not stressed at this level of ambient oxygen or that they can make physiological adjustments that make behavioural responses unnecessary.

These observations led to a series of studies designed to measure the physiological responses of skipjack, yellowfin and bigeye tunas to reduced ambient oxygen (Bushnell et al., 1990; Bushnell and Brill, 1991, 1992). The overall objective was to learn the physiological basis for the differences in the behavioural reactions of yellowfin and skipjack tunas. In the first study (Bushnell and Brill, 1991), spinally blocked (i.e. paralysed and restrained[4]) skipjack, yellowfin and bigeye tunas were all found sensitive to even mild reductions of ambient oxygen. Reductions to 4.9 mg l^{-1} (3.7 ml l^{-1}, 115 mm Hg, 75% saturation) were enough to cause significant cardiorespiratory adjustments. All three tuna species are, therefore, as sensitive to reductions in ambient oxygen as other marine and freshwater teleosts (Doudoroff and Shumway, 1970; Davis, 1975; Heath, 1987) and display physiological adjustments at ambient oxygen levels above those necessary to elicit changes in swimming speed.

Bushnell et al. (1990) showed, besides an increase in mouth gape and ventilation volume, that tunas reduce heart rate in response to lowered ambient oxygen. This is a common reaction in both teleosts and elasmobranchs. The hypothesized advantages of a lowered heart rate include longer residence of blood in the gills to aid oxygen uptake by haemoglobin, diminished work load of the heart, and longer residence of blood within the heart to allow sufficient oxygen uptake from venous blood by heart muscle itself (Randall and Shelton, 1963; Short et al., 1979; Farrell et al., 1985; Glass et al., 1991; Rantin et al., 1992; Rantin, 1993). The exact physiological functions of this response, however, remain unclear (Farrell, 1984; Rantin, 1993). Although other fish species maintain cardiac output at reduced heart rates by increasing stroke volume (i.e. the volume of blood pumped per beat), skipjack, yellowfin and bigeye tunas cannot (Farrell et al., 1992). Cardiac output therefore falls with heart rate (Bushnell et al., 1990).

To ensure that their observations were not artefacts of the fish being paralysed, Bushnell and Brill (1991) measured the physiological responses of swimming skipjack and yellowfin tunas to reduced ambient oxygen.[5] The physiological responses of swimming fish closely matched those of paralysed fish (Bushnell et al.,

1990; Bushnell and Brill, 1991), showing the suit- ability of the former technique. These experiments, however, did not support the conclusion of Dizon (1977) that yellowfin tuna are tolerant of lower ambient oxygen levels than skipjack tuna. Most important, the data from these experiments were used to expand a model, first created by Dizon (1977), that predicted oxygen demand (i.e. metabolic rate) and the ability of the cardiorespiratory system to deliver oxygen at various combinations of swimming speed and ambient oxygen. The model, and its implications for predicting suitability of tuna habitat based on ambient oxygen levels, are explored more fully below.

The third series of experiments (Bushnell and Brill, 1992) involved spinally blocked skipjack and yellowfin tunas and simultaneous measurement of dorsal (i.e. arterial) and ventral (i.e. venous) aortic blood pressures, arterial and venous blood gases, blood acid–base status, and cardiac output. Whereas the first two studies were intended to find at what ambient oxygen levels tunas begin to effect physiological and behavioural changes aimed at maintaining oxygen delivery to the tissues, this study was undertaken specifically to see how effective these physiological changes were in achieving this end. In other words, the objective was to learn how well the cardiorespiratory systems of skipjack and yellowfin tunas function in fully oxygen-saturated seawater and under reduced ambient oxygen conditions.

Fish were tested at three levels of reduced ambient oxygen considered mild, moderate, and severe (5.6, 3.9, 2.1 mg l^{-1}; 4.3, 3.0, 1.6 ml l^{-1}; 140, 90, 50 mm Hg; 91%, 58%, 32% saturation, respectively). As in the first study (Bushnell et al., 1990), decreases in heart rate were not accompanied by increases in stroke volume, and cardiac output fell. Because arterial oxygen content also diminished, both species were forced to reduce the substantial oxygen content of venous blood to maintain metabolic rate. Significant reductions in venous oxygen content occurred at moderate reductions in ambient oxygen (3.9 mg l^{-1}) in skipjack tuna but only at severe reductions (2.1 mg l^{-1}) in yellowfin tuna. The need to draw down venous oxygen reserves would make it difficult to meet the oxygen demands engendered by the increased swimming speeds seen in both species by Bushnell and Brill (1991). Because yellowfin tuna did not use venous oxygen reserves until 3.9 mg l^{-1}, they could probably at least survive this level of reduced ambient oxygen indefinitely under laboratory conditions. Skipjack tuna probably could not. This conclusion agrees with lethal oxygen levels for skipjack tuna observed by Gooding et al. (1981).

Figure 6. Dizon's (1977) model of oxygen demand (solid line) and delivery (dashed and dotted lines) for a 1.4 kg skipjack tuna at two mouth cross-sectional areas (1 and 2 cm²). Upper dashed and dotted lines show oxygen delivery in oxygen-saturated seawater (6.6 mg l^{-1}, 5.0 ml l^{-1}, 154 mm Hg, at 25°C). Arrows show changes in oxygen delivery predicted to occur when ambient oxygen is reduced to 3.6 mg l^{-1} (2.8 ml l^{-1}, 85 mm Hg, 55% saturation). Swimming speeds are in body lengths per second (BL s^{-1}).
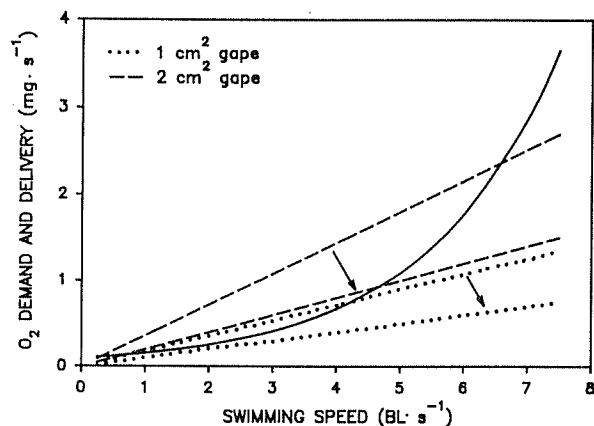
Model of cardiorespiratory function in skipjack and yellowfin tuna in fully saturated and reduced ambient oxygen conditions

Using lethal oxygen levels to determine tuna habitat results in simple two-state models (e.g. Barkley et al., 1978; Sharp, 1978). In other words, models that say fish can be found 'here' but not 'there'. A primary goal in modifying the model of oxygen demand and delivery for skipjack tuna first created by Dizon (1977) was to create a model providing a continuous function that realistically described changes in habitat suitability with reductions in ambient oxygen.

Dizon's model (Fig. 6) was created to predict the relationship among swimming speed, mouth gape (expressed as mouth cross-sectional area), oxygen demand and oxygen delivered to the gills by the inhalant water. The model predicts that oxygen delivery rises linearly with speed, whereas oxygen demand rises exponentially (based on data from Gooding et al., 1981). A point is reached, therefore, where oxygen demand exceeds delivery. This was considered the maximum sustainable swimming speed for skipjack tuna. Reduction in ambient oxygen to 3.6 mg l^{-1} (2.8 ml l^{-1}, 85 mm Hg, 55% saturation) was predicted to reduce maximum sustainable swimming speed and force skipjack tuna to increase gape to meet oxygen demand.

Dizon's model contained two important parameters subsequently shown to be incorrect. First, Boggs (1984)

and Olson and Boggs (1986) showed the oxygen demands of both skipjack and yellowfin tunas to increase as a power function, not as an exponential function of speed. Second, Bushnell and Brill (1991) showed in tunas, as in other fishes (e.g. Kerstens *et al.*, 1979; Smith and Jones, 1982; Steffensen *et al.*, 1982; Le Moigne *et al.*, 1986), that utilization (i.e. the fraction of oxygen removed from the ventilatory water stream) is inversely proportional to ventilation volume and directly proportional to ambient oxygen. Utilization is not fixed at 75% as Dizon assumed based on data presented by Stevens (1972). Bushnell and Brill (1991) therefore created a model predicting oxygen demand based on Boggs' (1984) and Olson and Boggs' (1986) data, and oxygen delivery that incorporated measured values for utilization and ventilation volume at various oxygen levels and swimming speeds for both skipjack and yellowfin tunas. However, it should be noted that the model was constructed from data taken over a narrow range of swimming speeds (≈ 0.7–1.9 BL s^{-1}), metabolic rates, and ventilation volumes because swimming speeds could not be controlled (Bushnell and Brill, 1991). Measurements of cardiorespiratory function of tunas over a larger range of oxygen demands are clearly warranted.

As shown in Fig. 7, the new model has several noteworthy features. First, because the oxygen delivery line is above the oxygen demand line for all speeds until well below U_{100}, minimum swimming speeds of both species are predicted to be set by the need to maintain buoyancy through lift generated by the pectoral fins, and not by oxygen demand. Second, maximum sustainable speeds (i.e. aerobically sustainable speeds) are reduced at a 2 cm^2 mouth gape in skipjack tuna because utilization decreases faster than ventilation volume increases, resulting in a net decrease in oxygen delivery. Obviously under these circumstances, skipjack tuna would decrease mouth gape to optimize oxygen delivery. Third, maximum predicted rates of oxygen delivery match the apparent maximum metabolic rates of skipjack tuna (Gooding *et al.*, 1981).

The new model also seems to predict that there is tremendous excess capacity in the oxygen delivery system. At slow swimming speeds, oxygen delivery may exceed demand by up to several hundred percent. This could suggest an error in the model. As discussed previously, it is energetically very expensive to have the ability to take up oxygen at high rates. The requisite large thin gills (and/or other adaptations) apparently engender a high SMR (Brill, 1979, 1987; Bushnell and Brill, 1992). Why would such an energetically expensive ability be present? Note that because of the steep rise in oxygen demand with speed at high swimming
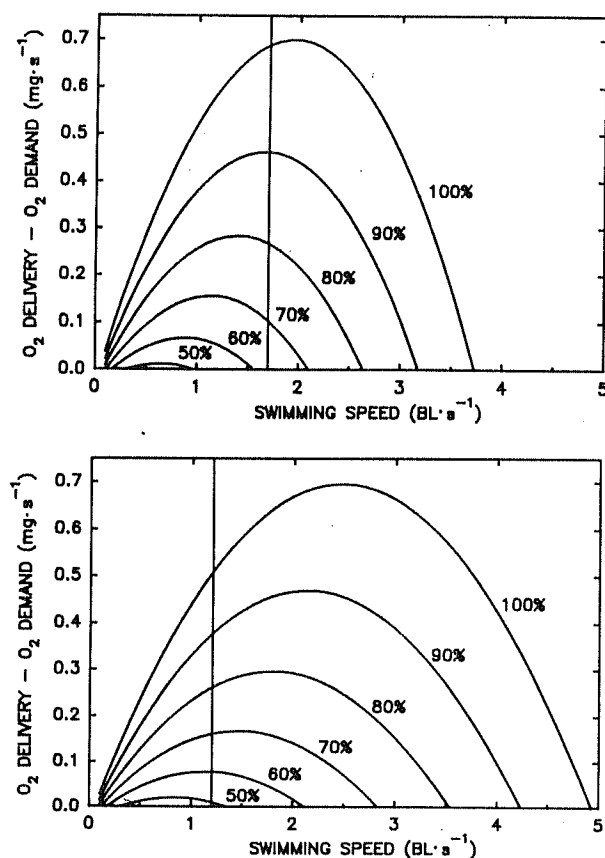
Figure 7. Model of the maximum rate of oxygen delivery, at two mouth cross-sectional areas, for 1.2 kg (40 cm fork length) skipjack tuna (upper panel) and 1.2 kg (40 cm fork length) yellowfin tuna (lower panel). Oxygen demand data (solid lines) are from Boggs (1984). Vertical lines indicate minimum hydrostatic equilibrium swimming speeds (Magnuson, 1973). The model predicts that the cardiorespiratory systems of both species can deliver oxygen at rates far exceeding demand. Swimming speeds are in body lengths per second (BL s^{-1}). (Redrawn from data presented by Bushnell and Brill, 1991.)
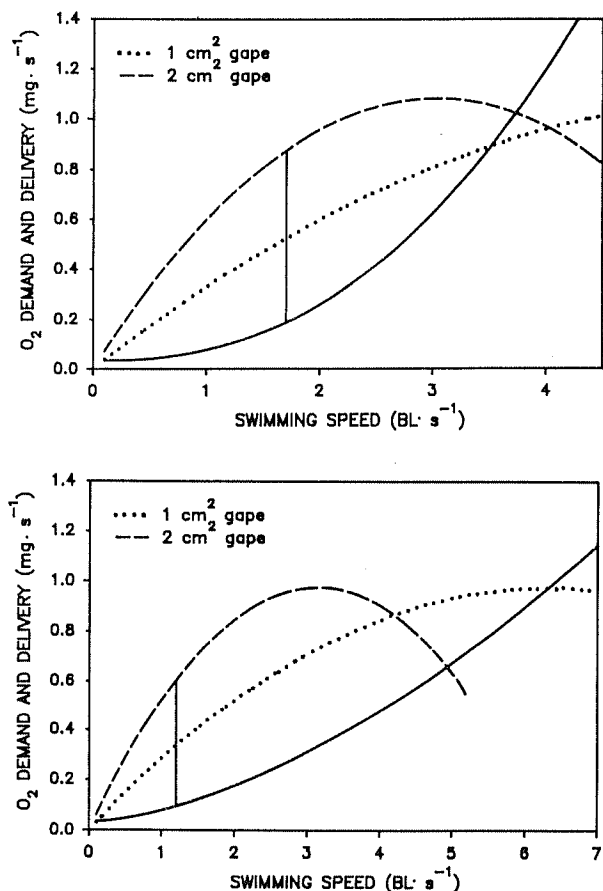
speeds, higher maximum metabolic rates result in only modest increases in predicted maximum sustainable swimming speeds. As explained by Brill (1987) and Pauly (1981), high maximum metabolic rates more likely result from the selective advantages conferred on tunas by quick recovery from strenuous exercise, rapid digestion, and elevated gonadal and somatic growth rates. All involve energy-consuming processes requiring oxygen delivery at rates exceeding those needed by the swimming muscles (Koch and Wieser, 1983; Armstrong *et al.*, 1992).
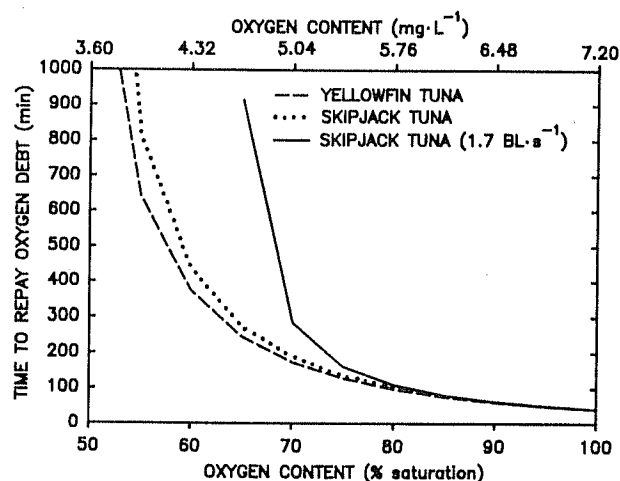
More important, the Bushnell and Brill oxygen demand and delivery model[6] can be run at various levels

Figure 8. The predicted difference between the rate of oxygen demand and the rate at which the cardiorespiratory system can deliver oxygen at various ambient oxygen levels in 1.2 kg skipjack (upper panel) and yellowfin (lower panel) tunas. Vertical lines indicate minimum hydrostatic equilibrium swimming speeds (Magnuson, 1973). The maximum differences between oxygen demand and delivery rates occur above the minimum hydrostatic equilibrium swimming speed down to 50% saturation in yellowfin tuna, but not skipjack tuna. The model, therefore, predicts that yellowfin tuna will swim more slowly at lower ambient oxygen levels after strenuous exercise in order to minimize the time required for recovery. Swimming speeds are in body lengths per second (BL s^{-1}).

Figure 9. Predicted time required for 1.2 kg skipjack and yellowfin tunas to metabolize 100 μM lactate g-1 and 5 μM creatine g-1 white muscle back to pre-exercise levels (7 μM g-1 lactate and 30 μM g-1 phosphocreatine). Data are based on the maximum differences between oxygen demand and delivery rates shown in Fig. 8. Because swimming speeds maximizing the difference between oxygen demand and delivery occur below the minimum hydrostatic equilibrium speeds of skipjack tuna (1.7 body lengths s-1), the time for recovery (solid line) is significantly prolonged compared with the hypothetical time for recovery if skipjack tuna could swim at speeds which maximize oxygen demand and delivery difference (dotted line).

of ambient oxygen, and the difference between the oxygen demand and delivery line plotted as a function of ambient oxygen and swimming speed (Fig. 8). The result is testable hypotheses about swimming speeds of tunas at various ambient oxygen levels following strenuous exercise. The model (Fig. 8) predicts that yellowfin and skipjack tunas should swim more slowly at lower ambient oxygen levels to minimize the time required to recover from strenuous exercise (i.e. metabolize lactate back to glycogen and resynthesize phosphocreatine). This would be the exact opposite to behaviour seen in

rested tunas, where reductions in ambient oxygen cause increased swimming speeds (Dizon, 1977; Bushnell and Brill, 1991). Tests of these predictions are clearly needed.

The ability to recover quickly from strenuous exercise best fits other well-established parameters of tuna physiology and biochemistry (Barrett and Connor, 1964; Guppy and Hochachka, 1978; Guppy et al., 1979; Hulbert et al., 1979; Abe et al., 1986; Weber et al., 1986; Brill et al. 1992; Dickson, 1994). Figure 9, therefore, presents results of the model when it is used to predict the time required to metabolize 100 μM lactate g^{-1} and 5 μM creatine g^{-1} white muscle (seen in post-exercise skipjack tuna) back to pre-exercise levels (7 μM lactate g^{-1} and 30 μM phosphocreatine g^{-1} white muscle; Arthur et al., 1992) at various ambient oxygen levels. At full oxygen saturation, the predicted time required for skipjack tuna to recover to pre-exercise levels (42 min) agrees reasonably well with the actual time required for these processes (about 80 min; Arthur et al., 1992).[7] The maximum difference between oxygen demand and delivery rates occurs below the minimum hydrostatic equilibrium swimming speed of

skipjack tuna (Fig. 8). Therefore, the time required to metabolize lactate is significantly increased from the theoretical time required if they could swim at speeds where the difference between oxygen demand and delivery rates are maximal. The model also predicts that the inability of skipjack tuna to swim slowly enough to maximize the difference between oxygen demand and delivery makes this species less tolerant of reduced ambient oxygen, because the time required to recover from strenuous exercise is significantly prolonged.

Little is known about the increase in oxygen demand engendered by digestion, gonadal synthesis and somatic growth in tunas. The energy required by these processes has only been estimated for tunas (Kitchell et al., 1978), although it has been measured in other teleosts (e.g. Brown and Cameron, 1991; Armstrong et al., 1992). Metabolic rates may approach maximum aerobic metabolic rates in some fishes following a large meal (Armstrong et al., 1992). Studies to quantify the energy demand engendered by both digestion and anabolism are clearly needed in tunas. For the present, rates of lactate metabolism and phosphocreatine synthesis (i.e. the time to recover from strenuous exercise) at various ambient oxygen levels are assumed to be reasonable surrogate measures for these processes.

The model is limited, however, in that it cannot be extrapolated to other species or to larger fish because there are no data available on how ventilation volume and utilization scale with body size in tunas. As with gill surface areas (Hughes, 1977) and standard metabolic rates (Brill, 1979, 1987), both will most likely scale non-linearly. Also, minimum hydrostatic equilibrium swimming speeds change uniquely and non-linearly with size in different tuna species (Magnuson, 1973). As the model shows for skipjack tuna (Fig. 8), the ability to swim at speeds where oxygen delivery maximally exceeds oxygen demand can have a significant impact on predicted low ambient oxygen tolerance.

It is at present difficult to test the model directly with field observations of skipjack and yellowfin tuna behaviour because there are only a few telemetry studies where both swimming depth and ambient oxygen data are given (e.g. Carey and Olson, 1982). Cayre (1991) recently published an ultrasonic telemetry study of 41–52 cm (fork length) skipjack and 73–105 cm yellowfin tunas including data on swimming depths and ambient oxygen levels. Skipjack tuna spent less than 10% of their time at depths where ambient oxygen levels were below about 5.0 mg l^{-1} (about 3.8 ml l^{-1}, about 75% saturation). Since water temperatures were 23–24°C at these depths, temperature per se was obviously not limiting depth distribution. Yellowfin tuna tracked during the same study spent less than 10% of their time at

depths where ambient oxygen levels were below about 4.3 mg l^{-1} (about 3.3 ml l^{-1}, about 65% saturation). Since water temperatures were 24–25°C at these depths, temperature was again obviously not limiting depth distribution. The apparently limiting oxygen levels are those at which the predicted time required to recover from strenuous exercise curves sharply upward in both species (Fig. 9). Field observations, therefore, appear to support the model's conclusions for small skipjack and yellowfin tuna at 23–25°C.

Although some data on the effects of temperature on metabolic rates and physiological processes of skipjack and yellowfin tuna are available (Brill, 1987; Brill and Bushnell, 1991; Brill et al., 1992), nothing is known about how temperature may influence low ambient oxygen tolerance. Because reductions in temperature and ambient oxygen most often parallel each other (e.g. Gundersen et al., 1972; Cayre and Marsac, 1993), studies on the interactive effects of simultaneous reductions in ambient temperature and oxygen are clearly needed.

SUMMARY AND CONCLUSIONS

Since oceanographic conditions can significantly modify the distribution of tunas and their vulnerability to specific fishing gear, catch per unit effort data (i.e. fisheries data) alone can be insufficient to measure abundance. The common assumption in tuna stock assessment models, that tunas are randomly and uniformly distributed, is simply never fulfilled. Models and stock assessments that ignore basic biological, physiological, and oceanographic data are, therefore, at risk of being misleading because they cannot readily differentiate changes in stock size from the continually changing distribution and gear vulnerability of tunas in a highly variable environment. The development of effective fishery management schemes similarly depends on the ability to differentiate overfishing from changes in distribution and gear vulnerability. Models correcting for changing distribution and gear vulnerability can, of course, be no better than the environmental and physiological data used to construct them. Good fisheries and oceanographic data lead to predictions of limited accuracy unless used with credible information on the physiological abilities and tolerances of tunas. As shown in this review, accurate data on certain aspects of the thermoregulatory abilities and low ambient oxygen tolerances of some tuna species are now available. Our understanding of tuna physiology is, however, far from complete. Research is still needed on (1) fishes other than small skipjack and yellowfin tunas, (2) the interactive effects of simultaneous reductions in temperature

and oxygen, (3) minimum tolerable temperatures, and (4) energetic costs of digestion, and somatic and gonadal growth.

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NOTES

1. Sharp (1978) estimated that if yellowfin tuna (*Thunnus albacares*) in the eastern tropical Pacific, an area of extensive purse seine fishing, were randomly and uniformly distributed there would be only one 10 kg fish per 2.8 km^2 of ocean. He concluded, "If tunas were truly uniformly dispersed in their habitat they would be so rarely encountered as to be virtually nonexistent." Specific examples of how catch per unit effort for tunas may reflect fish distributions, oceanographic conditions, and gear vulnerability, rather than true fish abundance, can also be found in Green (1976), Ingham *et al.* (1977), Evans *et al.* (1981), Hanamoto (1987), Sakagawa *et al.* (1987), Forsbergh (1989), Cayre (1991), and Cayre and Marsac (1993).

2. Brill *et al.* (1994) explain the various techniques (and their limitations) for examining the physiological thermoregulatory abilities of tunas.

3. Oxygen levels in water may be expressed as either partial pressure (expressed as millimetres of mercury or kilopascals; abbreviated mm Hg and kPa, respectively; 1 mm Hg = 0.1333 kPa) or some measure of concentration. Partial pressure and concentration are related by solubility. Oxygen solubility is, in turn, affected by temperature and salinity. Oceanographers generally report oxygen levels as mg l^{-1} (i.e. parts per million) or occasionally ml l^{-1}. The former unit is preferable because it is independent of temperature. Texts dealing with ambient oxygen tolerances of aquatic organisms also use percent saturation. Physiologists, however, generally use partial pressure because that is the common unit for expressing blood O_2 and CO_2 levels. Oxygen levels will be given in all units whenever possible to simplify comparisons among published studies.

4. Tunas are obligate ram ventilators and normally rely on forward movement to develop the head pressure necessary to move water over the gills (Brown and Muir, 1970; Roberts, 1978). In this experimental system, instead of the fish moving through the water, the fish is stationary and water is moved past the fish.

5. Bigeye tuna near the Hawaiian Islands spend most daylight hours below 200 m (Holland *et al.*, 1990). They are, therefore, only rarely captured by the commercial live bait (i.e. surface) fishery returning live tunas to the Kewalo Research Facility. Bigeye tuna were unavailable for the subsequent experimentation. This species is probably the most interesting in terms of low ambient oxygen tolerance (Boggs, 1993) and clearly deserves further laboratory study.

6. For the purposes of calculating the differences between oxygen demand and delivery at various levels of ambient oxygen, equations 9 and 10 in Bushnell and Brill (1991) have been replaced with the following:

for skipjack tuna

$$U = (PiO_2 \times 0.0029) - (V_\mu \times 1.27)$$
$$+ \{0.427 - [0.00425 \times (154 - PiO_2)]\}$$

and for yellowfin tuna

$$U = (PiO_2 \times 0.0029) - (V_\mu \times 1.27)$$
$$+ \{0.383 - [0.00279 \times (154 - PiO_2)]\}.$$

These equations are based on the rate of decrease in utilization (*U*) with reductions in ambient oxygen measured in restrained yellowfin and skipjack tunas by Bushnell and Brill (1992). I assume maximum utilization to decrease linearly from 75% in fully oxygen-saturated seawater (oxygen levels are expressed as partial pressure, PiO_2, in mm Hg) at 0.00279 $\Delta U/\Delta PiO_2$ in yellowfin tuna and 0.00425 $\Delta U/\Delta PiO_2$ in skipjack tuna. V_μ = ventilation volume in l s^{-1}.

7. The equations and constants required to calculate the amount of oxygen needed to convert lactate to glycogen and creatine to phosphocreatine are given in detail by Bushnell and Jones (1994).

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