

Review

Overview of research on tuna thermo-physiology using electric tags

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(Received April 17, 2003; Accepted July 22, 2003)

Abstract: The behavioral physiology of bigeye tuna was investigated using acoustic tags in the 1990s. They spend most of the daylight hours below the thermocline but make regular brief excursions into the mixed layer. In doing so, they reduce the efficacy of their vascular countercurrent heat exchangers while gaining heat from the warmer environment and then increase it again when they return below the thermocline. Recently, archival tags have been used on a range of tuna species including bluefin. This tag, recovered when the tuna is harvested, yields time-series data over longer periods than acoustic tags. Although immature Pacific bluefin spend most of their time at the surface, they often dive below the thermocline, maintaining a peritoneal temperature. This might be due either to heat conservation or high heat production. Further, while giant Atlantic bluefin show an ability to maintain their temperature above the ambient, there are occasions in cold water when some physiological process is clearly limiting their dive time. Solution of the growth conundrum that their warm body temperature may pose an ecological problem as they grow in body mass, should be clarified by using tag data. This will lead to investigation of their adaptation mechanisms to their habitats.

key words: archival tag, tuna, thermo-physiology, acoustic tag, adaptation mechanisms

Introduction

The Scombridae, which include *Thunnus* spp. (tuna), are unique among teleost fishes because of their elevated body temperatures (Kishinoue, 1923; Barrett and Hester, 1964; Carey *et al.*, 1971; Carey, 1973; Stevens *et al.*, 1974, 2000). This “endothermy” results from a suite of specializations that increases internal heat production and reduces heat loss. The elevated muscle temperatures are facilitated by internalization of the aerobic locomotor muscle, higher aerobic capacities compared to exothermic fish, and the elaboration of vasculature into counter-current heat exchangers that decouple heat production in the muscle from heat loss. A number of hypotheses have been proposed regarding the ecological or physiological importance of the maintenance of body temperature above ambient water temperature (Carey, 1973; Brill, 1996; Carey and Teal, 1966; Neill and Stevens, 1974; Graham, 1975; Sharp and Vlyman, 1978; Carey *et al.*, 1984; Block *et al.*, 1993; Brill, 1994a, 1996; Stevens

Table 1. The thermal boundaries of occurrence for 5 tuna species in the North Pacific according to Collette and Nauen (1983) and Uda (1957).

Species	Thermal boundaries of occurrence (°C)
Pacific bluefin tuna (<i>Thunnus thynnus orientalis</i>)	12–22
Albacore (<i>Thunnus alalunga</i>)	13.5–25.2
Bigeye tuna (<i>Thunnus obesus</i>)	13–29
Yellowfin tuna (<i>Thunnus albacares</i>)	18–31
Skipjack tuna (<i>Katsuwonus pelamis</i>)	14–30

et al., 2000). These include the possibilities that the ability to maintain temperatures higher than ambient may enable rapid digestion of food, more rapid growth, rapid recovery from exhaustion, and the possibility that a warmer locomotor muscle may develop more power. Northern bluefin tuna, *Thunnus thynnus*, are highly migratory predators; this is permitted in part by their speed and power, a result of their large size (over 680 kg, Collette and Nauen, 1983), high body temperature and streamlined body shape. It has been considered that their elevated body temperature enabled them to extend their range from a pan-tropical distribution to the coldest latitudes within the genus *Thunnus* (Carey and Teal, 1969; Block *et al.*, 1993, Table 1). However, all these hypotheses need to be verified by insights from field data.

Carey and Lawson (1973) observed thermoregulation in Atlantic bluefin weighing more than 250 kg. However, in such a large fish, thermoregulation could not be unequivocally separated from the simple effect of thermal inertia (Neill and Stevens, 1974). Neill *et al.* (1976) postulated that skipjacks (*Katuwonus pelamis*) could face an overheating problem, limiting their activity in warm waters, because of their elevated muscle temperature. Since then, laboratory studies have been undertaken to detect the physiological basis of the thermoregulatory abilities of skipjack or yellowfin, *T. albacares* (Dizon *et al.*, 1978; Brill *et al.*, 1978; Dizon and Brill, 1979; Schaefer, 1985; Dewar *et al.*, 1994; Korsmeyer and Dewar, 2001; Brill and Bushnell, 2001). Information about the mechanisms regulating the body temperature of free-swimming tuna in the wild is for this reason very scarce, and the environmental stimuli affecting tuna body temperature (such as seasonal and spatial changes in oceanic conditions) are not fully understood. Recent technological advances in electric tags, *e.g.* acoustic, archival, and pop-up tags (Hunter *et al.*, 1986; Koido and Miyabe, 1990; Miyabe and Okamoto, 1998; Arnold and Dewar, 2001; Gunn and Block, 2001) have made it possible to monitor the swimming behavior of various species of fish in the wild by measuring external (physical) and internal (physiological) information simultaneously. At present, there are some data for bigeye (*Thunnus obesus*) in the wild, based on both acoustic and archival tags (Holland *et al.*, 1992; Holland and Sibert, 1994; Brill and Bushnell, 2001; Schaefer and Fuller, 2002), but few reports have been published about bluefin. The present review summarizes pertinent research on tuna thermal physiology, especially thermoregulation, using electric tag data. We also suggest directions for future research in investigating the behavioral and physiological characteristics that permit this extreme evolutionary success.

Studies on the mechanisms of tuna thermoregulation using acoustic tags

An acoustic (ultrasonic) tracking system consists of a transmitter attached to the fish and

a directional hydrophone and receiver system installed on a tracking vessel. In some instances, pressure and/or temperature sensors can be installed in some types of transmitters, allowing the depth at which the fish is swimming and the ambient water temperature to be transmitted to a receiver system on board. The location of the fish is also measured using a GPS on the vessel.

Carey and Lawson (1973) first measured the ambient water and internal temperatures of 230–270 kg Atlantic bluefin (*T. t. thynnus*) in large pens. Stevens *et al.* (2000) demonstrated the capacity of giant bluefin to regulate their internal temperature using data collected by Carey *et al.* (1984). A bluefin made an abrupt dive from the surface where the water temperature was 18°C to the thermocline at 4 to 5°C. When the fish was released, its stomach temperature was 21°C. During a four-hour stay in the colder water, the temperature of its stomach gradually fell to about 19°C. After that, the fish returned to the warmer side of the thermocline and remained in water that was between 13–14°C. In spite of a change in water temperature of nearly 10°C, the stomach temperature of the fish remained around 18°C. The authors stated that the fact that the deep-body temperature of the fish remained nearly constant over extended periods in both cold and warm water was due to thermoregulation—an ability to vary the efficiency of the counter-current heat exchangers. This interpretation was, however, pointed out by Neill and Stevens (1974) as incorrect, the body temperature of bluefin being maintained not by physiological but by the physical means of their “thermal inertia”.

Nonetheless, in the 1990s Holland *et al.* (1990, 1992), using acoustic tags attached to free-ranging bigeye (7.0–12 kg), measured simultaneously the swimming depth and muscle temperature of the fish. They found that bigeye tunas spend most of the daylight hours well below the thermocline (in 14–17°C water) but made regular, brief excursions up into the mixed layer. The observations reported can be explained if the tuna reduce the efficacy of their vascular counter-current heat exchangers while they are gaining heat from the environment but increase it again when they return below the thermocline. This is known as “physiological behavioral thermoregulation” (Holland *et al.*, 1992; Holland and Sibert, 1994; Brill, 1994a, b). Holland *et al.* (1992) and Holland and Sibert (1994) actually developed a model that proved that the thermal rate coefficient of an index of heat transfer changed dramatically and that this can be explained by active control of heat transfer.

Recently, Marcinek *et al.* (2001) tracked bluefin (*T. t. orientalis*) in the Pacific (11.8–57.6 kg). The behavior of this species is almost the mirror image of that of bigeye. Bluefin spend over 80% of their time at the top of the water column and make occasional dives into deeper, cooler water. Although the mean muscle temperatures of three fish were 22.0–26.1°C in water temperatures that averaged 15.7–17.5°C, variations in their muscle temperatures were not correlated with water temperature or swimming speeds. This indicates an ability to control the efficiency of their heat exchanger that is similar to that of yellowfin, as was demonstrated in a laboratory study (Dewar *et al.*, 1994).

Some of the weak points of studies using acoustic tags are:

- The durations of all successful tracks are less than one week. This is due to the practical difficulty of tracking a target continuously over long periods in rough seas, which often results in the loss of the target.
- Only a single fish at a time can be tracked.
- Since fish may show abnormal behavior in the first few days after release, a longer

monitoring period is essential to estimate their natural behavior, particularly for investigations of seasonal change and development of their behavior.

Studies on tuna thermo-conservation mechanisms using archival tag data

The archival tag (data storage tag, micro data logger) is an electronic device that measures environmental variables and records raw or processed data in its memory. When an archival tag is attached to an animal, it allows direct examination of the relationship between animal behavior or physiological conditions and the environment. In addition, some versions of archival tags allow a rough estimation of fish location every day between sunrise and sunset using a light sensor (Block *et al.*, 1998b; Gunn and Block, 2001). These tags record data that are subsequently downloaded when the fish is recaptured and the tag recovered. Archival tags, therefore, enable us to record the detailed behavior of individual fish over longer periods and regardless of where they go, with less effort than previous tracking studies using acoustic transmitters.

In most recent years, archival tags have been applied to salmon *Oncorhynchus keta*, plaice *Pleuronectes platessa*, yellowtail *Seriola quinqueradiata*, Atlantic cod *Gadus morhua*, and atka mackerel *Pleurogrammus monoptyerygius* (Nichol and Somerton, 2002) and to elasmobranchs, crustaceans and tuna *Thunnus spp.* (reviewed in Arnold and Dewar, 2001; Gunn and Block, 2001). Gunn *et al.* (1994) first applied archival tags to southern bluefin (*T. maccoyii*). Kitagawa *et al.* (2000) analyzed time-series data on the swimming depth of Pacific bluefin and the ambient water temperature, recorded every 128 seconds by archival tags, retrieved from 15 fish in the East China Sea (data length about 80 days at maximum). Though making frequent feeding dives to depths of 120 m during the day, Pacific bluefin remained predominantly in the surface mixed layer (Fig. 1). The average swimming depths were much shallower during summer (6.1 m by day) than in winter (39.1 m by day) when there was no thermal stratification (Kitagawa *et al.*, 2000). These results suggest that the vertical water structure influences the behavior of young bluefin, which prefer the mixed layer. Kitagawa *et al.* (2000) also found that the peritoneal cavity temperature of bluefin tuna in the winter was maintained $\sim 1.5^{\circ}\text{C}$ higher than ambient temperature (around 17.5°C) and increased by $\sim 2^{\circ}\text{C}$ in the daytime (Fig. 1a, b). In addition, the difference between the peritoneal cavity (around 26°C during the daytime and 24°C during the night) and ambient temperatures (around 21°C) during the summer was much larger than in winter (Fig. 1b); this suggests that activity of the tuna and consequent heat production increased from winter to summer and that this increase in the daytime probably resulted mainly from greater heat production due to more activity.

Kitagawa *et al.* (2001) investigated thermo-conservation mechanisms of the bluefin under low ambient temperature by analyzing archival tag data. Over the summer, the difference between the ambient and peritoneal cavity temperatures became considerable as the ambient temperature decreased. This was because the fish made repeated dives below the thermocline for short periods (~ 640 s), perhaps for feeding (Fig. 2). This suggests that peritoneal cavity temperature is maintained constant during dives. A heat budget model revealed that thermal inertia, or internal heat production in the daytime, was important for thermo-conservation during dives. As bluefin could only maintain body temperature for a short period, they had to avoid rapid temperature change at the thermocline through behavioral ther-

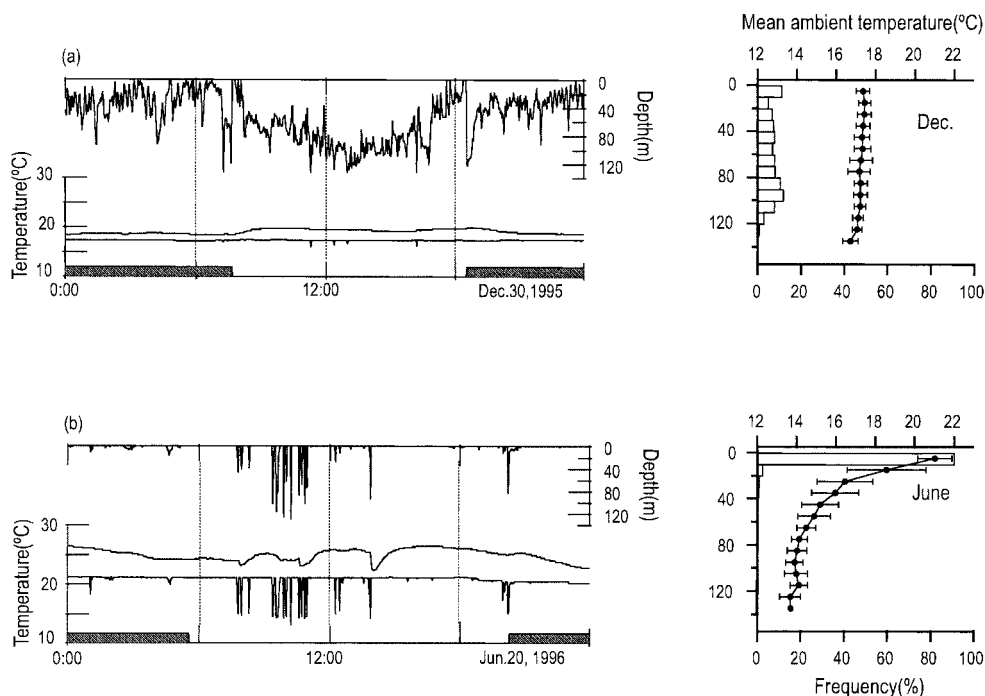


Fig. 1. (a) Time-series data on 30 December 1995, for depth (upper), peritoneal cavity temperature (middle), and ambient temperature (lower) obtained from Bluefin 177 swimming in the East China Sea. Shaded time zones indicate nighttime (left panel). Frequency distributions of the swimming depth and vertical profiles of mean ambient temperature (and standard deviation SD) in the daytime are shown in the right panel, modified from Kitagawa *et al.* (2000). (b) Time-series data on 20 June 1996, for depth (upper), peritoneal cavity temperature (middle), and ambient temperature (lower) obtained from Bluefin 177. Shaded time zones indicate nighttime (left panel). Frequency distributions of the swimming depth and vertical profiles of mean ambient temperature (and standard deviation SD) in the daytime are shown in the right panel, modified from Kitagawa *et al.* (2000).

moregulation. This is quite different from the situation for bigeye tuna, as reported elsewhere (Holland *et al.*, 1992).

Furthermore, Kitagawa *et al.* (2002) analyzed the archival tag data for an individual that migrated to the Sea of Japan, where the oceanographic characteristics are quite different from other seas and more than 90% of the sea is occupied by water colder than 5°C (Yasui *et al.*, 1967). Figure 3 illustrates the relationship during the daytime between mean ambient water and mean peritoneal cavity temperatures for individuals in the East China Sea, the Kurohio-Oyashio transition region and the Sea of Japan. Though the ambient temperatures for the fish in the Sea of Japan were significantly lower (11–17°C) than those for the others (18–22°C), the difference between two was about 5°C for all individuals. This indicates that they actively produce heat even in colder waters such as the Sea of Japan and that they have evolved tolerance to low ambient temperatures in addition to their elevated body temperature in order to extend their habitat into colder waters.

Block *et al.* (1998a, b, 2001a, b) and Gunn and Block (2001) applied archival tags to Atlantic bluefin (medium 61–141 kg, and giant >141 kg) and intensively examined their ther-

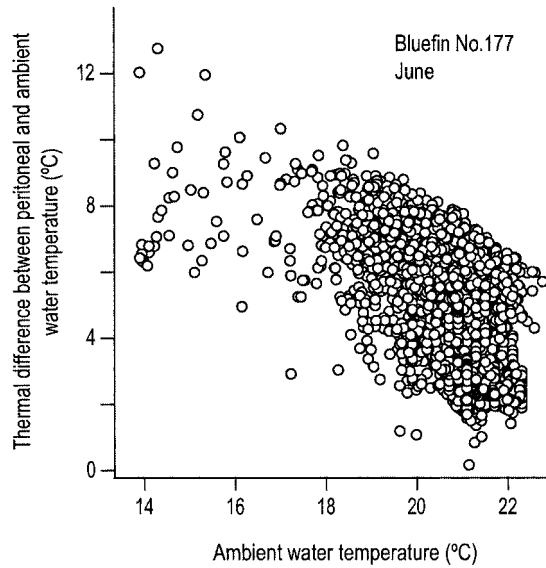


Fig. 2. Relationship between temperature difference (peritoneal cavity temperature minus ambient water temperature) and ambient water temperature for daytime data in June, for Bluefin 177 (modified from Kitagawa *et al.*, 2001).

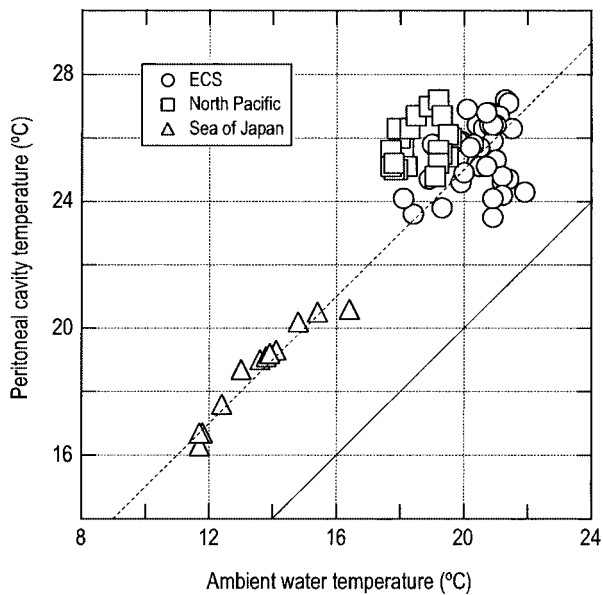


Fig. 3. Relationship between ambient water temperature and peritoneal cavity temperature (mean values for daytime). The solid line indicates a peritoneal-cavity temperature equal to ambient water temperature. The dashed line indicates a peritoneal-cavity temperature 5°C higher than ambient water temperature. ECS, North Pacific, and Sea of Japan indicate individuals swimming in the East China Sea, the North Pacific and the Sea of Japan, respectively (modified from Kitagawa *et al.*, 2002).

mal preference and physiology. They reported that bluefin experienced a wide range of environmental temperatures (2.8–30.6°C) but maintained a relatively constant peritoneal temperature (~25°C). The thermal excess could be up to 21°C above ambient. In warm Gulf Stream waters (20–26°C), peritoneal temperatures were 3–6°C above ambient, and bluefin often dive to 300–1000 m, maintaining relatively constant peritoneal temperature. In contrast, when some individuals were challenged by extremely cold surface waters, ranging from 5–10°C, for prolonged periods the core body temperature dropped to 13°C. Gunn and Block (2001) hypothesized that the bluefin may be dumping heat from the locomotor muscle and viscera to the cardiac system to protect the heart during long periods of cold. In addition, some bluefin often returned to the surface repeatedly when deep dives were made in cool surface waters (5–10°C). This behavior is similar to that of bigeye and is indicative of thermal limitation and behavioral thermoregulatory responses (Holland *et al.*, 1992). Thus, there are occasions in cold water when a physiological process is clearly limiting the bluefin's dive time while they show a remarkable ability to maintain that thermal excess above ambient (Gunn and Block, 2001). This information is still fragmentary and there is a need to continue to investigate detailed behavior and thermoregulation mechanisms in giant bluefin.

Directions for future research: investigating the reason for the evolutionary success of tuna and the importance of research using archival tags

As mentioned in the previous section, sufficient archival tag data to analyze bluefin thermo-physiology are gradually being accumulated. However, the conundrum of Neill *et al.* (1976) has not as yet been examined; large thermal inertia and high metabolic rate would pose a problem of overheating as tuna grow in body mass. Does overheating really happen to giant bluefin tuna? To solve this problem, it is necessary to clarify the development process of the thermo-conservation system with growth. This problem has been examined by Kitagawa *et al.* (2003). The mean thermal differences between peritoneal and ambient temperatures for Pacific bluefin are correlated to their body size. However, this is not a linear correlation and appears to reach an asymptote at approximately 8°C (Fig. 4). This suggests that the overheating problem does not seem to happen to bluefin. This observation is also given support by the results of Block *et al.* (1998a, b, 2001a, b), Block (2003), and Gunn and Block (2001) for giant bluefin. The detailed thermo-physiological mechanisms required to avoid overheating, and the developmental processes that result in these mechanisms, should be considered further, by analyzing relationships between the ambient temperature, fishes' development of thermo-conservation ability, and their rates of metabolism using retrieved archival tags data. This approach will in turn lead to investigation of their adaptation mechanisms to temperate waters.

Few studies of thermoregulation mechanisms in free-ranging tropical tuna, such as yellowfin or skipjack, have been carried out despite the reporting of many laboratory or tracking studies mentioned above. It is important to investigate their behavior and/or thermoregulation mechanisms, not only to elucidate the thermoregulation mechanisms that lead to a preference for certain waters but also for detailed elucidation of the evolution and significance of endothermy among fish.

Although ambient water preference in tuna species has been described in the literature (Suda *et al.*, 1969; Uda, 1973; Kawai, 1980; Koido and Mizuno, 1989; Ogawa and Ishida,

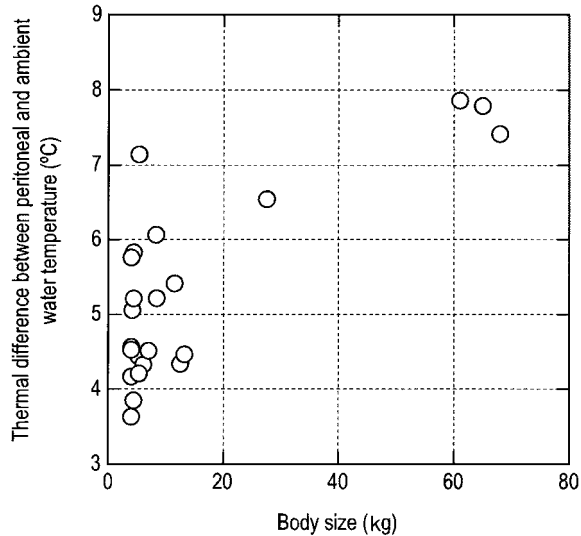


Fig. 4. Relationship between body size (kg) of bluefin tuna at the time of recapture and the mean thermal difference of peritoneal cavity temperature from the ambient water temperature recorded during about an hour from noon.

1989a, b), this was done from the viewpoint of fishing ground formation and was insufficient to inform us of the detailed behavioral and physiological ecology of the fish. Archival tags, however, provide a fisheries-independent measurement of fish behavior with environmental and physiological information. Therefore, if tags can be retrieved, it will be possible to collect detailed information, for longer durations and at higher resolutions compared to previous fisheries data analysis or acoustic tracking studies. In the future, tag data will also bring us new knowledge about thermoregulation mechanisms, and the importance of processes affecting bluefin migration over distances as great as 8000 km.

Acknowledgments

We wish to thank Prof. Y. Naito, Drs. K. Sato and A. Kato of the National Institute of Polar Research, Japan and Dr. H. Tanaka of Kyoto Univ., Japan for their advice on techniques for tag data analysis and other helpful comments. We would like to thank Dr. B. Block, Hopkins Marine Station of Stanford University, USA, for her encouragement. We are also grateful to Drs. Y. Uozumi, J. Suzuki, Y. Ishizuka, S. Tsuji, T. Itoh, and Mrs. M. Takahashi, National Research Institute of Far Seas Fisheries, Japan, and to Mr. A. Nitta, Japan NUS Co., for their support. T. Kitagawa was financially supported by a Research Fellowship from the Japan Society for the Promotion of Science for Young Scientists, Japan.

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