HOW WATER TEMPERATURE REALLY LIMITS THE VERTICAL MOVEMENTS OF TUNAS AND BILLFISHES - IT'S THE HEART STUPID

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Introduction

Accurate population assessments, especially for highly mobile pelagic species such as tunas (family *Scombridae,* tribe *Thunnini*) and billfishes (family *Istiophoridae*), require the ability to differentiate changes in abundance from changes in vulnerability to capture resulting from the natural variability in oceanographic conditions. Numerous studies have attempted to delineate the temperatures and oxygen levels that tunas and billfishes prefer, can withstand, or will avoid by employing catch statistics and oceanographic data averaged over time and space. Unfortunately, averaging catch statistics and environmental data can sometimes obscure, rather than elucidate, the relationships between species density and environment conditions. This occurs because fisheries and oceanographic data are often gathered separately in time and space, and because the inherent variability in both averages is usually too broad to clarify exact meaningful relationships (Sharp, 1978). More important, correlations of environmental data and catch rates do not prove causation and perpetuate a sort of circular logic. For instance, if tunas are rarely or never caught under a particular set of environmental conditions we assume the conditions are unsuitable. How it is known that they are unsuitable? -- because tunas are rarely or never caught when and where they occur. Entrapping circular arguments, missing data, limitations of catch per unit effort (CPUE) indexes, and the enormous difficulty of producing integrative models are just some of the obstacles fisheries biologists and fisheries managers face when attempting to resolve pelagic fish population assessment issues and resource allotment questions with some confidence. The immediate objective of our research is, therefore, to combine laboratory and telemetry studies to investigate the interactions between environmental conditions and pelagic fish movements, distribution, and vulnerability to capture by specific fishing gears. Our overall objective is, however, ultimately to improve current tuna and billfish stock assessment methods.

Water Temperature Limits the Vertical Movements of Tunas and Billfishes

Ultrasonic depth telemetry studies of yellowfin tuna (*Thunnus albacares),* skipjack tuna (*Katsuwonus pelamis*), blue marlin (*Makaira nigricans*), and striped marlin (*Tetrapturus audax*) all suggest that water temperature 8°C colder than surface water temperature limit vertical movements in spite of wide differences in body mass and surface water temperatures (Brill et al., 1993, 1998). Recent studies of the behavior of adult (estimated body mass 60-90 kg) yellowfin tuna the near the Hawaiian Islands revealed that these fish spend the majority of their time in upper uniform temperature layer (i.e., shallower than 120 m). Moreover, their depth distribution was found to be essentially identical to that of the juvenile yellowfin tuna (body mass approximately 2-5 kg) followed in the same area some years earlier (Holland et al.1990). These observations, however, contradict much of what was thought to be understood about the thermal physiology of tunas.

Tunas have vascular counter-current heat exchangers which decouple heat production in the muscle and heat loss at the gills. These unique structures thus allow tunas to keep their muscles significantly warmer than the surrounding water. Vascular counter-current heat exchangers also slow the rate at which the tunas' muscle temperatures change when going from the warm surface layer to deeper, colder waters. Neill et al. (1976) were the first to propose that this enhanced "thermal inertia" should allow tunas to spend more time in deeper, colder water and to exploit more effectively whatever food resources are found there. Large yellowfin tuna should, therefore, have greater vertical mobility (i.e., ability to spend more time in deeper and colder water) then juvenile fish because their greater body mass affords even slower rates of muscle temperature change following abrupt decreases in ambient temperature. Yet, as stated, direct observations of adult and juvenile yellowfin tuna carrying depth sensitive ultrasonic transmitters showed identical vertical movement patterns in spite of the body mass of the adult fish being approximately 10-20 times larger than that of the juvenile fish. In summary, neither differences in body mass, nor the presence of vascular heat exchanges in tunas and their absence in billfishes, appears to influence the limiting effect of water temperature on the vertical movements of these pelagic fishes.

A fresh perspective (or maybe we've been looking at the wrong end of the horse)

The basic premise underlying the idea that larger tunas should be able to spend more time in deeper, colder water is that body (i.e., swimming muscle) temperature is the most important factor limiting vertical movements. Our experiments, however, imply that it is the temperature of the heart that really limits the vertical movements of tunas and (by implication) billfishes. The heart is on the "water" side of tunas' vascular counter-current heat exchangers. This means its temperature will follow directly changes in water temperature regardless of the presence or absence of vascular counter-current heat exchangers or the size of the fish. The relatively simple recognition that the temperature of the heart is a limiting factor in behavior is a novel idea, but can it really explain the observed vertical movements of tunas and billfishes in the open ocean?

A nearly completed series of experiments on the effects of rapid ambient temperature change on the cardio-respiratory function of tunas revealed that reductions in water temperature result in an immediate and parallel decrease in heart rate. Figure 1 shows the response of a yellowfin tuna

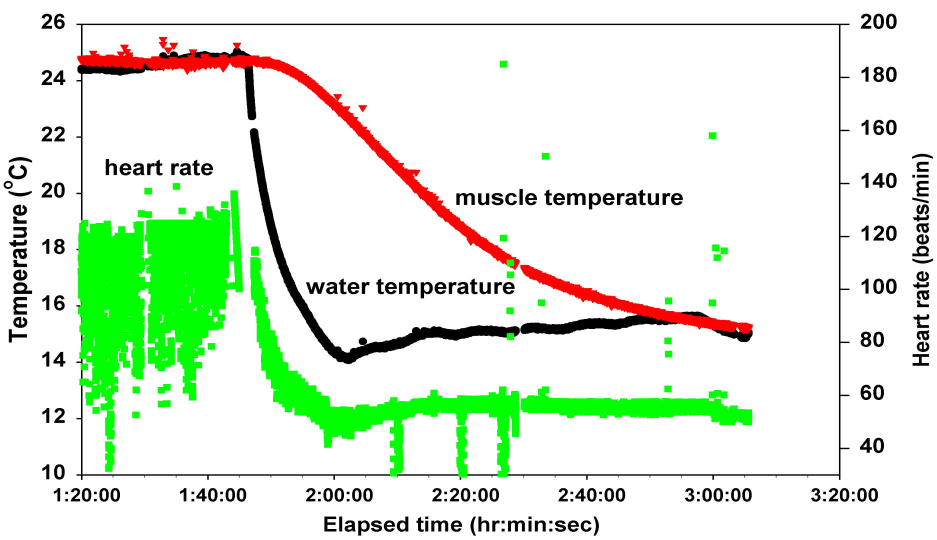

Figure 1. Effect of an abrupt change in water temperature (25 to 15° C) on heart rate in a yellowfin tuna. Note that heart rate follows the change in water temperature, not muscle temperature. Cardiac output (data not shown) follows heart rate because of tunas' limited ability to increase stroke volume.

exposed to an abrupt 25 to 15° C change in water temperature (skipjack tuna respond in essentially the same manner). Note that heart rate follows the change in water temperature not the change in muscle temperature, which lags significantly behind. Because of tunas' limited ability to increase stroke volume (i.e., the volume of blood pumped per heart beat), cardiac output falls with heart rate (Farrell et al., 1992). Reductions in water temperature, therefore, directly and immediately impact the cardiac output of tunas (and by implication billfishes), thereby limiting swimming performance.

A second key observation is that at 15°C, tunas have no ability to increase heart rate. Unlike most other teleosts, tunas increase heart rate rather than stroke volume during periods requiring elevated cardiac output (Farrell et al. 1992). In tunas, as in other vertebrates, the vagus nerve (i.e., the 10th cranial nerve) acts as a regulatory "break" on heart rate and increases in heart rate result from reductions in vagal nerve activity. The actions of the vagus nerve can be blocked pharmacologically with atropine. When tunas are given atropine at 25° C, heart rate approximately doubles. Yet at 15° C, atropine has no effect (Fig. 2). In other words, at 15° C, tunas have no ability to increase heart rate or cardiac output and, therefore, little or no ability to meet any increase in oxygen demanded by the swimming muscles while chasing prey, escaping a predator, or metabolizing lactate (i.e., recovering from exhaustive exercise). Hence, the effect of temperature on heart rate and cardiac output appears to explain the limiting effects of water temperature on the vertical movements of tunas and (by implication) billfishes.

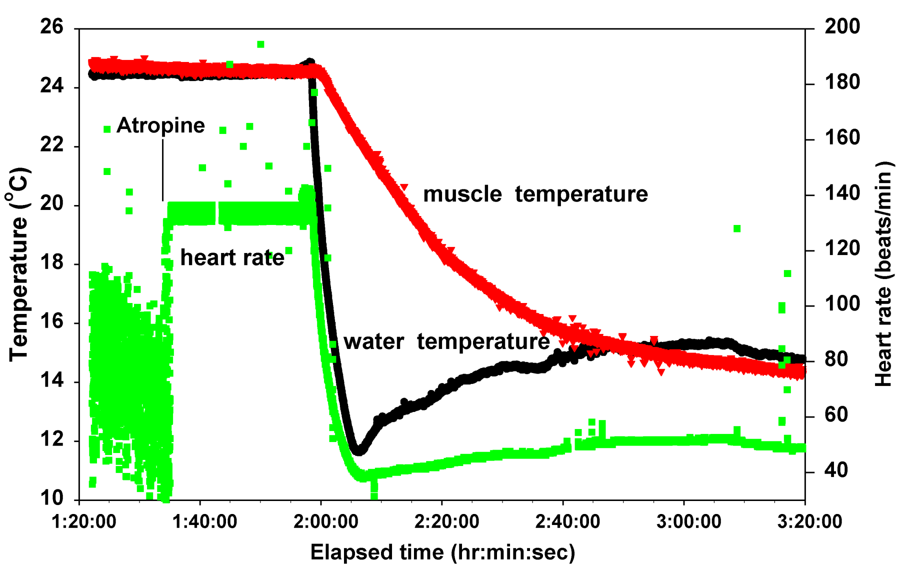

Figure 2. Effect of an abrupt change in water temperature (25 to 15°C) on heart rate in yellowfin tuna treated with atropine. Note that the heart rate is the same at 15°C is as in a yellowfin tuna not treated with atropine (Fig. 1). These data show that yellowfin tuna at 15°C have no ability to increase their heart rate or cardiac output.

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Acknowledgments

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