Into the deep

understanding swordfish eco-physiology

Cold-blooded vertebrates, such as fish, are extremely susceptible to changes in the temperature of their surroundings. Yet one successful ocean predator, the swordfish, migrates from tropical to temperate seas, and dives daily from warm surface waters to cooler depths, with seeming ease. ***Drs Diego Bernal*** *and* ***Chugey Sepulveda*** *of the University of Massachusetts Dartmouth and the Pfleger Institute of Environmental Research (PIER), are working together to explain the physiological mechanisms underpinning this ability, with implications for understanding vertebrate respiratory and muscle function, and for maintaining healthy populations of swordfish and other marine species.*

As terrestrial animals, we are accustomed to an environment that undergoes dramatic temperature change that occurs over both long (i.e., from summer to winter) and short time frames (from day to night). As warm-blooded mammals, we have the capacity to regulate our body temperature to mitigate the physiological effects of these environmental changes. Other groups, like marine fish, aren't so lucky, as drastic changes in temperature can have lethal repercussions.

In the marine realm, the high heat capacity of water provides fish with a buffer against rapid changes in environmental temperature. For this reason, most marine species have evolved to inhabit relatively narrow and homogeneous thermal niches. Thus, even though most fish do not have physiological control over their body temperature, they still are able to maintain a relatively constant thermal environment in which metabolic processes are optimised. However, certain fish species do not follow this trend, with body temperatures and physiological processes subject to extreme thermal variation on both a daily and seasonal basis. These thermal fluctuations are primarily in response to daily and seasonal migrations in search of rich prey sources that aggregate in temperate and polar regions as well as the waters well beneath the thermocline.

A LIFE OF EXTREMES

One remarkable species has been shown to possess great tolerance to changing thermal environments. The swordfish (*Xiphias gladius*) – a large marine predator that roams all the world's oceans – is among the few fish species known to traverse extreme thermal barriers on a daily basis, spending prolonged periods hunting both at the surface at night and at great depth during the day. This diurnal activity pattern results in extreme thermal fluctuation, with physiological processes subject to temperature changes in excess of 15°C within a matter of minutes. Although many fish species also exhibit tolerance to short-lived changes in temperature, the swordfish has been shown to reside and hunt for prolonged periods in very disparate conditions, providing a daily pattern that subjects physiological processes to extreme and contrasting conditions. This daily pattern provides swordfish with a unique foraging opportunity that allows them to feed on rich prey resources both during the day and at night.

Swordfish caught using deep-set techniques developed by the PIER team.

Understanding how swordfish tolerate extreme conditions and segregate from other species has also led to the development of selective, low-impact fishing gears. By documenting depth trends and dive characteristics, researchers have been able to identify times and locations that lead to increased selectivity in swordfish fisheries. This is critical given that world-wide swordfish fisheries have been routinely implicated with high levels of bycatch of sensitive species like sea turtles and marine mammals.

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From a physiological perspective, understanding how swordfish tolerate extreme thermal conditions and how they transition rapidly between them, offers insights not just into this species, but also into how other organisms respond physiologically to changing environmental temperatures. It may even help managers of fisheries develop new, more sustainable fishing practices. Drs Bernal and Sepulveda are bringing their complementary expertise in physiology, ecology, and marine resource conservation together to answer these fascinating questions.

MUSCLE MATTERS

A diving swordfish faces two fundamental issues as it moves from warm to cool water and back again. Firstly, the effect that changing temperatures may have on the muscles that power swimming – particularly significant in such fast-moving predators – and secondly the low levels of oxygen experienced at the depth where swordfish hunt during the day.

Every sprinter knows that muscles work better when they are warm. In their US National Science Foundation-funded project, Dr Bernal and Dr Sepulveda aim to quantify this effect in swordfish. Their work documents any changes in muscle temperature in free-swimming fish during dives and subsequently assesses *in-vitro* muscle performance at the same range of temperatures in a laboratory setting.

Swordfish have several anatomical adaptations that may help maintain their swimming muscles at temperatures that are warmer than their surroundings: the main swimming muscles are held close to the centre of the body and are supplied with blood via an elaborate network of vessels that act as a heat exchanger, effectively conserving body heat. This mechanism, known as 'regional muscle endothermy', clearly enables swordfish to maintain high swimming performance while at depth in cold water, but it does not fully account for their ability to

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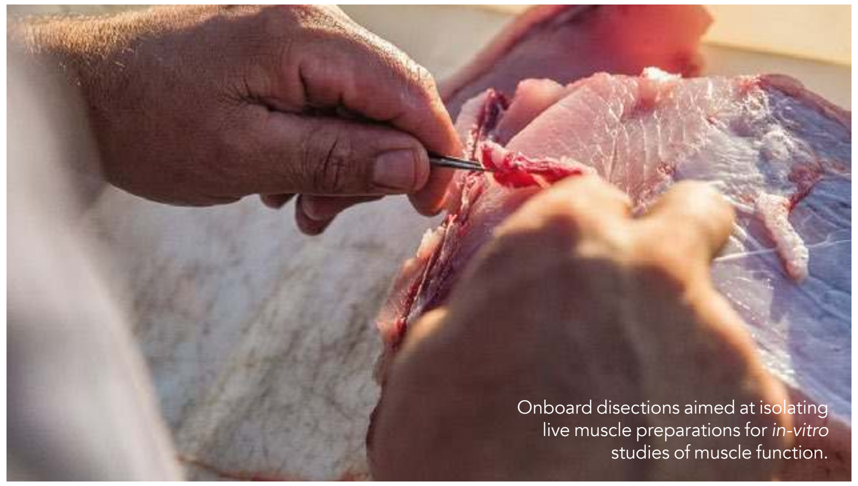

Onboard disections aimed at isolating live muscle preparations for *in-vitro* studies of muscle function.

survive such rapid dives and to spend such long periods at depth. In fact, other predatory fish including tuna and some sharks have a much greater capacity for regional muscle endothermy than swordfish, however, they cannot sustain such long dives.

Drs Bernal and Sepulveda proposed an explanation for this discrepancy: from the data collected to date, the team has proposed that swordfish use physiological thermoregulation coupled with muscles that operate across a large range of environmental temperatures. When their empirical measurements of body and water temperature from free-swimming diving swordfish were put into computer-generated thermodynamic models, they found that swordfish can alter and control the rate at which their entire body exchanges heat with the surrounding water, effectively slowing down the rate at which their body cools during a dive and accelerating the rate of rewarming when they return to the surface. Their work has also shown that swordfish muscle can function at a range of temperatures, including very cold conditions that have been shown to be lethal to many other pelagic fish.

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PERFECT PREDATOR

Bernal and Sepulveda postulate that the basis for physiological thermoregulation in swordfish lies in their complex, two-part circulatory system. When diving into cooler water, the fish may slow down cooling by routing blood through vessels armed with heat-exchanging manifolds deep inside their bodies, keeping them warmer and defending against the cold. Conversely, when returning to warm surface waters, swordfish may accelerate heat exchange with their surroundings by routing blood through vessels that short-circuit the heat exchange systems. The net result is that swordfish operate at warmer temperatures than their surroundings for a longer proportion of the time than other fish. This may give them a competitive advantage relative to other predators and their prey. In addition, the ability to warm up rapidly decreases the amount of time swordfish spend 'basking' on the surface, freeing up more time to exploit the rich food resources of the ocean depths.

The next question for the research team is how these prolonged dives influence the swordfish's muscle function and its ability to uptake oxygen from the water. Certain layers of the deep oceans tend to be lacking in dissolved oxygen compared to the surface waters, and in most fish the ability of the blood to bind oxygen varies with temperature, producing a complex set of interactions for fish to tend with. Bernal and Sepulveda have teamed up with colleagues in the US and Canada to examine how temperature affects the oxygen-binding capacity of swordfish blood, and to explore potentially unique ultrastructural adaptations in their gills and muscles that enhance their oxygen-transporting ability. They hope to shed light on the physiological basis of swordfish tolerance to extremes of temperature and oxygen deficits: as the researchers describe it, "adaptations for life on the edge."

FINE-TUNING FISHERIES

A final, fundamental aspect of Bernal and Sepulveda's research lies in how the detailed physiological and ecological data garnered during the study relate to local fisheries. Sepulveda and his team at PIER have dedicated much of the past decade trying to develop alternative means to harvest swordfish, ones that are more selective than some of the more traditional fisheries used around the world. The key to this work is understanding where and when swordfish segregate from other species and developing alternative fishing gears that selectively target swordfish at depth. Increasing gear selectivity and minimising unwanted interactions with protected species like sea turtles and marine mammals is a win-win scenario for both managers and fishers. It is the teams hope that new knowledge on their physiological specialisations can be used to develop cleaner fisheries that offer new opportunities for dwindling fishing communities.

The collaborator's physiological data may also provide crucial insights into how swordfish movements and behaviours change with our changing climate. As our oceans change with time, factors including prey distribution and abundance, oxygen availability and sea temperature can influence the movements of this global resource. They hope their research may provide a set of biological insights that help explain how swordfish are capable of the feats they accomplish daily and how this information may help keep populations of swordfish and other marine species at sustainable levels in the future.

Behind the Bench

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Research Objectives
This collaborative work is focused on documenting and better understanding the physiological specialisations that allow certain fish species to exploit some of the harshest conditions on the planet. The work specifically tests hypotheses related to the effect that temperature has on muscle and cardio-respiratory performance in pelagic fish species. Additionally, this work has coupled these physiological investigations with movement studies to aid in the development of new, low-impact fishing gears that increase selectivity and reduce bycatch in modern-day fisheries.

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Collaborators
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Bio
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Q&A

The swordfish is clearly a unique species. How did you first discover its remarkable combination of behaviours?
Despite the presence of global fisheries dedicated to the harvest of swordfish, very little biological information exists for this species. Since the 1960s, there have been numerous reports from the open-ocean fisheries showing that swordfish were captured at depth during the day and in shallower water at night. That work indicated their capacity to move extensively up and down the water column. Then, in the 1970s and 80s, there were a series of papers by Francis Carey and his group that began to uncover some of the swordfishes unique physiological and morphological adaptations that allows them to be active predators in the deep, dark, and cold layers of the ocean. For example, they can warm their eyes and brain to enhance sensory perception. Since then, we have continued that line of work but have focused on how swordfish can sustain swimming during their descents into cold water and to try understand if, and how they can maintain their active swimming ecology, even when other top predators apparently cannot.

What are the implications of your findings for our understanding of muscle function in other species?
Swordfish are not the only fish that dive deep and cold, but they are unique in that they stay at depth for prolonged periods of time. How they can do that without markedly affecting their capacity to swim is what makes them unique. By learning how swordfish muscles can continue to function, even when facing rapid and large changes in temperature and potentially under low oxygen conditions, we will better understand how animals have adapted to inhabit environmental conditions that should be limiting.

How do swordfish cope with the longer-term changes of temperature they experience during migration between cooler and warmer latitudes?
We do know that many migratory fishes appear to acclimate their bodies throughout their slow progression to cooler waters. However, some other species that migrate more rapidly (tunas and swordfish) and appear to spend more time in cooler waters have evolved a suite of unique adaptations to stay warm. This allows them to potentially swim longer and faster, and increase sensory perception and maybe enhance their rate of growth. Although we are just beginning to understand how these animals can cope with short-term (minutes) changes in environmental conditions, we still have more to learn about their long-term (months) strategies to deal with these changes, which takes on a new sense of importance in the face of the potential oceanographic shifts associated with global climate change.

How would you like to see fishing practices change as a result of your studies?
We hope that our work will help provide fisheries with species-specific information that can lead to increased gear selectivity and reduced bycatch. Furthermore, we hope that this type of data can also be collected from other species and used to increase fishery selectivity based upon ecological and physiological differences. Expanding the scope of traditional fisheries and looking outside of the box for bycatch solutions continues to be a goal of both Sepulveda and Bernal's laboratories.

What do you each bring to the project? And what can you achieve together that you could not achieve alone?
The two laboratories have unique attributes and areas of expertise. Bernal has spent more than a decade working in the laboratory coupling his work with the field. In contrast, Sepulveda has diverged from his colleagues' path and focused more heavily on field studies that have fishery relevance. The coupling of the Bernal and Sepulveda laboratories has resulted in some strong well-rounded studies that tie the field to the laboratory. This synergistic research has bridged the traditional gap that separates field and laboratory investigation and broadened our understanding that allows us to work on questions that others cannot.