

## The Effect of Ocular Heating on Vision in Swordfishes

*Kerstin A. Fritsches, Richard W. Brill & Eric J. Warrant*

Pelagic fishes such as billfishes, tuna and some sharks have among fishes the unusual ability to maintain all or part of their bodies warmer than the ambient water temperature. While the extent of the warming varies between species, eyes and brains are always target organs for the warming. In swordfishes (Fig. 1), for example, Carey (1989) managed to insert thermistors in the heads of subsequently tracked animals and recorded cranial temperatures 10–15°C above water temperatures in the free-swimming fish.

But why do these fishes maintain elevated eye temperatures? There have been a number of suggestions, one of which is related to the animal's ability to detect fast movements in time (Block and Carey 1985; Block 1986; Tatler et al. 2000). Photoreceptors, the cells in the retina that convert light information into a neural signal, do so within discreet integration times, analogous to the shutter speed in a camera. Low temperatures decrease the “shutter speed” and the receptor collects light information (or photons) over longer time intervals before responding with a neuronal signal. While this means more photons will be collected, two different events occurring during one integration time will be summed to one neural response. With long integration times (i.e., slow shutter speed) the visual system loses resolution of events in time (temporal resolution) and this, in turn, reduces an animal's ability to detect fast moving objects.

The effect of temperature on temporal resolution of the visual system has been described in a wide range of animals, both in vertebrates and invertebrates. The humble blowfly, for example, has a warm head at high ambient temperatures and this significantly increases the animal's resolution in time (Tatler et al. 2000). In experiments made possible by access to the NOAA research vessels *Townsend Cromwell* and *Oscar E. Sette* and the unique opportunity to undertake electrophysiological experiments on-board ship with animals caught on longline gear, we have been able to show that temperature also substantially affects temporal resolution in swordfishes and tunas (Fritsches et al. 2005).

For the experiments we removed the retina from freshly caught fish and maintained the tissue alive for electrophysiological recording (electroretinogram, ERG). The retina was shown a light stimulus flashed at different frequencies and the response of the retina was recorded (for more detailed methods see Fritsches et al. 2005). When the light was flashing at low frequencies the retina's responses followed the increasing and decreasing light levels accurately (Fig. 2). As the flash frequency was increased, however, the



**Figure 1.** Swordfish have large eyes and a well-developed visual sense.

retina eventually failed to distinguish individual flashes. This frequency is termed the Flicker Fusion Frequency (FFF) and is used as an indicator of temporal resolution in a visual system. By recording the FFF with the retina held at different temperatures we were able to show clearly a reduction in FFF at cold temperatures (Fig. 2). In swordfishes, the FFF was over 40 flashes per second (Hz) at 22°C, which was reduced to 5 Hz or less at 10°C. This represents a substantial effect of temperature on a physiological process (more than twice what we expected) and shows that the swordfish seem to be particularly sensitive to changes in retinal temperatures.

We could therefore conclude that the heater organ allows higher temporal resolution in swordfishes, just as a warm head allows a blowfly to avoid being swatted even more efficiently. But unlike a fly moving around in bright sunlight, the swordfish uses its heater to keep the eyes warm when diving into deep, cold and also dark water. Decreasing light intensity has the same effect on temporal resolution as decreasing temperature: temporal resolution is reduced. In dim light, the visual systems of all animals studied so far decrease the “shutter speed” of their photoreceptors

(continued on page 2)

### CONTENTS

<b>U.S. Pacific Island Fishery Managers</b>	
<b>Address Overfishing of Bigeye Tuna</b> .....	4
<b>Publications of Note</b> .....	4
<b>Fishing Regulations Recommended For</b>	
<b>Proposed NWHI Sanctuary</b> .....	5
<b>Upcoming Events</b> .....	5

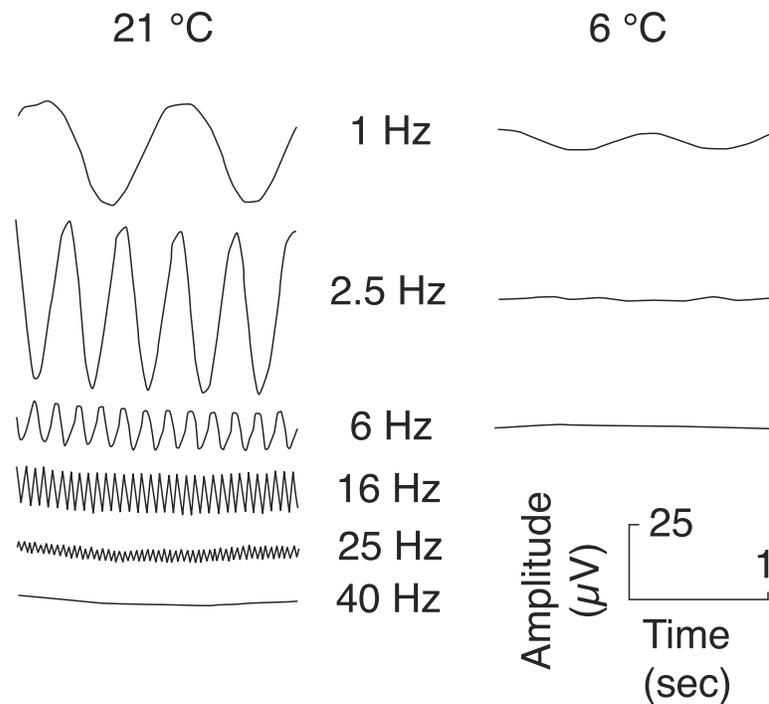


Figure 2. Electretinogram recordings of the swordfish retina responding to sinusoidal light stimuli of increasing frequency. At 21°C (left column) the FFF is reached when the light stimulus is flashed between 25 and 40 times per second (Hz, exact FFF was determined at 32 Hz). At 6°C (right column) the same retina has an FFF of 6Hz. Reprinted with permission from *Current Biology*.

to make vision more reliable. This reduces temporal resolution but allows the capture of the few photons available, a requirement for being able to see anything at all. The swordfishes' elevated eye temperatures would theoretically allow their retinas to have a higher temporal resolution, even at great depth. However, at depth, there might not be enough light to make high temporal resolution possible anyway. So we asked the question: If it also gets dimmer at depth as it gets colder, is there a net benefit for having warm eyes?

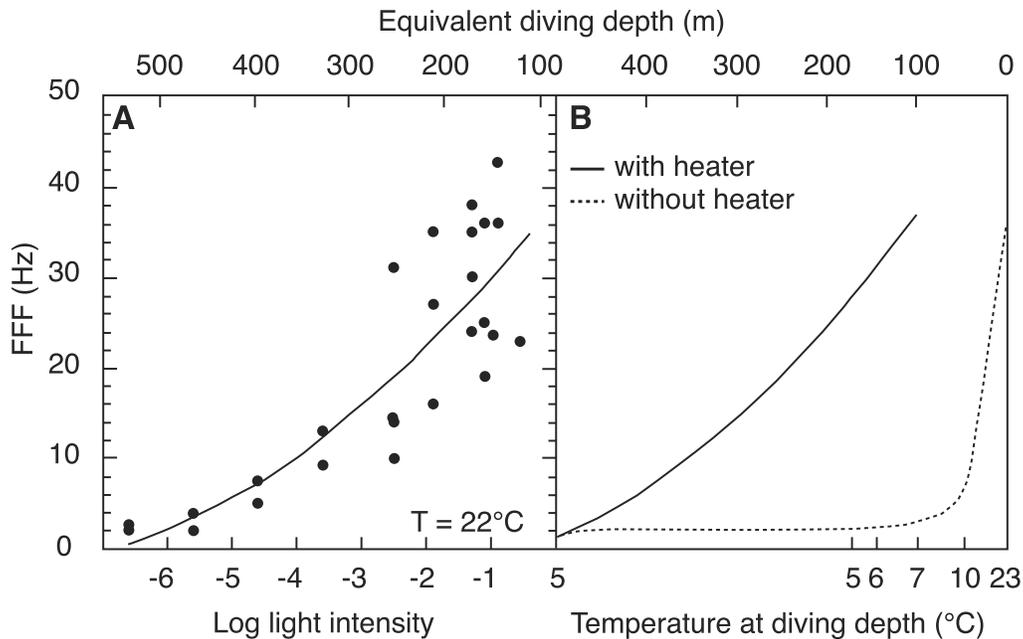
Additional ERG experiments allowed us to establish the effect of decreasing light intensity on the FFF in swordfishes (Fig. 3A). Our data revealed, as expected, a clear reduction of FFF with decreasing light intensity. Acoustic and archival tracking data from swordfishes (Carey and Robison 1981; Carey 1989; Takahashi 2003) provided us with a detailed picture of diving depths and ambient water temperatures experienced by swordfishes during their daily vertical movements. To this information we could add estimates of light intensities experienced by the fish at these depths (Warrant and Lockett 2004). By combining all these data sets we have been able to show that indeed swordfishes have much better temporal resolution with elevated eye temperatures at their common diving depths.

The effect is especially strong in the more temperate latitudes where thermoclines are steep and close to the water surface (Fig 3B). In these areas at 100 m, elevated eye temperatures will allow the swordfish to have an FFF 12 times higher than if the animal had no means of warming its eyes. At a diving depth of 300 m

the FFF is lower due to the reduced light intensities at this depth; however, a warm retina still allows an FFF seven times higher than that of a retina at ambient cold water temperatures. By 500 m light levels are so low that the eye's temporal resolution is no longer improved by warming the retina. It is interesting to note that in temperate regions swordfishes have been shown to spend more time in shallower waters to a few hundred meters, where the advantage of having elevated retinal temperatures on temporal resolution would be most pronounced.

The biological significance of high temporal resolution is an increased ability to see the movements of fast and agile prey, such as squid. Prey animals such as squid and smaller fishes, in turn, do not have the ability to warm their eyes and hence will have a reduced temporal resolution due to the cold ambient water temperatures, giving the swordfish and other warm-eyed predators, such as other billfishes, tuna and sharks, a crucial advantage in prey capture. Interestingly, the swordfish has the largest heater organ of the billfish group (Block 1986) and also the most temperate distribution of the group, underlining the importance of the heater for hunting in cold water.

Naturally there are also other advantages to maintaining the eyes and brain at warmer than ambient temperatures, thereby reducing or eliminating a rapid drop of neural tissue temperature as the fish descends. Function of the entire nervous system is sensitive to temperature changes and a cooling of the nervous system generally delays nervous responses. This, in turn, might interfere



**Figure 3.** A. The relationship of FFF and light intensity in swordfishes ( $n=5$ ), showing a clear reduction of FFF with decreasing light intensity. B. Our modelling results, considering the effects of light intensity at different depths and water temperatures on temporal resolution for a fish with warm eyes (solid line) and without heater (dotted line). Especially in areas with a near-surface thermocline, a fish with elevated retinal temperatures has significantly higher FFF than if the retina was at ambient temperature. Depth-temperature data were taken from Takahashi et al. 2003. Reprinted with permission from *Current Biology*.

with learning behavior and effective hunting (Prosser and Nelson 1981). However, as for learning in swordfishes, Carey (1982) pointed out that the brain of a swordfish is so small (0.002% of its body weight) that the heater organ is most likely “responding to requirements other than those of intellect.”

## References

Block, B. A. and Carey, F. G. 1985. Warm brain and eye temperatures in sharks. *J. Comp. Physiology B* 156, 229-236.

Block, B. A. 1986. Structure of the brain and eye heater tissue in marlins, sailfish and spearfishes. *J. Morph.* 190:169-189.

Carey, F. G. and Robison, B. H. 1981. Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fish. Bull.* 79, 277-292.

Carey, F. G. 1982. A brain heater in the swordfish. *Science* 216, 1327-1329.

Carey, F. G. 1989. Further acoustic telemetry observations of swordfish. In *Planning the Future of Billfishes: Research and Management in the 90th and Beyond. Proceedings of the Second International Billfish Symposium, Part 2: Contributed Papers* (ed. R. H. Stroud), pp. 103-122. Kailua Kona, Hawaii: National Coalition for Marine Conservation, Inc.

Fritsches, K. A., Brill, R. W. and Warrant, E. J. 2005. Warm eyes provide superior vision in swordfishes. *Current Biol.* 15, 55-58.

Fritsches, K.A. and Warrant, E. J. 2001. New discoveries in visual performance of pelagic fishes. *PFRP Newsletter*, Vol. 6, No. 3., 1-3.

Prosser, C. L. and Nelson, D. O. 1981. The role of nervous systems in temperature adaptation of poikilotherms. *Ann. Rev. Physiol.* 43, 281-300.

Takahashi, M., Okumara, H., Yokawa, K. and Okazaki, M. 2003. Swimming behaviour and migration of a swordfish recorded by an archival tag. *Mar. Fresh. Res.* 54, 527-534.

Tatler, B., O’Carroll, D. C. and Laughlin, S. B. 2000. Temperature and the temporal resolving power of fly photoreceptors. *J. Comp. Physiol.* 186, 399-407.

Warrant, E. J. and Locket, N. A. 2004. Vision in the deep sea. *Biol. Rev.* 79, 671-712.

## Acknowledgments

This project was funded by the National Marine Fisheries Service–Pacific Islands Fisheries Science Center; the Australian Research Council, GFAA R&D Foundation and Tailored Marine Accessories (SPIRT grant to KAF) and the Swedish Research Council and the Swedish Foundation for International Cooperation in Research and Higher Education (STINT to EJW).

*Kerstin A. Fritsches is a Research Fellow at the Vision, Touch and Hearing Research Centre, University of Queensland, Australia. Richard W. Brill is with the Virginia Institute for Marine Science and NOAA Fisheries, Northeast Fisheries Science Center. Eric J. Warrant is Professor of Zoology at the Department of Cell and Organism Biology, University of Lund, Sweden.*

## U.S. Pacific Island Fishery Managers Address Overfishing of Bigeye Tuna

A suite of domestic and international initiatives to address overfishing of bigeye tuna in the Pacific Ocean met with unanimous vote by the Western Pacific Regional Fishery Management Council last month. Overfishing of the species was recognized by the National Marine Fisheries Service (NMFS) in its annual report to Congress last June.

In December 2004, NMFS notified the Council that it and the Pacific Fishery Management Council had to take action to end overfishing of the species by June 14, 2005. At the same time, the Inter-American Tropical Tuna Commission (IATTC) is requiring large-scale tuna longline vessels fishing in the Eastern Pacific Ocean (EPO) to limit their 2004, 2005 and 2006 catch levels to their 2001 level. The 2001 harvests in the EPO are: Japan 34,076 mt (metric tonnes); Korea 12,576 mt; Taiwan 7,953 mt; China 2,639 mt; and U.S. 150 mt.

The Council recognizes that any unilateral action it takes will not stop the overfishing of the species in the Pacific. The fisheries under its jurisdiction account for only four to five percent of the bigeye tuna caught in the Pacific.

Still, the Council will develop a plan that would require the Hawai'i offshore, small-boat tuna handline fishery operating in the exclusive economic zone (EEZ), where appropriate, to be federally permitted with mandatory logbooks, limited entry and observers. The plan includes an international component that will engage the efforts of the NMFS Pacific Islands and Southwest Fisheries Science Centers, the Pelagic Fisheries Research Program,

the Western and Central Pacific Fisheries Commission (WCPFC) and the IATTC.

Actively involved in the international management of fisheries in the Pacific, the Council made numerous recommendations regarding U.S. representation on the WCPFC, the Interim Scientific Committee for Tuna and Tuna-like Species in the North Pacific (ISC) and the IATTC, as well as the implementation of the decisions made by these international organizations as they relate to domestic fisheries. The Council concluded that domestic fishing regulations resulting from international treaties should be implemented through the Council process.

Members highlighted the need for scientific research to better define the stock structure of bigeye tuna to ensure implementation of appropriate management regimes. Likewise, the Council recommended that reports be prepared on the status of the North Pacific albacore stock and on the potential impacts to Hawai'i pelagic fisheries of international management measures for this species.

At its June 2005 meeting, the Council will review alternatives for a phased approach for obtaining commercial and recreational catch and fishing effort data for all types of fishing on pelagic fishes. Noted was the progress already made in obtaining this type of information from commercial and recreational pelagic fisheries in American Samoa, Guam and Commonwealth of the Northern Mariana Islands.

The Western Pacific Regional Fishery Management Council is the agency responsible for preparing fishery management plans for federal waters (generally three to 200 miles offshore) surrounding the U.S. Pacific islands. For more information, please visit the Council website at [www.wpcouncil.org](http://www.wpcouncil.org).

PFRP

## PUBLICATIONS OF NOTE

Executive Summary of the Second International Fishers' Forum held at the Hawai'i Convention Center in Honolulu, Hawai'i, November 2002. PDF file available online at <http://www.fishersforum.org>.

Hinke, J. T., I. C. Kaplan, K. Aydin, G. M. Watters, R. J. Olson, and J. F. Kitchell. 2004. Visualizing the food-web effects of fishing for tunas in the Pacific Ocean. *Ecol. Soc.* 9(1):10.

Langley, A., Hampton, J. and Williams, P. 2004. The Western and Central Pacific Tuna Fishery: 2002: Overview and Status of Stocks. *Tuna Fisheries Assessment Report 5*. Noumea, New Caledonia: Secretariat of the Pacific

Community. PDF file available online at <http://www.spc.org.nc/OceanFish/Docs/Research/wcptf.htm>.

PREPCON Documents of the Preparatory Conference for the Establishment of the Commission for the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific. PDF or Word files available online at <http://www.ocean-affairs.com>

*Tuna Market News*, monthly price and volume trends in world and regional tuna markets, available on the Pacific Islands Forum Fisheries Agency website. PDF file available online at <http://www.ffa.int/node/246>

PFRP

## Fishing Regulations Recommended For Proposed NWHI Sanctuary

The Western Pacific Fishery Management Council has decided on draft fishing regulations for the proposed Northwestern Hawaiian Islands (NWHI) National Marine Sanctuary (NMS). The regulations would allow bottomfish and pelagic fisheries to continue under existing federal regulations with some modifications.

A moratorium would be established for all other commercial, recreational, subsistence and sustenance fisheries in the NWHI until such fisheries are covered by a science-based, fishery ecosystem management plan developed by the Council in consultation with the NMS Program and implemented by NOAA Fisheries. Native Hawaiian subsistence use would be allowed by local communities eligible under a Western Pacific Community Development Program. NWHI fisheries would continue to be managed by the Council under the Magnuson-Stevens Fishery Conservation and Management Act.

Under the NMS Act, Regional Fishery Management Councils have the opportunity to draft fishing regulations for sanctuaries that are being designated. The Secretary of Commerce determines whether the draft regulations are compatible with the goals and objectives of the NMS Act and of the sanctuary being designated. The overarching goal of the proposed NWHI NMS is the long-lasting protection of the coral reef ecosystem.

Under existing federal regulations up to 17 bottomfish vessels of under 60 feet in length are permitted to fish in the NWHI. Nine bottomfish vessels are currently active. They provide about one-third of the Hawai'i commercial landings of opakapaka, onaga and

(continued on page 6)

### Pelagic Fisheries Research Program Newsletter

Volume 10, Number 2

April-June 2005

**Editors** Priscilla Billig, John Sibert  
**Writers** Kerstin A. Fritsches, Richard W. Brill, Eric J. Warrant, Priscilla Billig, and John Sibert  
**Layout** May Izumi  
**Printing** Service Printers, Honolulu, HI 96819

#### For more information

Pelagic Fisheries Research Program  
Joint Institute for Marine and Atmospheric Research  
University of Hawai'i at Mānoa  
1000 Pope Road, MSB 313  
Honolulu, HI 96822  
TEL (808) 956-4109 FAX (808) 956-4104  
E-MAIL [sibert@hawaii.edu](mailto:sibert@hawaii.edu)  
WWW <http://www.soest.hawaii.edu/PFRP>

## UPCOMING EVENTS

### 56th Tuna Conference

May 23-26, 2005, Lake Arrowhead, CA  
Contact: Kevin T. Hill at (858) 546-7170  
Online information: <http://www.swfsc.nmfs.noaa.gov/tunaconf.html>

### Fourth World Recreational Fisheries Conference

June 12-16, 2005, Trondheim, Norway  
Contact: [wrfc2005@nina.no](mailto:wrfc2005@nina.no) or call 47 7380 1621  
Online information: <http://www4.nina.no/WRFC2005>

### National Marine Educator's Conference

July 14-16, 2005, Maui Community College, Kahului  
Contact: Ann Coopersmith at [coopersm@hawaii.edu](mailto:coopersm@hawaii.edu)  
Online information: <http://www.hawaii.edu/mcc/oceania/NMEA05.html>

### Coastal Zone 2005

July 17-21, 2005, New Orleans  
Contact: Jan Kucklick at [Jan.Kucklick@noaa.gov](mailto:Jan.Kucklick@noaa.gov)  
Online information: <http://www.csc.noaa.gov>

### American Fisheries Society

#### 135th Annual Meeting

American Fisheries Society 135th Annual Meeting  
September 11-15, 2005, Anchorage, Alaska  
Contact Bill Wilson at [bill.wilson@noaa.gov](mailto:bill.wilson@noaa.gov) or (907) 271-2809  
<http://www.wdafs.org/Anchorage2005>

### Third International Fishers Forum

September 2005, Tokyo, Japan  
Contact Paul Dalzell at [Paul.Dalzell@noaa.gov](mailto:Paul.Dalzell@noaa.gov)  
<http://www.fishersforum.org>

### Fourth International Billfish Symposium

October 31-November 3, 2005  
Avalon, Santa Catalina Island, California  
Contact Michael Domeier at [Domeier@cs.com](mailto:Domeier@cs.com)  
[http://pier.org/billfish\\_symposium/index.htm](http://pier.org/billfish_symposium/index.htm)  
Abstracts due no later than July 15, 2005.  
(reduced rate if registering before May 15, 2005)

---

Fishing Regulations Recommended (continued from page 5)

other snappers, groupers and jacks from healthy stocks fished well below biologically safe levels of harvest. Scientists have determined that the bottomfish fishery has virtually no impact on the NWHI ecosystem or protected species found there.

In addition, recent research by the NOAA Fisheries Pacific Islands Fisheries Science Center shows that, if there is biological connectivity between the NWHI and the main Hawaiian Islands (MHI), it is unlikely the NWHI is a source of fish for the MHI. The dominant ocean currents run from the MHI to the NWHI and not vice versa.

The NWHI spans 1,200 miles, or about the length of entire East or West Coast of the United States. The proposed NWHI Sanctuary would be a 100-mile band covering the entire NWHI chain, an area of about 132,000 square miles or seven times the combined area of the 13 existing National Marine Sanctuaries combined.

PFRP



The diversity of fish and other reef organisms rival tropical rainforests. (Photo courtesy of OAR/National Undersea Research Program, Woods Hole Oceanographic Institution.)



### Pelagic Fisheries Research Program

Joint Institute for Marine and Atmospheric Research  
University of Hawai'i at Mānoa  
1000 Pope Road, MSB 313  
Honolulu, HI 96822

