

A RAPID INCREASE IN WATER TEMPERATURE ALTERS THE
SWIMMING PERFORMANCE OF STRIPED BASS (MORONE SAXATILIS)

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ABSTRACT

We tested the effects of rapid temperature increases on the swimming behavior and locomotor performance of striped bass (*Morone saxatilis*). Individuals were swum in a flow tank while being videotaped from lateral and ventral perspectives. From the video, we recorded the fraction of time spent swimming in transient burst-and-glide mode and conducted computer-aided motion analysis of sequences of steady swimming. From the kinematic data, we calculated tail-beat frequency, tail-beat amplitude, propulsive wavelength, caudal fin trailing-edge depth and hydrodynamic power. Our results showed that striped bass spent less time cruising steadily as the water temperature increased relative to the baseline (50% at the baseline of 21°C, 3% at the highest temperature of 29°C). During steady-swimming episodes, we found that propulsive wavelength and total power output increased with increases in water temperature. These results suggest that striped bass swimming into regions of rapidly increasing water temperature, such as electric generating station discharges, will suffer dramatic reductions in locomotor performance.

TABLE OF CONTENTS

Abstract V-3
Table of Contents V-5
List of Figures V-6
Introduction V-7
Methods V-9
Results V-12
Discussion V-15
Acknowledgments V-16
Literature Cited V-17

LIST OF FIGURES

| | |
|---|------|
| Figure 1. Burst time as a function of water temperature..... | V—13 |
| Figure 2. Propulsive wavelength as a function of water temperature..... | V—14 |
| Figure 3. Hydrodynamic power as a function of water temperature..... | V—14 |

INTRODUCTION

Ectothermic animals face a continual physiological challenge: any change in environmental temperature alters body temperature and, in turn, metabolic and enzymatic processes. This challenge is particularly acute for highly mobile ectotherms such as fish, whose ability to migrate or forage is dependent on effective functioning of the locomotor system. While fishes can acclimate to seasonal changes in temperature, abrupt fluctuations in temperature pose the most serious challenge. Abrupt temperature changes may be encountered by fishes as they alter depth or move into regions where two sources of different temperature converge (Wootton, 1990). Thus the goal of this study is to determine how acute fluctuations in water temperature alter the swimming performance of fish.

We chose a highly mobile, migratory species from the Hudson River, the striped bass (*Morone saxatilis*). A popular sport fish, striped bass use the Hudson River as one of their primary spawning sites on the East Coast of the United States, with individuals ranging as far south as North Carolina and as far north as Nova Scotia (Waldman *et al.* 1990). This is a species likely to encounter thermal pollution on the Hudson River as it travels past thermal discharges.

From 1975 to 1987, water temperature in the Hudson River between the Newburgh-Beacon and Mid-Hudson bridges varies from around 0°C in January to 28°C in July and August (measured at river mile 66 by Mancroni *et al.* 1992). Seasonal changes are gradual, with increases of 15°C occurring over a period of about three and a half months. Central Hudson Gas and Electric operates two fossil-fueled steam electric generating stations on the Hudson River. Together, Roseton and Danskamer Point stations take in about 3.6 million liters of water a minute and discharge it at significantly warmer temperatures (Normandeau Associates, 1989). The water temperature of discharge plumes are regulated, to a maximum of 20°C above ambient in the winter and

to 10°C above ambient in the summer. Because the water temperature of discharge plumes on the Hudson is not regularly monitored, the actual temperatures are not known.

The swimming performance of fish is largely determined by the ability of cellular chemical processes to function smoothly and to operate a compliant mechanical framework. Specifically, muscular enzymatic activity runs a complex architecture of bone, septa, and other tissues. The behavior of both mechanical and chemical interactions have been found to be temperature dependent (Wainwright *et al.* 1976). The cumulative effects of such interactions can be seen in the effects of temperature on whole organisms. Beamish (1970) found that oxygen consumption in swimming largemouth bass, Micropterus salmoides, increased linearly with water temperature in acclimated individuals between 10°C and 34°C.

The relationship between enzymatic activity and temperature is typically characterized by exponentially increasing activity with increasing temperature, followed by a steep decline in activity correlated with denaturation (Wootton, 1990). Muscle performance in fishes appears to follow the same trend. Rome *et al.* (1992) found that muscle fiber bundles of scup (Stenotomus chrysops) at 20°C generate force over a wider range of shortening velocities than muscle at 10°C. Although the warmer muscle did not generate significantly greater maximum force production, when stimulated appropriately locomotor muscle can generate more net force in a tail-beat cycle at higher temperatures. Although not tested, one would expect an eventual drop-off in this relationship, as seen with enzymatic activity. In addition to the enzymes associated with active muscle, one must also consider the temperature dependence of the biomechanical materials which support and are operated by muscle tissue. Passive muscle tissue, bones, and septa are all structures which have mechanical properties dependent on temperature (Vincent 1990).

In addition to altering physiological processes, temperature changes the physical properties of the water itself. An increase in temperature of 20° C, from 20 to 40 ° C for example, decreases the water's kinematic viscosity ($m^2 s^{-1}$) by 34 % (Vogel 1981). This

decrease in kinematic viscosity is inversely proportional to Reynolds number, the ratio of inertial to viscous forces encountered by an animal swimming at constant velocity (Vogel 1981). Thus, for a fish, a 20° C increase in water temperature results in a 50 % increase in Reynolds number. Thus, independent of physiological considerations, we would expect an increase in water temperature to require a striped bass to swim differently; exact predictions cannot be made since the required thrust varies non-linearly with Reynolds number (Vogel 1981).

METHODS

Fish Swimming

Six striped bass, Morone saxatilis, were collected by seine net from Long Island Sound on the coast of Port Washington, New York; water temperature was 20°C. Within six hours, the fish were transported to and held at Olmsted Hall, Vassar College, in tanks of salinity and temperature equal to that at the collection site. Fifteen days after obtaining the fish, post-absorptive individuals were swum at a water temperature of 21°C over a range of swimming speeds; these data served as the baseline at acclimation temperature. Two days later, experiments with temperature changes took place over a continuous 8-hour period; we allowed fish to rest at least an hour at 21°C between bouts of swimming at higher temperatures.

To simulate rapid water temperature change, individuals were placed from a 21°C holding tank into the flow tank with heated water. We then swam each individual at a flow speed of 2.0 body lengths/sec (BL s^{-1}). We chose this speed for three reasons: (1) it is in the region of speeds for which striped bass ram ventilate, (2) it is below the critical swimming speed of striped bass (Freadman 1979), and (3) it is above the range of undulatory swimming speeds accompanied by pectoral rowing. Three individuals swam steadily in the following water temperatures (in order of experiments): 31°, 29°, 26°, 24°,

and 21°C. The swimming of the final sequence was compared to the swimming recorded at the same water temperature two days earlier. This comparison served as a control for effects of stress incurred on the fish during handling and experimentation. Using analysis of variance, we could not detect a significant difference between pre-trial and experimental swimming. On this basis, neither the handling or temperature fluctuations permanently altered swimming physiology.

For each bout of swimming we videotaped the locomotor behavior of the fish. To characterize the locomotor behavior, we measured, from videotape, the proportion of time each individual spent accelerating compared to the time it spent swimming steadily. This "burst time" gives an indication of the locomotor effort required by the white, anaerobic muscle of the body, which operates at faster contraction frequencies and is used when red muscle alone cannot produce sufficient power (Rome *et al.* 1992).

To characterize the locomotor motions of the body, we measured the kinematics of the axial wave of bending during steady swimming. To minimize turbulence and standardize flow conditions, sequences were analyzed only when the individual swam between 5 and 15 cm off the floor of the working section and in flow velocities within 10% of the mean velocity of that 10 cm section of the water column. The position of the axial midline through time was measured from the video sequence using a video overlay system composed of a freeze-frame video deck (Sony, model SVO-9200-MDR SVHS), overlay board (Mass Microsystems, model Colorspace Iii), and a computer (Apple, model Mac Centris 650). For each frame in a sequence, the coordinates of desired points were recorded with a software-generated cursor (National Institutes of Health, model Image 1.51). Fifteen points were traced down the central body axis of the ventral surface of a fish in addition to two points taken on the lateral view of tail. Only sequences of steady swimming sustained for at least three tail-beat cycles were analyzed. From these midlines, viewed over the complete bending cycle for that speed, individual, and temperature, we calculated the following kinematic variables: (1) tail-beat frequency

(Hz), (2) tail-beat amplitude (m), (3) propulsive wavelength (m), (4) depth of the trailing edge of the caudal fin (m), (5) and the hydrodynamic power output (W).

Tail-beat frequency was the inverse of the average time of three tail-beat cycles. Tail-beat amplitude was the half the average peak to trough displacement of three tail-beats. Propulsive wavelength was twice the half-wave components of the propulsive wave, a standard kinematic variable that is the apparent wavelength of the body when midline images are superimposed about the axis of progression (Webb 1986; Webb 1988). Depth of the trailing edge of the caudal fin was the maximal dorso-ventral length of the caudal fin, as viewed laterally, during a tail-beat cycle.

Using those kinematic variables, hydrodynamic power output was calculated using elongated-body theory, a standard hydrodynamic model for undulating fish (Lighthill 1970). The small-amplitude form of this theory can be derived as follows (see Webb *et al.* 1984). From conservation of energy, the thrust power, P_{thrust} , at steady speeds is the total power generated by the swimmer, P_{tot} , minus the power lost as kinetic energy in the wake, P_{ke} :

$$P_{thrust} = P_{tot} - P_{ke} \quad (1)$$

where

$$P_{tot} = m\omega WV \quad (2)$$

and

$$P_{ke} = \frac{1}{2} m\omega^2 V \quad (3)$$

The virtual mass of the water per unit length is m , ω is the velocity given to the water at the trailing edge, W is the lateral velocity of the trailing edge of the tail, and V is the forward velocity of the fish. These variables, in turn, are approximated as follows:

$$m = \frac{\rho\pi D^2}{4} \quad (4)$$

and

$$\omega = \frac{W(F\lambda - V)}{F\lambda} \quad (5)$$

and

$$W = \frac{\pi F A}{\sqrt{2}} \quad (6)$$

where ρ is the density of the water, D is the depth of the trailing edge of the caudal fin, F is the tail-beat frequency, l is the propulsive wavelength of the body, and A is tail-beat amplitude. These quantities (Eqs. 4 to 6) are measured from films of swimming fish and used to calculate thrust power.

RESULTS

Changing water temperature alters the swimming performance of striped bass in a flow tank. No fish were capable of swimming either transiently or steadily at or above water temperatures of 31°C. Individuals were observed to fatigue and lose equilibrium (the ability to resist body roll) within the first minute of exposure. With increasing water temperature, striped bass increase the proportion of time they spend accelerating, as measured by the relative burst time (Fig. 1). Since burst and glide swimming is generated by white, anaerobic muscle (Rome *et al.* 1992), this increased burst time is associated with a decrease in the use of the aerobic red muscle.

The relationship between water temperature and burst time can be summarized by the following regression equation ($n = 4$, $r^2 = 0.906$, $p = 0.048$):

$$y = -0.865 + 0.065x$$

where y is the burst time (%) and x is the water temperature (°C).

Of the four kinematic variables — tail-beat frequency, tail-beat amplitude, propulsive wavelength, tail depth — only propulsive wavelength varies significantly with increasing water temperature (Fig. 2). The propulsive wavelength at 29°C is greater than that at either 21° or 26° C. This result was determined using analysis of variance and was robust; it existed with data at 21° C pooled from pre-trial and experimental data, with pre-trial data removed, and with pre-trial and experimental data separated.

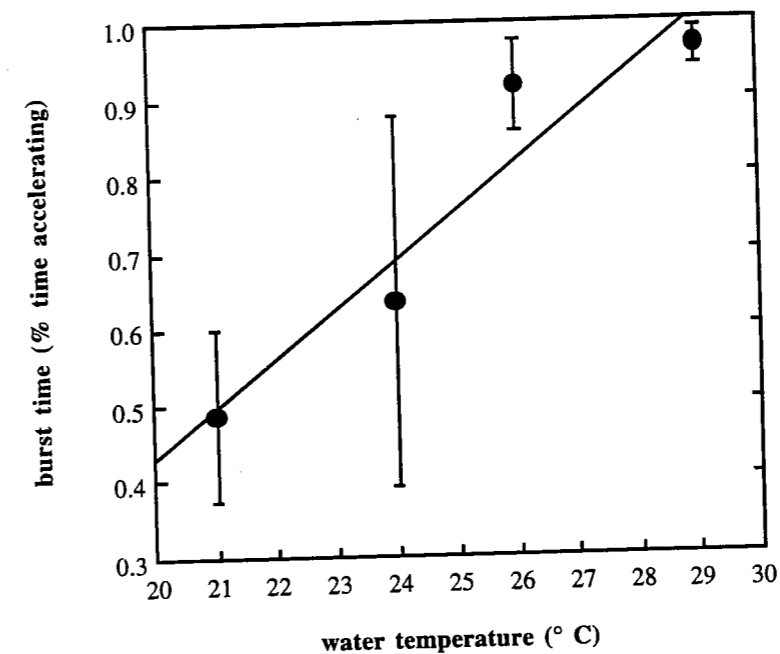


Figure 1. Burst time as a function of altered water temperature. As water temperature fluctuates over a short time period, with 21°C as the baseline temperature, time spent swimming in the burst and glide mode (accelerating) increases. The line is a significant linear regression ($p < 0.05$).

The total hydrodynamic power and its components (see Equations 1 - 6) did not vary significantly with water temperature. Statistical significance was not detected with either regression analysis or analysis of variance. Nonetheless, all three components of hydrodynamic power mirror the significant changes in propulsive wavelength (compare Fig. 2 with Fig. 3). In fact, propulsive wavelength is an excellent predictor of total hydrodynamic power ($n = 4$, $r^2 = 0.975$; $p = 0.012$):

$$y = -0.024 + 0.141x$$

where y is the total power and x is the propulsive wavelength. Given the relationship between propulsive wavelength and power, as calculated using elongated-body theory, this relationship is not surprising.

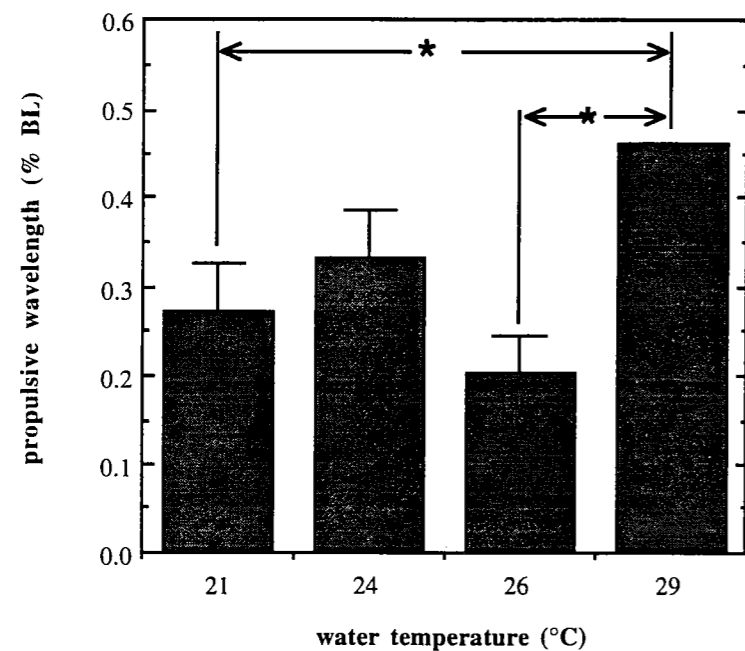


Figure 2. Propulsive wavelength as a function of altered water temperature. Sample sizes at each temperature were 5, 2, 3, 1. Temperature varied from a baseline of 21°C.

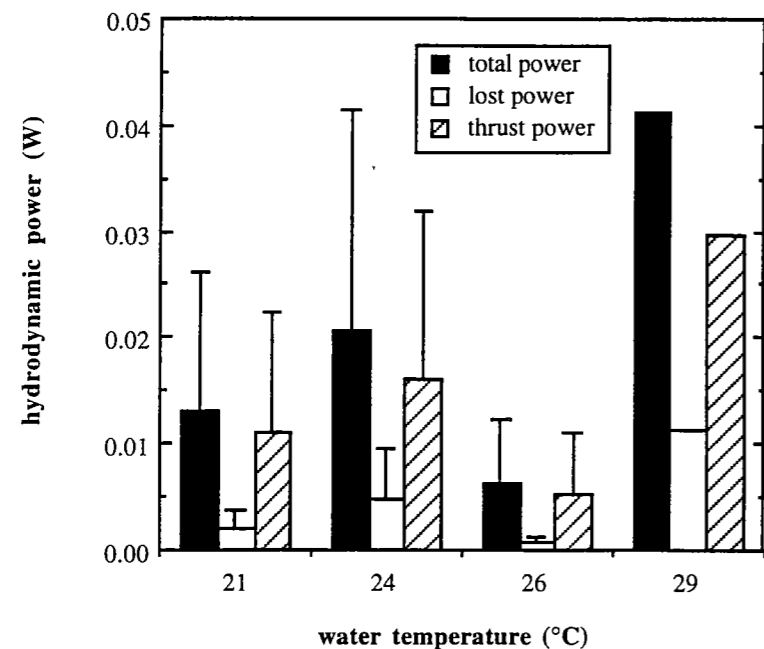


Figure 3. Hydrodynamic power as a function of water temperature. Total power, lost power, and thrust power do not change significantly with water temperature. Total power is predicted, however, by propulsive wavelength (see text for details). Sample sizes are the same as those indicated in Fig. 2.

DISCUSSION

In response to fluctuating water temperatures, striped bass alter their swimming performance. As the increment of temperature change increases from the acclimation temperature of 21°C, bass respond by increasing the time spent swimming in burst and glide mode relative to steady swimming mode (Fig. 1). Steady swimming motion changes with increasing temperature change as well; the propulsive wavelength of the body axis increases at 29° C (Fig. 2). The propulsive wavelength, in turn, is an excellent predictor of the total hydrodynamic power output of the fish (Fig. 3). These results suggest that the swimming performance of striped bass could be altered as they swim in or near the heated water discharged from electrical power plants of the Hudson River.

Perhaps the most striking result in the present study is the inability of individuals to swim in either mode at or above a water temperature of 31°C, 11°C above acclimation temperature. It is probable that the intensity of rapid temperature increase necessary to cause such paralysis is dependent on other variables such as acclimation temperature and fish body mass. However, it is currently possible for such a shift in ambient water temperature to occur in the Hudson.

While we have documented changes in the swimming performance of striped bass with fluctuating temperatures, several important questions remain. What is the physiological basis of the change in performance? What is the nature of the temperature fluctuations encountered by striped bass normally and in association with the water discharged by electrical power plants? Do the changes in swimming performance associated with increasing temperature place striped bass, and other fish as well, at risk of impingement or predation? Answers to these questions are needed in order to formulate sound policy for the regulation of thermal pollution in the Hudson River.

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