

Behavioral and Physiological Responses of Smallmouth Bass to a Dynamic Thermal Environment

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Abstract.—In general, temperature and activity levels of fish are highly correlated, and this has important implications to the management of fish populations exposed to elevated and dynamic thermal systems due to anthropogenic perturbations. In this study, the behavior and physiology of smallmouth bass *Micropterus dolomieu* were monitored in the discharge canal of a thermal generating station on Lake Erie during two critical thermal periods; winter and summer. The spring transition was also monitored. Behavioral responses were quantified by monitoring movement, distribution, and abundance with traditional radio telemetry, underwater videography, and activity transmitters. Cardiac function was monitored with hard-wired Doppler flow probes to assess physiological adjustments. At lower temperatures during the winter and spring, smallmouth bass spent most of their time in the warmest and most thermally variable areas of the discharge canal and made few behavioral adjustments on both large- and fine-scales. At these times cardiac function was highly correlated with temperature. As temperatures increased in the summer this trend began to reverse with a decrease in the correlation between cardiac function and temperature until a critical point at approximately 25–30°C where most smallmouth bass attempted to locate thermal refugia by leaving the untempered areas of the discharge canal. Cardiac function of bass experimentally forced to stay in the high and dynamic thermal conditions was completely independent of temperature. This work illustrates the variation in behavioral and physiological responses associated with exposure to different thermal regimes and indicates the utility of integrative studies in assessing the impacts of anthropogenic influences.

Introduction

Rates of activity and physiological processes of ectothermic organisms, including most fish, are influenced principally by temperature. Important life history factors including growth, reproduction, geographic distribution, and feeding rates are all profoundly influenced by water temperature (Fry 1971; Magnusson et al. 1979). The upper and lower thermal tolerances of different fish vary considerably and are somewhat flexible as fish may acclimate seasonally to different extremes (Fry 1958; Crawshaw 1977, 1979; Barans and Tubb 1973; Beitinger et al. 2000). With the capacity to detect temperature changes as small as 0.03°C (Bull 1936), it is clear why fish respond in real time and throughout their lives to thermal variation.

Three major mechanisms permit fish to respond to changes in thermal environments (Crawshaw et al. 1990; Hazel 1993). The first is behavioral thermoregulation (Neill and Magnusson 1974; Neill 1979) which can occur on the scale of seconds to minutes in response to sensory input from thermoreceptors (Crawshaw et al. 1990). Behavioral adjustments usually include displacement to regions with more preferential water temperatures. The second mechanism is physiological in nature and alters the rate of chemical reactions within the organisms (Hochachka and Somero 1984). This type of response is also activated quickly (seconds to minutes) and is evidenced at the metabolic level by altered respiratory and cardiovascular rates and efficiencies (Crawshaw 1976). The final mechanism occurs over longer time periods (organism's lifetime through to evolutionary time) and involves acclimatory and adaptational changes

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to variable temperatures (Fry 1947). Research to date has pointed towards a series of phenotypic and genotypic adaptations that may occur to permit fish to reside in thermally variable environments until conditions exceed their tolerances (Huey and Kingsolver 1993). All of these mechanisms are influenced by the magnitude of temperature change, the thermal history of the individual (Beitinger et al. 2000), the direction of temperature change (Crawshaw 1977), and the thermal preferences and tolerances of the organism (Fry 1947; Coutant 1977).

Under natural conditions, fish generally experience gradual changes in seasonal temperature, but over shorter time-periods, water temperatures may be relatively stable. However, major short-term water temperature fluctuations, including some that are potentially lethal, do occur. In natural systems these thermal changes are often driven by climatic conditions (Shuter and Post 1990). Anthropogenic influences have increased the frequency with which fish may face thermally extreme conditions (Regier et al. 1990). For example, widespread development has led to frequent flash floods and groundwater depletion and deforestation has increased the daily temperature fluctuations in riverine systems. Water is also used in various manufacturing and utility industries resulting in the release of heated discharges into receiving waters.

Coal, natural gas, and nuclear power generating stations use water for cooling purposes. As demand for power fluctuates hourly, daily, and seasonally, so does the amount of water required for condenser cooling. Fish living in receiving waters must therefore contend with variable heated discharges. Not only does this typically result in an increase in the temperature of the receiving water body and subsequent effects on biota, but it also may attract fish into the discharge channel or plume where fish are exposed to elevated and fluctuating thermal conditions (Coutant 1970). One of the factors limiting our understanding of how dynamic thermal conditions affect organisms is the difficulty in monitoring the physiological responses and behavior of free-swimming fish in their natural environment (Claireaux et al. 1995). Technological developments have provided scientists with a series of tools to monitor fish behavior and physiology remotely and in real time (Lucas et al. 1993), thus permitting investigations of thermal responses at finer spatial and temporal scales (Cooke and McKinley 1999).

The objective of this study was to examine the response of smallmouth bass to thermal variation

in a power generating station effluent on Lake Erie. To this end, behavior and physiology were monitored using several different techniques during two critical thermal periods, winter and summer, as well as the spring transition. Winter (January to March) studies focused on: Movement, distribution, and abundance with traditional radio telemetry and underwater videography; fine-scale movements and activity with activity transmitters; and cardiac function with Doppler flow probes. In the spring and summer (April to August), we monitored abundance with underwater videography, and cardiac function with Doppler flow probes. The results from this work provide insight into the ability of fish to respond to different thermal regimes, and additionally provide insight into the management and regulation of thermal effluents.

Methods

From January to August 1999, we conducted a variety of studies to examine the behavioral and physiological responses of smallmouth bass residing in the Nanticoke thermal generating station discharge canal, located on the north shore of Lake Erie (Figure 1). Site descriptions and station operations are discussed in Wiancko (1981). Both angling and modified hoop nets were used to capture fish. General temperature patterns were monitored by the station every hour just upstream of the oil booms in the discharge canal and in the lake influent (Figure 1). Temperatures for locomotory activity and cardiac function experiments were monitored every five minutes with submersible, archival temperature recorders (Hobo Temo Loggers, Onset Inc., Massachusetts, USA) at various locations (see figure captions). The focus of this study was on the extremes, i.e. the coldest periods of winter and the warmest periods of summer. However, several of the monitoring techniques employed were used for both periods and the spring transition. In the winter (January to March) underwater videography and traditional radio telemetry were used to monitor fish movement, distribution, and abundance; locomotory activity transmitters were used to assess fine-scale and localized movements; and Doppler flow probes were used to measure cardiac function. In the spring and summer (April to August), abundance was monitored with underwater videography and cardiac function was measured with Doppler flow probes. Although this work focused on the response of fish in the discharge canal, locomotory activity and cardiac function were also monitored in the adjacent lake water.

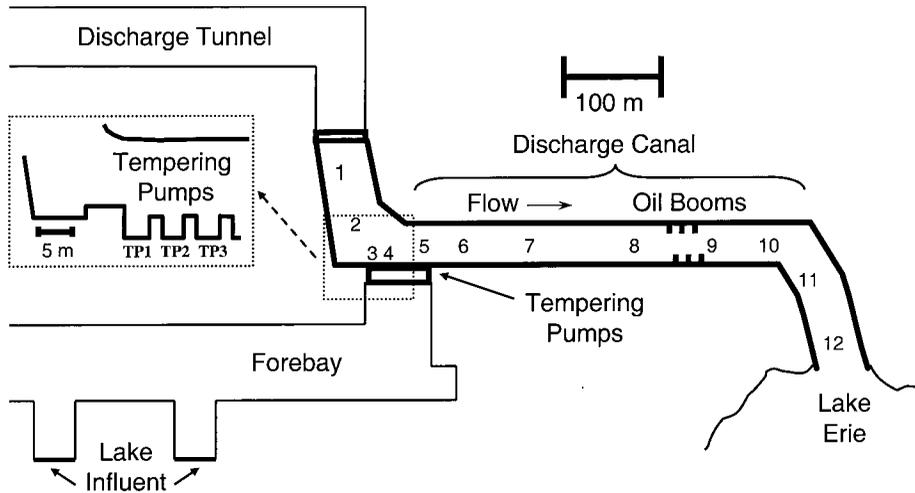


Figure 1. Overhead schematic of the thermal generating station discharge canal complex detailing the locations of the telemetry antenna array. The numbers 1–12 denote antennas for monitoring movements with conventional radio telemetry. Antennas 3, 4, 8, 9, 10, 11, and 12 were underwater whereas antennas 1, 2, 5, 6, and 7 were aerial. Cooler lake water enters the discharge canal through a series of 8 tempering pumps that are linked to an adjacent forebay. The forebay is supplied with water via two intakes in the lake. Tempering pumps one and two were not operational throughout this study.

Videography

To assess relative abundance of fish in the upper reaches of the discharge canal, we employed underwater videography (see Cooke and Schreer 2002 for complete methodology). Briefly, a wide-angle, low light sensitive underwater color camera (Deep-Sea Camera and Light Inc., San Diego, California, USA) in a sealed housing (8 cm diameter, 25 cm length) was lowered to a depth of 3 m in the upper reaches of the canal, at tempering pump 1 (Figure 1). Video was generally recorded from 0900–1500 hours at least weekly. For each tape, data was tabulated for three 10 minutes observation periods. Tapes were viewed at slow speeds (1/5 and 1/30 normal) and the number of each species of fish that swam by the camera during the observation period was recorded.

Radiotracking

To determine residency and movement patterns of adult smallmouth bass in the discharge canal, conventional radio telemetry was employed. A total of 29 fish (Mean \pm SE: TL = 349 \pm 6 mm, Wt = 689 \pm 44 g) were implanted with radio transmitters (MCFT3em, 8.9 g in air, 11.0 mm (Diameter) \times 49.0 mm (Length), Lotek Engineering, Newmarket, Ontario, Canada) in December 1998 and January 1999. Detailed descriptions of surgical techniques are provided in Cooke and Bunt (2001). Briefly, the fish were anesthetized with clove oil and a radio

transmitter package was placed in the intraperitoneal cavity. The whip antenna exited the body through a small puncture caudal to the transmitter. An array of antennas, configured similarly to Cooke et al. (2000) was employed (Figure 1). This included an array of five underwater antennas in the mid to lower reaches of the canal (antennas 8–12), and an extensive grid of both aerial (antennas 1, 2, 5, 6, and 7) and underwater (antennas 3 and 4) antennas in the upper reaches of the canal. Two digital receivers (SRX_400, Lotek Engineering, Newmarket, Ontario, Canada) with code discrimination software, one in the upper and one in the lower portion of the canal, continuously scanned the antenna array for fish with radio transmitters.

Locomotory Activity

Smallmouth bass were captured from both the discharge canal ($n = 5$, Mean \pm SE: TL, 372 \pm 9 mm, Wt, 841 \pm 73 g) and the lake ($n = 5$, Mean \pm SE: TL, 369 \pm 8 mm, Wt, 806 \pm 69 g) in January and February 1999. Fish were anesthetized with clove oil, implanted with locomotory activity transmitters (EMGi, 13 mm (diameter) \times 51 mm (length), weight = 18.0 g in air, Lotek Engineering, Newmarket, Ontario, Canada), and released into large cages (12 m³) in their respective sites of origin. Cages were necessary to ensure continuous data collection from several individuals in a somewhat controlled environment. Surgical and anesthetic procedures are

described in Cooke et al. (2001) and general activity transmitter theory is described in Beddow and McKinley (1998, 1999). Briefly, two gold electrodes attached to an epoxy coated transmitter were implanted into the axial red musculature. The entire procedure lasted less than five minutes and fish recovered quickly when returned to fresh oxygenated water. Resting activity values were collected during a two hour recovery period in a large, 100 L cooler. Activity values were standardized according to the methods of Cooke et al. (2001). This resulted in resting values being assigned a value of zero with increasing activity being expressed as a percent increases over resting. Field measurements were collected continuously using two underwater antennas, one placed in each cage, and a receiver (SRX_400-W20, Lotek Engineering, Newmarket, Ontario, Canada).

Cardiac function

A total of 16 fish from the discharge canal (Mean \pm SE: TL, 326 \pm 11 mm, Weight, 583 \pm 6 g) and three fish from the lake (Mean \pm SE: TL, 313 \pm 7 mm, Weight, 448 \pm 31 g) were captured and held at a mobile field station for a minimum of two days prior to experimentation. Fish from the discharge canal were held in a 1000 L flow-through tank continuously supplied with discharge water under natural photoperiod conditions in an on-site laboratory. Fish from the lake were held under identical conditions except that the tank was supplied with lake water. For six fish (three discharge and

three lake) in March 1999, water sources were switched midway through the trial. The other 12 fish were held in discharge water at three different periods from May to July. Detailed descriptions of surgical procedures and general measurement theory are provided in Schreer et al. (2001). Briefly, fish were anesthetized with clove oil and a flexible silicone cuff-type Doppler flow probe (subminiature 20 MHz piezoelectric transducer: Iowa Doppler Products, Iowa City, Iowa, USA) was placed around the ventral aorta. Internal diameter of the cuffs ranged from 1.4 to 2.2 mm. Cardiac output was monitored and recorded by a hard-wired flowmeter (545C-4 Directional Pulsed Doppler Flowmeter: Bioengineering, The University of Iowa, Iowa City, Iowa, USA) and a digital strip-chart recorder (LabVIEW, Version 4.0.1, National Instruments Corporation, Austin, Texas, USA). Fish were held in 70 L flow-through tanks (50 cm \times 50 cm) with a darkened area covering approximately 30 percent of the tank to provide cover. Cardiac output (CO) was calculated by averaging the flow index per unit time and heart rate (HR) was determined by counting peaks. The quotient of CO divided by HR yielded stroke volume (SV). Where possible, actual flow rates were calculated directly through a postmortem calibration.

Results

Water temperature in the discharge canal was generally 10°C higher than the adjacent lake water and

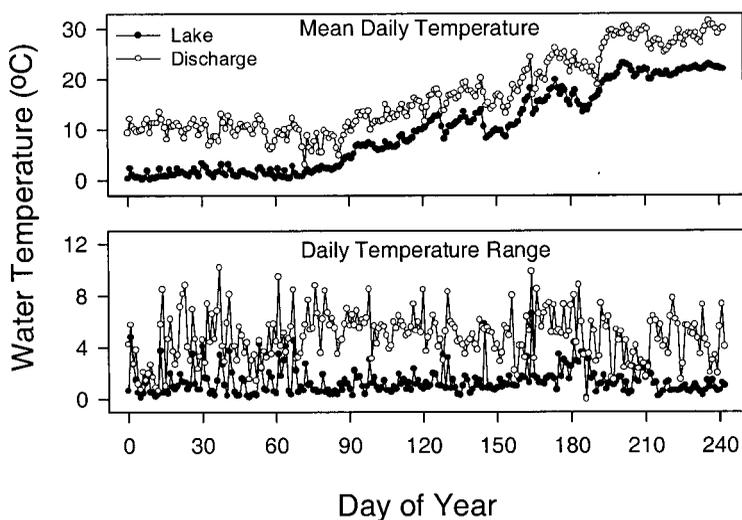


Figure 2. Daily temperature patterns in the thermal generating station discharge canal and the adjacent lake water (forebay) from January to August 1999. Temperature was monitored every hour just upstream of the oil booms in the discharge canal and in the lake influent (Figure 1).

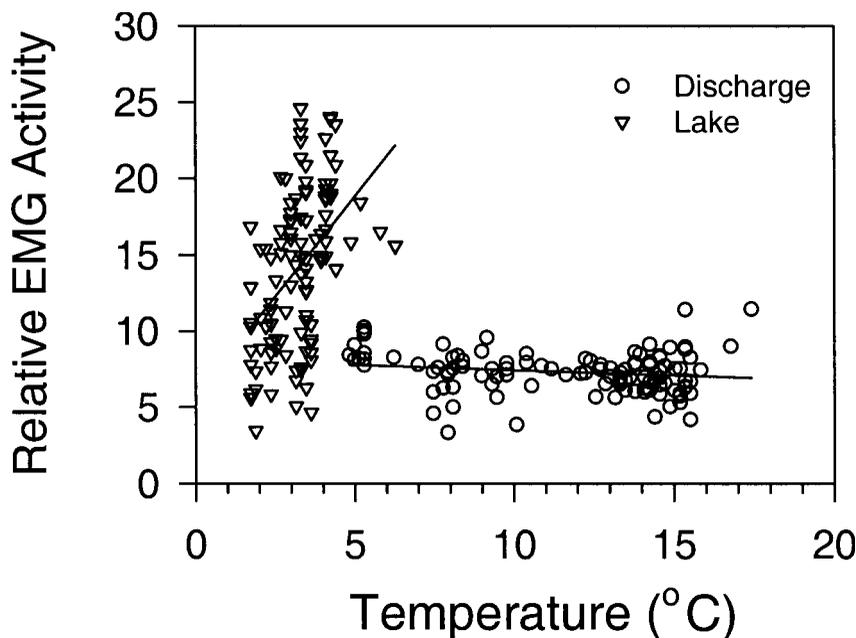


Figure 5. An example of the relationship between temperature and electromyogram (EMG) activity for smallmouth bass in the thermal generating station discharge canal and the adjacent lake water (forebay). Relative EMG activity (five minute mean) is a percent increase above resting values (resting = 0). Fish were held in cages in tempering pump 1 and in the adjacent forebay area (Figure 1). Temperature was recorded every five minutes with archival recorders in each cage. The linear relationships for lake and discharge fish are $y = 2.616x + 5.737$, $r^2 = 0.215$ and $y = -0.068x + 8.130$, $r^2 = 0.028$, respectively.

was considerably more variable (Figure 2). Mean daily water temperatures were relatively constant during January and February (10°C and 2°C for discharge and lake water, respectively), and then increased in a fairly linear fashion from March to August ($10\text{--}30^{\circ}\text{C}$ and $2\text{--}22^{\circ}\text{C}$ for discharge and lake water, respectively). As temperatures were monitored downstream of the tempering pumps, it needs to be noted that water temperatures upstream of the tempering pumps can be $2\text{--}3^{\circ}\text{C}$ higher (Cooke et al. 2000). There was some variation in daily temperature range, although no trends could be seen throughout the study period except that discharge water always had a larger temperature range than lake water.

Winter

From January to March there was little behavioral response to elevated and variable water temperatures. More than 90 percent of the telemetrically recorded locations of fish were in the warmest and most thermally variable regions of the discharge canal in or upstream of the tempering pumps (Figures 1 and 3). Videographic observations also indicated that relative abundance was high in

untempered areas (tempering pump 1) when water temperatures were below 20°C (January to April) (Figure 4). Fine-scale movements of discharge fish, as monitored by locomotory activity, were minimal and independent of temperature from 5°C to 18°C (Figure 5). Conversely, locomotory activity was relatively higher and more closely coupled to temperature for lake fish residing in water between 2°C and 6°C (Figure 5).

Despite the lack of behavioral responses to elevated and variable water temperatures, physiological adjustments were strongly linked to temperature. Cardiac output for both discharge and lake fish was strongly coupled with water temperature and this was almost entirely due to changes in HR (Figure 6). Stroke volume varied little with temperature with a weak inverse relationship for lake fish exposed to discharge water. When water sources were switched (lake to discharge and vice versa), no acclimation or recovery period was observed (i.e., no elevation in cardiac function in response to the thermal shock). The relationship between cardiac output and temperature was stronger for discharge fish in discharge water than lake fish in discharge water (Fig-

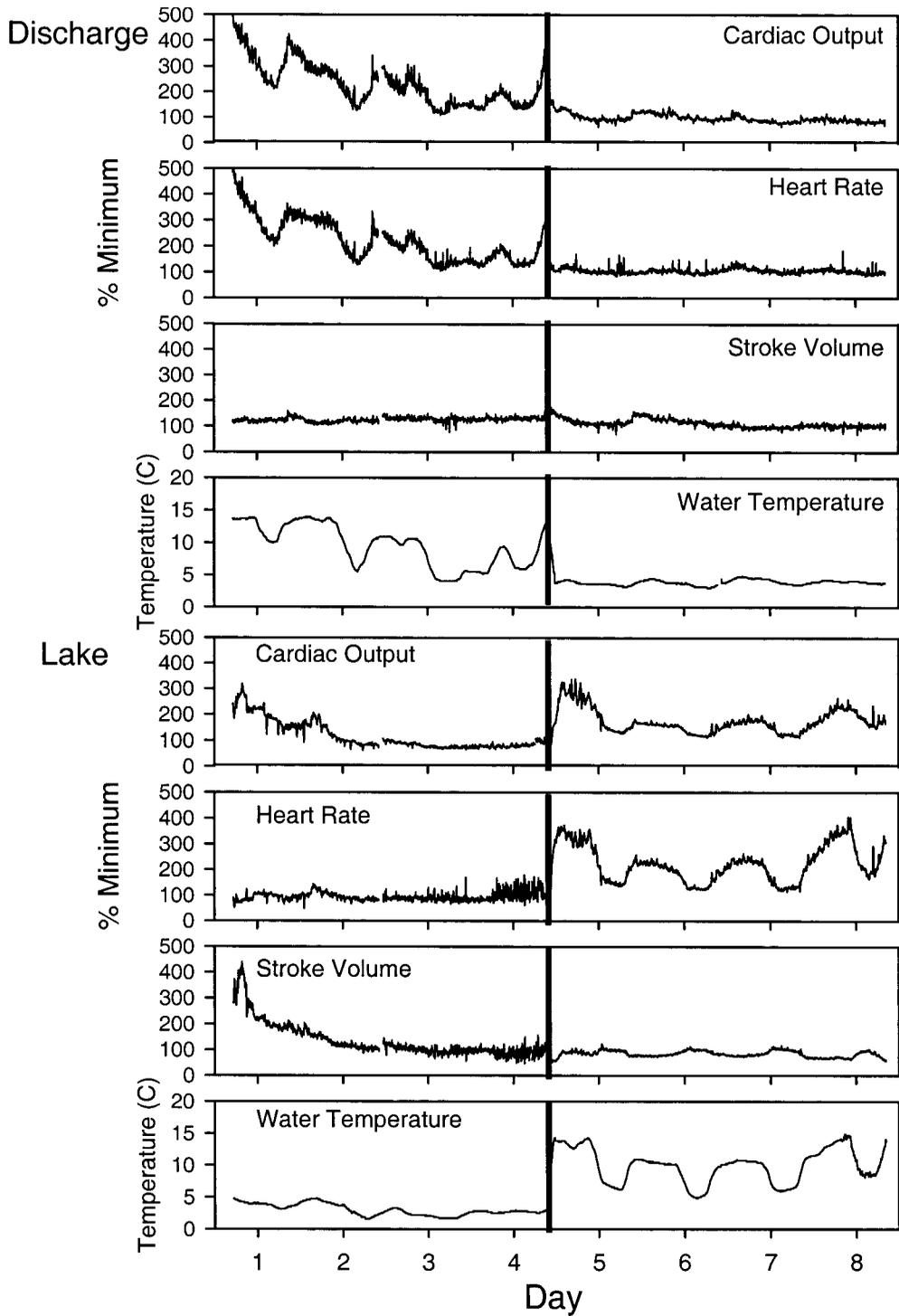


Figure 6. Example traces for cardiac function for smallmouth bass exposed to discharge and lake water. For comparative purposes, all values are five minute mean percent change from a prolonged minimum value set at 100 percent. The shaded lines denote the point at which the discharge water was changed to lake water and vice versa. Temperature was recorded every five minutes with archival recorders located in the discharge canal just downstream of the tempering pumps and in the adjacent lake water (forebay) (see Figure 1).

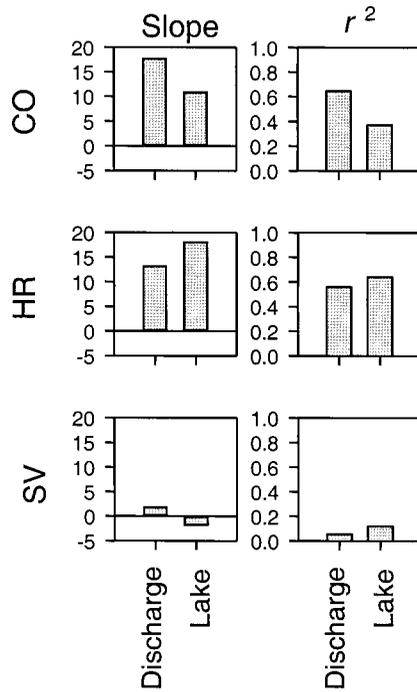


Figure 7. Relationships between cardiac function and temperature for smallmouth bass from the discharge canal and the lake (forebay) exposed to discharge water (see Figure 6). For comparative purposes, relationships were calculated from five minute mean values scaled as a percent change from a prolonged minimum value set at 100 percent.

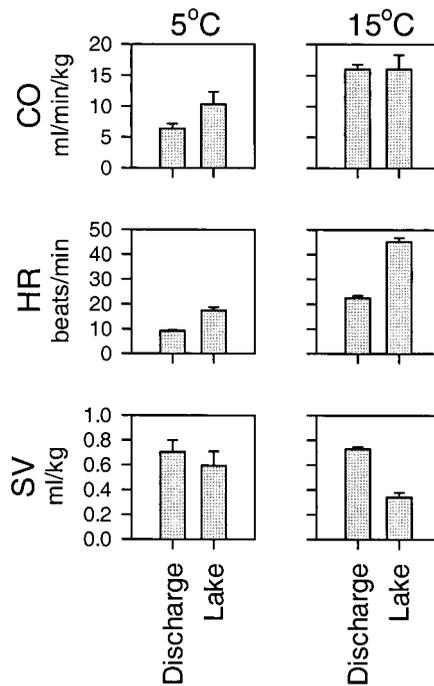


Figure 8. Real cardiac values for smallmouth bass from the discharge canal and the lake (forebay) adjusted to 5°C and 15°C (see Figure 7).

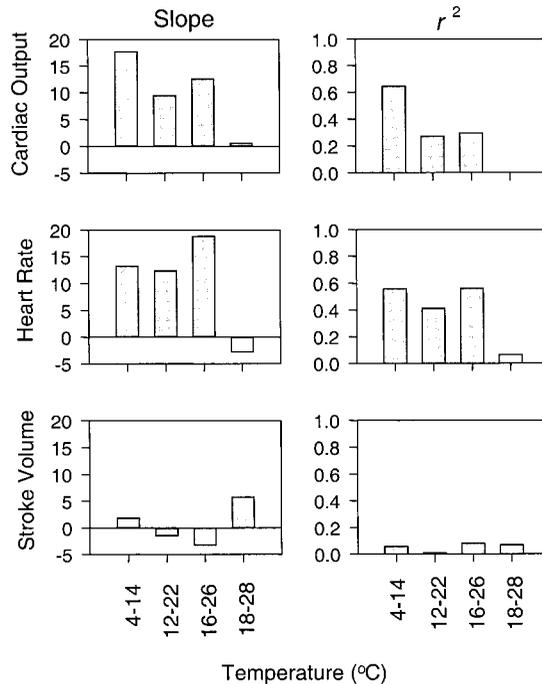


Figure 9. Relationships between cardiac function and temperature for smallmouth bass during four different temperature ranges. For comparative purposes, relationships were calculated from five minute mean values scaled as a percent change from a prolonged minimum value set at 100 percent. All fish were captured and held in water from the discharge canal. March = 4–14°C, late May and early June = 12–22°C, mid June = 12–26°C, late June and early July = 18–28°C.

ure 7). The weaker CO relationship to temperature in lake fish was due to an initially higher and a more rapid increase in HR resulting in a decrease in SV (Figure 8).

Spring and Summer

Videographic results show that following a period of relatively high abundance during winter and spring (10–20°C, January to April), numbers of fish decreased until almost no smallmouth bass were present from 25°C to 30°C in mid July (Figure 4). While the relationship between CO and temperature was relatively strong for May and early June (12–22°C), and mid June (16–26°C), these values were lower than winter measurements (Figure 9). Similar to the lake versus discharge comparison during the winter (Figure 7 and 8), the weaker relationship between CO and temperature during May and June was due to a more rapid increase in HR and higher absolute HR resulting in a decrease in SV with increasing temperature. In late June and early July (18–28°C), this relationship broke down completely with all cardiac parameters varying little and independently of temperature.

Discussion

Although temperature influences many aspects of an organism's behavior and physiology, adjustments can vary depending on absolute temperature and range. The general trend seen in this work was that most behavioral responses were minimal while physiological adjustments were maximal when temperatures were low and well within thermal tolerances of smallmouth bass. This was despite the highly dynamic thermal regime (ranging up to 10°C per day) and absolute temperatures 5–10°C above the adjacent lake water. However, as temperatures increased this trend began to reverse with a decrease in physiological adjustments with varying temperatures until a critical point where fish responded behaviorally by attempting to locate areas with more suitable temperatures (i.e., moving downstream of the tempering pumps) and eventually leaving the discharge canal. Laboratory held fish forced to stay in the warm and thermally dynamic water exhibited no relationship between temperature and cardiac function.

Winter

During the winter and early spring, conventional radio telemetry showed that not only are smallmouth bass movements not affected by temperature, but that they spend most of their time in or upstream of tempering pump 1, where no tempering occurs and temperatures are highest and most variable. There are two primary reasons why smallmouth bass may be spending so much time upstream of the tempering pumps during the winter.

First, numerous studies have suggested that preference for suitable physical structure and prey availability may override optimal temperature preferences (Bevelhimer 1990, 1996; Cooke et al. 2000). The area in and around the tempering pumps provide ample physical structure and velocity refugia for fish (Cooke et al. 2000) and many prey species (i.e., rainbow smelt *Osmerus mordax*, emerald shiner *Notropis atherinoides*, and alewife *Alosa pseudoharengus*) are killed, injured, or disoriented as they are pulled through the condenser cooling and tempering pumps (Kelso and Milburn 1979; Foster and Wheaton 1981), providing an abundant and easy-to-catch prey source.

Second, smallmouth bass may be selecting temperatures which are closer to their final preferendum (Cooke et al. 2000). At these higher temperatures metabolic rates will be higher and consequently fish will grow faster and become larger if provided with sufficient food (Coble 1967; Wrenn 1980). As well, the elevated temperatures may allow smallmouth bass to avoid going into a state of torpor or generalized inactivity at lower temperatures (Coble 1975; Crawshaw 1984).

Although residency patterns from the conventional radio telemetry were generally consistent, this only indicates that fish were not leaving certain areas for temperature refugia. Fish may still be quite active and move considerable cumulative distances within a localized area that would still indicate the temperature dependence of behavior (Cooke et al. 2000, 2001). However, when confined in the cages, the relatively low and invariable activity patterns indicate that discharge fish were not even making fine-scale movements within the caged region of the tempering pump. Locomotory activity patterns indicate that both discharge and lake fish were relatively inactive during the winter (as compared to a 40 percent increase over resting in muscle activity for burst swimming at 16°C) (Cooke et al. 2001). It would be expected that lake fish would be inactive during the winter when temperatures are low (Armour 1993) as has been illustrated by Demers et al. (1996) using activity transmitters in lentic

smallmouth bass. However, it is surprising that not only are the discharge fish inactive at higher and more variable temperatures, but they are less active than lake fish. Further, unlike lake fish, their activity is not coupled to temperature.

A possible explanation for the lower and temperature independent activity levels for discharge fish is synonymous with why fish spend so much time upstream of the tempering pumps; an abundant and easy to catch prey source and suitable velocity refuge (Cooke et al. 2000). Discharge fish have a unique situation where they can sit and wait for prey that have been injured, stunned, or freshly killed to be brought directly to them by the eddy within and around the tempering pump 1 area. Consequently, discharge fish could successfully forage at a wide range of temperatures with little or no movement. Conversely, lake fish would have to pursue active prey and this may only be feasible when temperatures are relatively high (i.e., above temperatures associated with inactivity – Armour 1993). Smallmouth bass food consumption rates and growth are severely limited at low temperatures (Armour 1993), although in lake Erie, smallmouth bass are readily angled at temperatures below 5°C and have prey items present in their stomachs (S.J. Cooke Personal Observation). This would explain not only why lake fish are more active than discharge fish, but also why their activity is more closely coupled to temperature.

An alternative, but less likely, explanation for why EMG activity is higher for lake fish than discharge fish may be due to the temperature dependent properties of the axial musculature (Beddow and McKinley 1998). Power output and maximum shortening speeds in axial muscle can decrease two- to threefold from 20 to 10°C (Rome 1983). Consequently, fish may recruit more muscle fibers and faster fiber types at lower swimming speeds to compensate for the reduction in power output (Rome et al. 1984). This would result in higher absolute EMG activity as well as a more rapid increase in relative EMG activity over resting.

Despite the limited behavioral responses observed, cardiac patterns indicate that fish are making large adjustments in CO that are strongly related to temperature. Almost all of the variation in CO is due to changes in HR while SV remained relatively constant. Interestingly, the relationship between CO and water temperature is stronger for discharge fish in discharge water than lake fish in discharge water. This suggests that discharge fish have acclimated to the higher and more variable temperatures. This is accomplished by having a

lower CO and HR (especially at lower temperatures) than lake fish, perhaps due to lower activity levels (see discussion on EMG activity above) or the resetting of pacemaker activity to a lower rate (Farrell 1997). Consequently, when temperatures increase, discharge fish have more of their metabolic scope available (Farrell 1997; Schreer et al. 2001) when an increase in metabolism is needed. Lake fish, conversely, are more limited by the mechanical properties of the heart. At higher HR's, ventricular filling time becomes severely limited and at a certain point will result in a drastic reduction in SV and a concomitant leveling off of CO (Farrell 1991; Farrell and Jones 1992; Schreer et al. 2001). These lake fish would have less of an activity range within the discharge canal.

Spring and Summer

Although behavioral responses were thermally independent whereas physiological adjustments were thermally dependent during the winter, these patterns reversed during the summer. Videographic results indicate that smallmouth bass were generally abundant until the end of June, after which time very few fish were observed in the upper reaches of the canal. Comparing this trend against water temperature indicates that fish abundance was relatively high until about 20°C, but then declined steadily until 25°C when numbers were near zero. Because temperatures were generally 2–3°C greater upstream of the tempering pumps (Cooke et al. 2001) (as compared to where temperature measurements were taken) and can vary up to 10°C per day, at 20°C (as measured by the downstream temperature probe), fish could be exposed to temperatures nearing 30°C. This is near or above the final preferendum for smallmouth bass (Armour 1993) and consequently, it would be expected that fish would begin to leave water of these temperatures. When temperatures (as measured by the downstream temperature probe) near 25°C, fish in the untempered areas could be exposed to temperatures as high as 35°C which is very near to the upper ultimate incipient lethal limit (Armour 1993) and consequently all fish would be expected to leave the untempered areas of the canal at this time. This trend in behavioral response was supported by the physiological results.

At lower temperatures (during the winter), CO was strongly correlated with water temperature. However, as temperatures increased to the mid teens and low twenties, the relationship between CO and temperature was diminished primarily due to an inverse relationship between SV and tempera-

ture. Because absolute HR would be higher at higher temperature (Farrell and Jones 1992), similar to the comparison of discharge and lake fish during the winter, ventricular filling time would be more limited resulting in a reduction in SV and a concomitant leveling off of CO (Farrell 1991; Farrell and Jones 1992; Schreer et al. 2001).

As temperatures increase to the mid twenties in late June and early July, when smallmouth bass abundance was minimal in the upper canal, fish were also no longer capable of physiologically adjusting to thermal variation. Cardiac output and HR varied little and independently from temperature. At these high temperatures, absolute CO and HR values would be near maximal and therefore when temperature increases there is no room in the metabolic scope for adjustments (Schreer et al. 2001). Consequently, the only option for a fish in this situation is to leave for cooler water which appears to be exactly what occurred.

Conclusion

This work has shown that despite an elevated and highly variable thermal environment in a discharge canal, smallmouth bass are capable of surviving in these conditions. In fact, during the winter and spring, most fish spend all of their time upstream of any tempering where thermal conditions are the most elevated and dynamic. Within limits it appears that these fish are able to respond to the elevated and variable temperatures through the appropriate cardiac adjustments while their behavior is independent of temperature. However, as temperature increases physiological adjustments decrease. When temperatures increased further (mid to late summer), the relationship between cardiac output and temperature broke down completely and only behavioral adjustments were available (i.e., attempting to locate thermal refugia, generally resulting in leaving the untempered regions of the canal). Because smallmouth bass can readily tolerate canal conditions during the winter and spring, spend most of their time upstream of any tempering, and appear to be able to immediately adjust to conditions simulating a potential cold shock (leaving the canal abruptly during winter), the benefits of tempering for reducing absolute water temperature and thermal variation appear to be minimal during the winter and spring (at least for smallmouth bass residing in the canal). However, during the summer as temperatures increase, maximum temperatures do become a limiting factor to the point where fish are excluded from the

canal. Under these conditions, tempering protocols appear to be ineffective at maintaining temperatures within a tolerable range for smallmouth bass within the upper reaches of the canal. Through an integrative approach, this work has demonstrated that management regimes must be flexible because as environmental conditions change so must the mitigating solutions.

Acknowledgments

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