RNA pieces in the spliceosome, has a domain V counterpart, containing a 2-nucleotide bulge located 5 base pairs away from an AGC triad (*10*). Formation of an analogous metal-binding platform in this region of U6 (*11*) may explain the apparent ability of spliceosomal RNAs to retain catalytic activity in the complete absence of the many protein components that usually accompany splicing (*12*). A domain V-like element could have played a major role during the RNA world era of evolution, serving as the catalytic center for RNA cleavage, transesterifiation, and polymerization reactions.

The new structure provides a powerful starting point for future investigations of group II introns and the spliceosome. The lack of electron density for domain VI, which is important for the first step of splicing in many group II introns, and the absence of exons from the structure preclude us from seeing how these elements dock onto the surface created by domains I to V. Thus, the structural details of substrate recognition and catalysis remain undefined. The nature of the conformational change known to separate the two steps of splicing (*13*) also remains unclear. Finally, it will be important for our understanding of group II intron self-splicing to capture the structures of the other intermediates along the splicing pathway and to pursue experiments that link features of these structures with functionally defined interactions.

References

1. A. M. Pyle, *Ribozymes and RNA Catalysis* (Royal Society of Chemistry, Cambridge, UK, ed. 2, 2008).
2. A. M. Pyle, A. M. Lambowitz, *The RNA World* (Cold Spring Harbor Laboratory, Cold Spring Harbor, NY, ed. 3, 2006).
3. N. Toor, K. N. Keating, S. D. Taylor, A. M. Pyle, *Science* **319**, xxxx (2008).
4. M. Stahley, S. Strobel, *Science* **309**, 1587 (2005).
5. T. Steitz, J. Steitz, *Proc. Natl. Acad. Sci. U.S.A.* **90**, 6498 (1993).
6. L. Zhang, J. A. Doudna, *Science* **295**, 2084 (2002).
7. R. Sigel *et al.*, *Nat. Struct. Mol. Biol.* **11**, 187 (2004).
8. P. Gordon, J. Piccirilli, *Nat. Struct. Biol.* **8**, 893 (2001).
9. P. Gordon, R. Fong, J. Piccirilli, *Chem. Biol.* **14**, 607 (2007).
10. G. Shukla, R. Padgett, *Mol. Cell* **9**, 1145 (2002).
11. S. Yean, G. Wuenschell, J. Termini, R. Lin, *Nature* **408**, 881 (2000).
12. S. Valadkhan, J. Manley, *Nature* **413**, 701 (2002).
13. G. Chanfreau, A. Jacquier, *EMBO J.* **15**, 3466 (1996).

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CLIMATE

Blooms Like It Hot

A link exists between global warming and the worldwide proliferation of harmful cyanobacterial blooms.

Hans W. Paerl[1] and Jef Huisman[2]

Nutrient overenrichment of waters by urban, agricultural, and industrial development has promoted the growth of cyanobacteria as harmful algal blooms (see the figure) (*1*, *2*). These blooms increase the turbidity of aquatic ecosystems, smothering aquatic plants and thereby suppressing important invertebrate and fish habitats. Die-off of blooms may deplete oxygen, killing fish. Some cyanobacteria produce toxins, which can cause serious and occasionally fatal human liver, digestive, neurological, and skin diseases (*1*–*4*). Cyanobacterial blooms thus threaten many aquatic ecosystems, including Lake Victoria in Africa, Lake Erie in North America, Lake Taihu in China, and the Baltic Sea in Europe (*3*–*6*). Climate change is a potent catalyst for the further expansion of these blooms.

Rising temperatures favor cyanobacteria in several ways. Cyanobacteria generally grow better at higher temperatures (often above 25°C) than do other phytoplankton species such as diatoms and green algae (*7*, *8*). This gives cyanobacteria a competitive advantage at elevated temperatures (*8*, *9*). Warming of surface waters also strengthens the vertical stratification of lakes, reducing vertical mixing. Furthermore, global warming causes lakes to stratify earlier in spring and destratify later in autumn, thereby lengthening optimal growth periods. Many cyanobacteria exploit these stratified conditions by forming intracellular gas vesicles, which make the cells buoyant. Buoyant cyanobacteria float upward when mixing is weak and accumulate in dense surface blooms (*1*, *2*, *7*) (see the figure). These surface blooms shade underlying nonbuoyant phytoplankton, thus suppressing their opponents through competition for light (*8*).

Cyanobacterial blooms may even locally increase water temperatures through the intense absorption of light. The temperatures of surface blooms in the Baltic Sea and in Lake IJsselmeer, Netherlands, can be at least 1.5°C above those of ambient waters (*10*, *11*). This positive feedback provides additional competitive dominance of buoyant cyanobacteria over nonbuoyant phytoplankton.

Global warming also affects patterns of precipitation and drought. These changes in the hydrological cycle could further enhance cyanobacterial dominance. For example, more intense precipitation will increase surface and groundwater nutrient discharge into water bodies. In the short term, freshwater discharge may prevent blooms by flushing. However, as the discharge subsides and water residence time increases as a result of drought, nutrient loads will be captured, eventually promoting blooms. This scenario takes place when elevated winter-spring rainfall and flushing events are followed by protracted periods of summer drought. This sequence of

Undesired blooms. Examples of large water bodies covered by cyanobacterial blooms include the Neuse River Estuary, North Carolina, USA (**top**) and Lake Victoria, Africa (**bottom**).

CREDITS: (TOP) HANS PAERL/UNIV. OF NORTH CAROLINA; (BOTTOM) SATELLITE PHOTO, DIGITALGLOBE

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events has triggered massive algal blooms in aquatic ecosystems serving critical drinking water, fishery, and recreational needs. Attempts to control fluctuations in the discharge of rivers and lakes by means of dams and sluices may increase residence time, further aggravating cyanobacteria-related ecological and human health problems.

In addition, summer droughts, rising sea levels, increased withdrawal of freshwater for agricultural use, and application of road salt as a deicing agent have led to rising lake salinities in many regions. Several common cyanobacteria are more salt-tolerant than freshwater phytoplankton species (*12*, *13*). This high salt tolerance is reflected by increasing reports of toxic cyanobacterial blooms in brackish waters (*2*, *6*).

Some cyanobacteria have substantially expanded their geographical ranges. For example, *Cylindrospermopsis raciborskii*—the species responsible for "Palm Island mystery disease," an outbreak of a severe hepatitis-like illness on Palm Island, Australia (*4*)—was originally described as a tropical/subtropical genus. The species appeared in southern Europe in the 1930s and colonized higher latitudes in the late 20th century. It is now widespread in lakes in northern Germany (*14*). Similarly, the species was noted in Florida almost 35 years ago and is now commonly found in reservoirs and lakes experiencing eutrophication in the U.S. southeast and midwest (*2*). It is adapted to the low-light conditions that typify eutrophic waters, prefers water temperatures above 20°C, and survives adverse conditions through the use of specialized resting cells (*14*). These bloom characteristics suggest a link to eutrophication and global warming.

More detailed studies of the population dynamics in cyanobacterial blooms are needed. For example, competition between toxic and nontoxic strains affects the toxicity of cyanobacterial blooms (*15*). Furthermore, viruses may attack cyanobacteria and mediate bloom development and succession (*16*). It is unclear how these processes are affected by global warming. What is clear, however, is that high nutrient loading, rising temperatures, enhanced stratification, increased residence time, and salination all favor cyanobacterial dominance in many aquatic ecosystems. Water managers will have to accommodate the effects of climatic change in their strategies to combat the expansion of cyanobacterial blooms.

References

1. J. Huisman, H. C. P. Matthijs, P. M. Visser, *Harmful Cyanobacteria* (Springer, Dordrecht, Netherlands, 2005).
2. H. W. Paerl, R. S. Fulton III, in *Ecology of Harmful Marine Algae*, E. Graneli, J. Turner, Eds. (Springer, Berlin, 2006), pp. 95–107.
3. I. Chorus, J. Bartram, *Toxic Cyanobacteria in Water* (Spon, London, 1999).
4. W. W. Carmichael, *Human Ecol. Risk Assess*. **7**, 1393 (2001).
5. L. Guo, *Science* **317**, 1166 (2007).
6. S. Suikkanen, M. Laamanen, M. Huttunen, *Estuar. Coast. Shelf Sci.* **71**, 580 (2007).
7. C. S. Reynolds, *Ecology of Phytoplankton* (Cambridge Univ. Press, Cambridge, 2006).
8. K. D. Jöhnk *et al.*, *Global Change Biol*. **14**, 495 (2008).
9. J. A. Elliott, I. D. Jones, S. J. Thackeray, *Hydrobiologia* **559**, 401 (2006).
10. M. Kahru, J.-M. Leppänen, O. Rud, *Marine Ecol. Prog. Ser.* **101**, 1 (1993).
11. B. W. Ibelings, M. Vonk, H. F. J. Los, D. T. van der Molen, W. M. Mooij, *Ecol. Appl*. **13**, 1456 (2003).
12. L. Tonk, K. Bosch, P. M. Visser, J. Huisman, *Aquat. Microb. Ecol.* **46**, 117 (2007).
13. P. H. Moisander, E. McClinton III, H. W. Paerl, *Microb. Ecol*. **43**, 432 (2002).
14. C. Wiedner, J. Rücker, R. Brüggemann, B. Nixdorf, *Oecologia* **152**, 473 (2007).
15. W E A Kardinaal *et al.*, *Aquat. Microb. Ecol*. **48**, 1 (2007).
16. M. Honjo *et al.*, *J. Plankton Res*. **28**, 407 (2006).

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DEVELOPMENT

Deconstructing Pluripotency

The requirements for reprogramming different somatic cell types to a pluripotent state may not be equivalent.

Anne G. Bang and Melissa K. Carpenter

In 2006 Yamanaka and colleagues (*1*) discovered that mouse fibroblasts could be reprogrammed to a pluripotent, embryonic stem (ES) cell–like state by the simple introduction of four transcription factors, Oct4, Sox2, Klf4, and c-Myc. This finding has since been reproduced (*2*–*6*) and extended to human fibroblasts using the same cocktail of genes (*7*, *8*) or one comprised of Oct4, Sox2, Nanog, and Lin28 (*9*). These so-called "induced pluripotent stem cells" (iPS cells) appear similar to ES cells in that they can give rise to all the cells of the body and display fundamental genetic and morphologic ES cell characteristics (see the figure). The concept of an iPS cell brings together decades of work in the fields of ES cell biology and nuclear reprogramming that predicted it might be possible to impose pluripotency upon a somatic cell (*10*). iPS cells not only have the potential to produce patient-specific stem cells, but they also provide a platform to study the biology of pluripotency and cell reprogramming. On page XXXX of this issue, Aoi *et al*. (*11*) broaden the application of iPS cell methodology to murine epithelial cell types, highlighting differences when compared with reprogramming of fibroblasts. And on page YYYY, Viswanathan *et al*. (*12*) address the role of one of the reprogramming factors, Lin28, in regulating microRNAs (miRNAs) in ES cells. The findings of Viswanathan *et al*., and recent work by Benetti *et al*. (*13*) and Sinkkonen *et al*. (*14*), advance our knowledge of the little-understood roles of miRNAs in ES cells. Collectively, these studies take us closer to understanding how ES cells maintain an undifferentiated, self-renewing, and pluripotent state, and to defining how pluripotency can be imposed on other cell types.

To date, fibroblasts and mesenchymal stem cells have been used to generate iPS cells (*1*-*9*). A next step is to determine whether other cell types are susceptible to reprogramming. Toward this end, Aoi *et al*. produced iPS cells from two epithelial cell populations, adult mouse hepatocytes and gastric epithelial cells, by expressing Oct4, Sox2, Klf4, and c-Myc. Like iPS cells generated from fibroblasts (iPS-fibroblast), those from primary hepatocytes (iPS-Hep) and gastric epithelial cells (iPS-Stm) were pluripotent and gave rise to adult and germline chimeras. However, iPS-Hep and iPS-Stm differ from iPS-fibroblast cells in several important respects, indicating that the dynamics of reprogramming may not be equivalent in these cell types. For instance, although c-Myc was used, iPS-Hep and iPS-Stm cell–derived chimeric mice did not display the c-Myc-dependent tumorigenicity observed in iPS-fibroblast derived chimeric mice. In addition, iPS-Hep and iPS-Stm cells could be generated using less stringent selection conditions. Thus, epithelial cell types may be more prone to reprogramming than fibroblasts.

How do these differences inform us about the mechanism of reprogramming? Given that ES cells are an epithelial population, characterized by cell adhesion (mediated by the membrane protein E-cadherin), one possibility is that epithelialization is an event required

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FACTORS INFLUENCING GROWTH AND SURVIVAL OF WHITE SUCKER, *Catostomus commersoni*

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ABSTRACT

Growth responses of the white sucker, Catostomus commersoni, were examined in relation to the influence of temperature, body size, season, daylength, light intensity, food ration level and food quality. Sucker growth was maximum at a temperature range of 19-26°C, depending upon experimental conditions. Fish reared under low light intensities grew an average 43% faster than those reared under unshaded conditions. Growth on various diets was best on live tubificid worms presented over sand substrate >tubificids (no soil substrate) >frozen Daphnia >Oregon Moist pellets >Glencoe Mills pellets. The optimum temperature for growth on excess rations of live tubificids was 25°C and was 19°C on restricted rations (1.5% fish body dry weight). Maximum specific growth rate decreased nearly 4-fold over a size range of 12 to 175g, but no difference in optimum temperatures were found. Fish of the same approximate size grew twice the rate in the spring as compared to other times of the year. Photoperiod showed little influence on growth rate, but fish exposed to shorter daylength showed a marked increase in time to achieve a maximum growth rate.

The ultimate upper incipient lethal temperature (UUILT), determined by slowly increasing (0.5°C/day) acclimation temperature to death, was 32.5°C for juvenile white suckers and 31.5°C for adults. The UUILT was 2-3°C higher than the upper lethal temperatures measured by the classical approach involving the direct transfer technique.

CONTENTS

FIGURES

TABLES

SECTION 1

INTRODUCTION

Growth of fish is affected by many variables including temperature, season, body size, and food quality and quantity. These factors influencing growth have been investigated with various species of salmonids (Brown 1946; Brett et al. 1969; Brett 1971 a, b; Shelbourn et al. 1973; Brett and Shelbourn 1975; Elliot 1975; Wurtsbaugh and Davis 1977). No studies have described the thermal responsiveness of cool- and warm-water species throughout an annual growth cycle.

The white sucker, Catostomus commersoni, is a widespread cool-water species important as a forage and bait fish. Both growth response as well as lethal limits are necessary criteria to identify thermal impact on the environment, to improve culture techniques for laboratory research and to enhance the bait industry. McCormick et al. (1977) have shown that sucker fry grow best at a temperature of 26.9°C and reported an upper incipient lethal temperature of 30.5°C for swim-up larvae acclimated to 21.1°C. Brett (1944) reported an ultimate upper incipient lethal temperature of 31.2°C for juvenile white suckers using a direct transfer technique from an acclimation temperature of 25°C. Hart (1947) indicated that the ultimate upper lethal temperature for juvenile suckers was 29.3°C. Hokanson (1977) noted that the upper incipient lethal temperature of a species may vary as much as 4°C. Highest values of the ultimate upper incipient lethal temperatures occurred for summer tests at the highest acclimation temperature increasing slowly to the lethal temperature.

The purpose of the present study was to investigate the growth and mortality rates of juvenile and adult white sucker under different temperature regimens as related to body size, season, daylength and ration level. Preliminary studies were conducted to determine conditions that maximize growth prior to initiation of experimental studies. The upper lethal temperatures of suckers of different sizes were estimated by the direct transfer method and by slowly raising the acclimation temperature 0.5°C/day until death occurred.

SECTION 2

CONCLUSIONS AND RECOMMENDATIONS

The growth optimum and ultimate upper incipient lethal temperature (UUILT) of a species are parameters used in derivation of summer temperature criteria for aquatic life. The growth optimum varied from 19-26°C for juvenile white suckers while the UUILT varied from 28.2 to 32.5°C depending on experimental conditions.

Growth of fish was best when reared without any discernible current flow.

Growth of fish reared under shaded conditions was increased by an average of 43% over those reared under unshaded conditions.

Maximum growth was observed at 25°C on excess rations (9.11% fish body dry weight) and at 19°C on restricted rations (1.5%). Best growth was observed with live tubificid worms presented over a natural sand substrate. Growth on various diets decreased in the following order: Tubificids (sand substrate) >Tubificids (no soil substrate) >frozen *Daphnia* >Oregon Moist pellets >Glencoe Mills pellets. Maximum gross food conversion efficiency was 26% at 22°C and 3.0% ration level of tubificids.

Maximum specific growth rate decreased nearly 4-fold over a size range of 12 to 175g. Optimum temperature for growth was not influenced over this size range. The weight exponent (slope) for this size range was -0.45 which decreased when smaller fish were included in the growth rate-body weight relationship.

Fish of a common size had a 2-fold increase in maximum growth rate in spring compared to other seasons. There was no difference in growth rate between summer and winter fish under a 15hL-9hD photoperiod. Maximum growth in summer occurred at 26°C and at 24°C in winter and spring tests.

Daylength changes had no significant effect on maximum growth rate or optimum temperature. However, attainment of maximum growth under test conditions was increased from 2 to 4 weeks when fish were reared under 15hL-9hD and 9hL-15hD photoperiods, respectively, in a winter test.

The highest UUILT (32.5°C) was achieved by slowly raising the test temperature 0.5°C/day until death. This approach measured an UUILT that was 2-3°C higher than that measured by the classical approach involving the direct transfer of fish from an acclimation temperature to a series of lethal levels.

The UUILT for newly hatched larvae, swim-up larvae, juvenile, and adults were 28.2, 30.5, 32.5, and 31.5°C, respectively.

It is recommended that each investigator run a series of preliminary tests to optimize culture conditions prior to measurement of the physiological optima for each respective species. Better control of light intensity in bioassays with nocturnal or deep-water organisms is especially encouraged.

Growth of white suckers on live tubificids should be compared to growth on natural components in their diet including live Cladocera and macroinvertebrates.

Future bioenergetic studies should cover a broader biokinetic range of temperatures to include the lower and upper limits of zero net growth.

The large variation in measurement of the physiological optima and UUILT for one species herein suggests that temperature criteria data base be critically appraised or revised before adaptation of any literature values to field problems (ie. 316a demonstrations).

Field validation of the laboratory data base on temperature criteria is needed to confirm the best test procedures.

SECTION 3

MATERIALS AND METHODS

EXPERIMENTAL TANKS AND WATER SUPPLY

All tests were conducted in 210 x 54 x 54 cm fiberglass tanks where a 30 cm standpipe at the downstream end of the tank maintained a volume of 340 liters. The water in each experimental tank, representing one test temperature, was supplied by its own head tank where dissolved oxygen and temperature were regulated. Water temperature in the head tank was regulated by either electrical immersion heaters as used by Smith and Koenst (1975) or a thermostatically controlled solenoid valve which allowed hot water to flow through a series of immersed stainless steel heating coils. Dissolved oxygen concentration was maintained near air saturation in the head tanks with the aid of airstones. An airstone also was placed in each experimental fish tank to increase the oxygen concentration and to prevent thermal statification. Water flowed by gravity from the head tank through garden hose to a horizontally placed polyvinyl chloride pipe with three constricted glass outlet tubes placed equally apart above the tank. These glass tubes dispensed a continuous flow of water into the fish tank at a rate of 1.8-2.0 l/min. The water supply was from a deep well and was transported to the head tanks through polyvinyl chloride pipe. A comprehensive analysis of the well water was reported by Smith et al. (1976). Temperature was measured daily with an immersion thermomemter graduated to 0.1^{o}C. A 24-channel temperature recorder monitored temperature variation at less precise levels. Daylength was maintained at a

15h light-9h dark photoperiod during acclimation and testing unless otherwise stated. Dissolved oxygen was measured twice weekly with the azide modification of the Winkler method (APHA et al. 1971). Total alkalinity was determined twice during each test. A weekly determination of pH was made with a pH meter. Temperatures fluctuated slightly (standard deviations ranged from 0.04 to 0.12); pH ranged from 8.18 to 8.30; dissolved oxygen ranged between 78-92% air saturation; and total alkalinity averaged 235 mg/l as $CaCO_3$.

EXPERIMENTAL FISH

All juvenile suckers were acquired from a bait dealer in Sherburne County, Minnesota. Large juvenile suckers (140-200 g) were secured from the same source, but after they had been maintained for one year in the ambient temperature study channels of the Monticello Ecological Research Station, U.S. Environmental Protection Agency, Monticello, Minnesota. Adult suckers (1000 g) were collected from Greenwood Lake, Cook County, Minnesota. Upon arrival at the University of Minnesota Fisheries Laboratory, all fish were given a routine prophylactic treatment of formalin plus malachite green oxalate for 3 days as prescribed by the Committee on Methods for Toxicity Tests with Aquatic Organisms (1975). Fish were kept in holding tanks at 11°C prior to acclimation.

FISH FOOD

Several types of food were given to the fish during holding and testing. During the initial holding period, fish were fed frozen adult brine shrimp (Artemia) and Oregon Moist pellets. Different types of food were presented to the suckers during the acclimation and testing period. During the initial 18 months of the study, Oregon Moist pellets (3/64) was primarily used for growth tests. During the second phase, live tubificid worms were fed to the fish. Along with the food previously mentioned, Glencoe pellets (#1 granules) and frozen adult Daphnia magna were also used in the specific food test.

An excess ration of Oregon Moist pellets was fed to the fish with the aid of an automatic clock feeder. This method was useful in presenting the food continuously over a long period of time and especially in dispensing the food at night during the white suckers' natural active feeding period.

Tubificid worms were collected from two sources: Raven Creek, Scott County, Minnesota, and in a trout hatchery. They were held in a holding tank with clean substrate and flowing water for several weeks prior to being fed to the fish. Subsamples of worms were analyzed for body constituents and were found to contain about 76% water, 7% fat, and 13% protein. Live worms were placed in the fish tanks and, thus, were available for feeding 24 hours per day. A fine granular sand substrate (1.5 cm deep) was placed in each experimental tank to aid in the acceptance of tubificids as a food.

Daphnia were captured in Raven Creek, Scott County, Minnesota, which was fed by an outfall from a sewage treatment pond. Daphnia were in abundance during May and June and large amounts were collected with drift nets in a short time. They were immediately frozen with dry ice at capture and were kept frozen until fed to the fish. Daphnia cubes were thawed and presented to the fish at least twice daily.

PROXIMATE ANALYSIS

Half of the fish were frozen at the end of each experiment for determination of fat and protein content. Water content was determined from fresh fish after each test and from frozen fish at a later date. Fish were oven-dried at 105°C for 24h to determine percentage water content. Fat content was determined from frozen samples which were oven-dried at 85°C to a constant weight. The dried samples were crushed and extracted with n-hexane (Brett et al. 1969). The residue remaining after fat-extraction was analyzed for nitrogen content by the micro-Kjeldahl technique for protein determination. A factor of 6.25 was used to obtain the mean protein value. Subsamples of tubificid worms were also analyzed for body constituents with the same procedures.

EXPERIMENTAL PROCEDURES

Generalized procedures are described herein. Specific details of the experimental design of each study will be described under the appropriate section.

All fish were transferred from holding tanks to experimental tanks within a period of 7 days after prophylactic treatment. Fish were randomly assigned to a test tank after screening for a relatively uniform size. The temperature was increased at a rate of 1^{o}C/day, and the fish were given an additional acclimation period of 2 weeks to experimental tanks after the final test temperature was reached.

To start the growth test, all fish were anesthetized with tricaine methanesulfonate (MS-222) and cold-branded with "liquid nitrogen". The branding was done with branding irons that were super cooled within a liquid nitrogen bath. The numerical brand was placed dorsally above the base of the pectoral fin. Fish were blotted with paper towels and weighed to the nearest 0.01 g and measured to the nearest mm during the marking procedures, and every 2 weeks throughout a 4- to 6-week growth period. Fish were fed daily during acclimation and testing, and observations were made for mortality. Growth in 2-week intervals was expressed as a specific rate (percent change in weight/time) after Brett et al. (1969). The specific growth rate is the slope of the regression of the natural log of weight on time multiplied by 100. All data were statistically examined to describe the optimum range by Analysis of Variance followed by Duncan's New Multiple Range Test (Steele and Torrie 1960). The data was reported as specific growth rate ± 2 standard errors.

The upper incipient lethal temperature (UILT) was determined by the method of Fry (1947) whereby fish were transferred directly from a constant acclimation temperature to a series of constant temperature baths bracketing the median response. The incipient lethal temperature was defined by Fry as the temperature beyond which 50 percent of the population cannot live for an indefinite period of time. The UILT was established for acclimation temperatures of 12, 16, 20, and 24^{o} C as an initial range finding test. The ultimate upper incipient lethal temperature (UUILT) is the highest UILT which can be raised by thermal acclimation. The UUILT was determined by exposing acclimated fish to a slow temperature rise (0.5^{o}C/day) until death after Cocking (1959) and Fry (1971). Percent survival and the corresponding mean daily temperature in the preceeding and final 24h interval was used to determine the temperature where 50 percent of the population would die by graphical interpolation. The UUILT was determined for white suckers of different sizes after a 4-week growth study for fish reared at constant temperatures near optimum (26 and 28 ^{o}C). Feeding was terminated above 30^{o}C since it could influence the response to the upper lethal temperature.

SECTION 4

FACTORS INFLUENCING GROWTH

PRELIMINARY OBSERVATIONS

During the first phase of the project, it became apparent that the white sucker would not achieve maximum growth in the laboratory using methods that have been previously demonstrated with other fish species. It was hypothesized that sucker growth could be maximized by controlling variables such as water current flow, temperature, light intensity, and diet quality. These variables can maximize sucker growth by influencing food acceptance and/or reducing their spontaneous activity and routine metabolism.

Water Current

Juvenile suckers placed in holding tanks did not readily accept pellet food (Oregon Moist) but did feed readily on adult frozen brine shrimp. The brine shrimp distributed more evenly in the tanks due to slight currents created by airstones and the fresh water inflow. A test was initiated to determine if current would enhance food acceptance. Water was circulated by a pump in a circular tank to achieve the desired current. Fish were tested under low light intensity (less than 5 ft-candles) at 22°C under both current and non-current conditions. Fish living without water current grew nearly twice the rate of fish living in a current (Table 1).

Temperature

A preliminary test was conducted to determine the optimum temperature for

TABLE 1. EFFECT OF CURRENT FLOW ON GROWTH OF WHITE SUCKERS*

	$\bar{x}$ Initial wet wt. (g)	Specific growth rate (%/day)
Current+	11.2	0.938
Non-current++	10.2	1.839

*Test conducted in summer at 22°C under a light intensity of less than 5 ft-candles. All fish fed an excess ration of Oregon Moist pellets.

+Water current was created by a pump in a circular tank to disperse food pellets and transport them to fish. Flow rate and velocity was not measured.

++Fish received a similar continuous flow of fresh water, but flow was adjusted to avoid creating any discernible current.

growth of white suckers fed to satiation on Oregon Moist pellets. A growth test was started with juvenile suckers (10 g) at eight different temperatures ranging from 12° to 29°C (Table 2). Fish grew best at 24°C and had an optimum temperature range of 20° to 26°C. Growth was significantly reduced above and below this temperature range ($P < 0.05$).

Light Intensity

The current (Table 1) and temperature (Table 2) experiments indicate that light intensity could be an important factor influencing growth. A comparison of growth rates at 22°C between the two types of tests indicate that suckers grew at a greater rate at low light intensity. It was observed by Stewart (1926) and Campbell (1971) that white suckers normally feed during darkness. Nocturnal activity was also noted by Spoor and Schloemer (1938) who found suckers to move inshore during evening hours and offshore during morning hours. A growth test with 35 g suckers was initiated to investigate the effect of

TABLE 2. EFFECT OF TEMPERATURE ON GROWTH RATE OF WHITE SUCKERS*

Temperature (C)	$\bar{x}$ Initial wet wt. (g)	Specific growth rate (%/day)+
11.9	10.72	0.140 ± 0.051
16.0	11.01	0.330 ± 0.122
18.0	10.74	0.669 ± 0.195
19.9	10.93	1.014 ± 0.223
22.0	10.93	1.032 ± 0.206
24.0	10.63	1.070 ± 0.200
26.0	10.41	0.931 ± 0.187
28.9	9.91	-0.032 ± 0.332

*Tests conducted during fall at a light intensity of 11.5 ft-candles. Fish fed an excess ration of Oregon Moist pellets over a 42-day period.

+Rate ± 2 SE; N = 20 for each treatment.

light intensity. After a two-week acclimation period to test conditions, fish were tested for growth for a two-week period under unshaded conditions (11.5 ft-candles). This was followed by a two-week growth period where shade was provided by placement of a black plastic cover over the lower two-thirds of the water surface. Light was supplied by two 40-watt fluorescent bulbs (Vita-Lite) providing a light intensity of 11.5 ft-candles in the unshaded portion and 0 ft-candles in the shaded portion. Fish were always observed at the lowest light intensity. Fish were tested at seven different temperatures ranging from 14° to 26°C (Table 3). For all temperatures combined, growth rate was increased by an average of 43% after shade was provided, even though these fish were a larger initial size than in the unshaded test. Growth rate was significantly greater under shaded conditions ($P < 0.05$). The unshaded test showed 22°C to be the optimum temperature for growth as compared to all other temperatures ($P < 0.05$), while the shaded test showed an optimum temperature of 24°C and an optimum temperature range of 18°C to 26°C ($P < 0.05$).

TABLE 3. GROWTH RATE OF WHITE SUCKERS AT DIFFERENT TEMPERATURES AND LIGHT INTENSITIES*

Temperature (C)	$\bar{x}$ Initial wet wt. (g)	Specific growth rate (%/day)+	
		Unshaded++	Shaded+++
14.0	37.48	0.34 ± 0.14	0.63 ± 0.26
16.0	35.30	0.52 ± 0.20	0.73 ± 0.21
18.0	34.28	0.67 ± 0.22	1.05 ± 0.27
20.0	35.39	0.79 ± 0.23	0.82 ± 0.24
21.9	34.19	1.22 ± 0.31	1.40 ± 0.35
24.0	34.43	0.87 ± 0.28	1.48 ± 0.34
26.0	33.57	0.87 ± 0.17	1.13 ± 0.25

*Fish tested in winter and fed an excess ration of Oregon Moist pellets.

+Rate ± 2 SE for N = 10 for each treatment.

++11.5 ft-candles.

+++0 ft-candles underneath shaded portion of tank (lower two-thirds area), and 11.5 ft-candles at upper end (one-third area).

Eisler (1957) concluded that high light conditions stimulated growth of chinook salmon fry. Conversely, suckers are nocturnal feeders and could be stimulated by low light conditions.

Diet Quality

It was thought food type could still be a significant limiting factor in achieving maximum growth rate (Brett 1971b). Furthermore, the amount of Oregon Moist consumed by the suckers would be difficult to quantify over time. Live food would be preferable in food ration tests. Tests were conducted to determine food type most suitable in obtaining maximum growth rates. The presence of a substrate with live food was also tested as a factor influencing growth or food acceptability. Juvenile suckers were tested for a two-week growth period at 22°C after a two-week acclimation period. Foods tested were

TABLE 4. GROWTH OF WHITE SUCKERS AFFECTED BY DIET QUALITY*

Food	Specific growth rate (%/day)
Live tubificid worms (sand substrate)+	4.33
Live tubificid worms (no substrate)	3.30
Frozen Daphnia	3.19
Oregon Moist	1.78
Glencoe Mills	-0.03

*Test conducted in spring at low light intensity (0 ft-candles under lower two-thirds tank) at 22°C. Initial wet weight was 10-11 g.

+A 1.5 cm layer of fine sand distributed evenly over bottom of tank.

Oregon Moist pellets, Glencoe pellets, frozen adult Daphnia and tubificid worms. The tubificids were presented as two treatments, one being a tank with no substrate and the other being a tank with a sand bottom. All fish were fed to satiation. Fish fed live tubificids over a sand substrate had a maximum growth rate of 4.3%/day (Table 4). Growth declined in decreasing order from tubificids (sand substrate) > tubificids (no soil substrate) > frozen Daphnia > Oregon Moist > Glencoe Mills.

As a result of the preliminary tests, culture techniques enhancing growth were incorporated into subsequent experimental procedures. All experiments were conducted under low light intensity (11.5 ft-candles at upper one-third tank; 0 ft-candles under shade cover over lower two-thirds tank), fish were fed live tubificid worms, and a sand substrate was provided for feeding.
A continuous flow-through (1.8-2.0 l/min) with no current was provided in the test chambers. These improvements in sucker culture increased growth rates

TABLE 5. EFFECT OF TEMPERATURE AND BODY SIZE ON GROWTH OF WHITE SUCKERS*

$\bar{x}$ Initial wet wt. (g)	N	Temperature	Specific growth rate (%/day)+
11.79	10	12.1	0.05 ± 0.05
10.79	10	17.0	0.55 ± 0.22
11.73	10	20.9	1.79 ± 0.25
10.71	10	24.0	1.80 ± 0.30
12.61	10	25.9	2.37 ± 0.27
12.29	10	28.1	1.33 ± 0.39
11.96	10	29.9	0.20 ± 0.21
166.39	5	12.1	0.40 ± 0.08
161.54	5	17.0	? 0.08 ± 0.06
172.96	5	21.0	0.54 ± 0.08
161.67	5	24.0	0.65 ± 0.15
175.06	5	26.1	0.68 ± 0.14
157.31	5	28.0	0.24 ± 0.09

*A summer test at low light intensity. Fish fed an excess of live tubificid worms.

+Rate ± 2 SE.

more than four-fold to a level that approximates growth rates observed under field conditions at low fish density (K.E.F. Hokanson, U.S. EPA, Monticello MN, personal communication). Mortality of fish was also negligible at all temperatures herein when growth conditions were optimized.

TEMPERATURE X BODY SIZE

The effect of body size of white suckers on growth rates were tested at excess rations of live tubificid worms at different temperatures during the summer. Two sizes of juvenile white suckers were tested (Table 5). Fish of both sizes showed an optimum temperature range for growth to be 21-26°C ($P < 0.05$). Maximum growth occurred at 26°C where the 12.6 g fish grew at a rate of 2.37%/day and the 175.1 g fish grew 0.68%/day. Juvenile suckers (mean wet wt. 25.6 g) tested at excess rations at 25°C grew at a maximum rate of 1.38%/day (see Ration Size X Temperature section, Table 8).

Brett and Shelbourn (1975) found that a log-log transformation provides a good linear relationship between maximum growth rate and body weight for salmonids. A similar relationship exists for juvenile white suckers (Fig. 1). The maximum growth rate relationship for white suckers fed excess rations at 26^{o}C for a weight range of 12.6-175.1 g was expressed by the linearized equation:

$$\ln G = 1.9160 - 0.4523 \ln W \qquad (1)$$

where G = specific growth rate (%/day)

W = initial wet weight (g)

The fitted regression line between the summer data points had an R^2 value of 0.967.

Suckers tested in the springtime showed a higher growth rate than at other seasons for similar sized fish (see Season X Daylength section, Table 6). The maximum growth rate - body weight relationship (10.1-53.6 g) was derived only for comparative purposes by the linearized equation:

$$\ln G = 2.3541 - 0.3391 \ln W \qquad (2)$$

Caution should be exercised in extrapolation of these data beyond the indicated size range as inclusion of smaller fish will reduce the size correction factor (slope) further. McCormick et al. (1977) observed a maximum specific growth rate of 14.8%/day for white sucker larvae with an initial wet weight of 4.1 mg. Addition of this data point to the spring growth rate-body weight relationship would give a slope of -0.168 with an R^2 = 0.972.

SEASON X DAYLENGTH

The effect of season and daylength on sucker growth was investigated. Fish were compared for growth at three different times of the year (spring, summer, and winter) and at three different temperatures (24, 26, and 28C) at

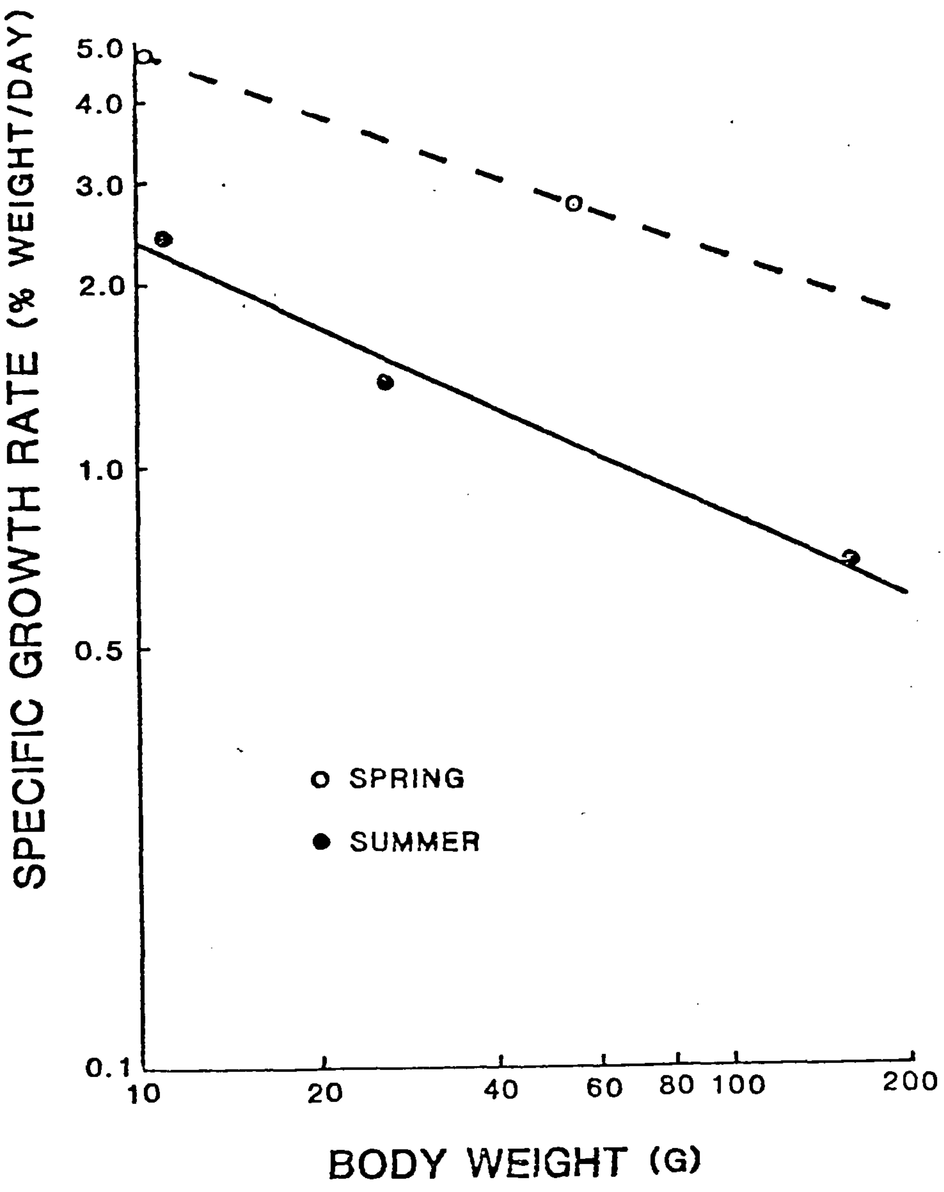

Figure 1. The relationship between initial body size and maximum growth rate of white suckers in the spring and summer.

at a 15h L-9h D photoperiod. Because of a possible effect of season and daylength on growth rate, winter fish were tested at two photoperiods: 15h L-9h D, and 9h L-15h D.

The time of year had a marked effect on growth rates of suckers. Fish during late spring (May-June) displayed nearly a two-fold increase in growth

TABLE 6. EFFECT OF SEASON AND DAYLENGTH ON MAXIMUM GROWTH OF JUVENILE WHITE SUCKERS AT THREE PRESCRIBED TEMPERATURES*

Season	Photoperiod h-L/h-D	x̄ Initial wet wt. (g)	Temperature (C)	Specific growth rate (%/day)+
Spring++	15/9	10.14	24.0	4.80 ± 0.41
	15/9	9.97	26.0	4.35 ± 0.43
	15/9	9.50	28.0	2.89 ± 0.34
	15/9	53.56	24.0	2.73 ± 0.22
	15/9	55.00	26.1	2.60 ± 0.18
	15/9	51.47	28.0	1.66 ± 0.26
Summer++	15/9	10.71	24.0	1.80 ± 0.30
	15/9	12.61	25.9	2.37 ± 0.27
	15/9	12.29	28.1	1.33 ± 0.39
Winter++	15/9	11.66	24.0	2.39 ± 0.26
	15/9	11.17	26.0	2.33 ± 0.22
	15/9	11.17	28.0	1.67 ± 0.34
	9/15	12.13	24.1	2.71 ± 0.29
	9/15	11.41	26.0	2.60 ± 0.28
	9/15	11.40	27.9	1.78 ± 0.24

*Fish fed an excess ration of live tubificid worms at low light intensity.

+Rate ± 2 SE for N = 20.

++28 day growth test began in late May, late July, and early January, respectively.

rate compared to growth during summer and winter (Table 6, Fig. 1). Large juvenile suckers (54 g) displayed a greater growth rate (2.73%/day at 24^{o}C) in the spring than did smaller 11 g individuals (1.80%/day at 24^{o}C) in the summer. The optimum temperature for growth on excess rations was 26^{o}C in summer and was reduced to 24^{o}C in winter and spring tests, although growth rates were not significantly different (P > 0.05). Fish (10-12 g) showed no significant differences in growth rate between summer and winter seasons for a 15h L-9h D photoperiod.

One phenomenon brought out by the winter test was that photoperiod played an important part in the acclimation rate to test conditions based on

TABLE 7. EFFECT OF PHOTOPERIOD AND TEMPERATURE ON GROWTH STANZAS OF WHITE SUCKERS*

Temperature (C)	Specific growth rates (%/day)			
	Photoperiod			
	15h L - 9h D		9h L - 15h D	
	I+	II++	I	II
24	2.37	2.40	1.46	2.71
26	2.34	2.33	1.85	2.60
28	1.74	1.59	1.14	1.78

*Fish fed an excess of live tubificid worms at low light intensity in winter.

+Period I - first two-week period of growth test, following an initial 12-day acclimation period to test tanks, temperature, and photoperiod.

++Period II - second two-week period of growth test.

maximum growth potential. All fish prior to acclimation and testing were treated alike and were exposed to a short daylength during holding. Upon placement in their respective tanks, the photoperiod was changed over a period of three days, fish were acclimated to test temperatures at a rate of $1^{o}C$/day, and held for two weeks before the growth test began.

Results showed that fish acclimated to their test conditions at a slower rate when exposed to decreased daylight (Table 7). Based on maximum growth rate, it took over four weeks for the fish to be fully acclimated to their test conditions during shorter daylength hours compared to two weeks acclimation at the longer daylength. No differences in growth rates were noted between the first two weeks and the second two weeks of the 15h L-9h D photoperiod ($P > 0.05$). Conversely, suckers exposed to the 9h L-15h D photoperiod showed nearly a two-fold increase in growth between Period I and II ($P < 0.05$).

Although no significant differences in growth rates were found due to photoperiod based on the last two weeks of the test ($P > 0.05$), there was a large difference in growth rate between suckers exposed to the two photoperiods for the first two weeks of the test ($P < 0.05$). Special precautions are needed to insure complete acclimation to test conditions if "aseasonal" growth studies are to be conducted in winter.

RATION SIZE X TEMPERATURE

Growth tests were conducted on white suckers (mean wet wt. 29 g) at different temperatures and reduced ration levels of live tubificid worms. Fish were tested at five different temperatures (16, 19, 22, 25, and 28°C) and five daily ration levels (0, 1.5, 3.0, 4.5%, and excess). The restricted ration was prescribed at the start of each two-week growth period and was based on estimated mean dry weights of fish at the mid-point of each interval. Mean dry weight was estimated from final weight (initial weight of current interval) and specific growth rate in the previous two-week interval). Subsequently, fish received a slightly higher portion of feed than the prescribed ration in the first week and a slightly lower portion in the latter week of the growth interval. Tubifex were weighed wet and fed daily to the fish. Subsamples of tubificid worms and fish were dried and weighed at the end of the study. Measured specific growth rates were used to estimate daily mean fish wet weights. These estimated fish wet weights and measured food wet weights were converted to dry weights to determine actual ration size per day. These measured ration sizes, test temperatures, and corresponding growth rates are reported in Table 8. Fish at 16°C did not consume their prescribed ration of 1.5% equally. Because half of the fish consumed little food, the mean growth rate (0.047%/day) was lower than expected while feeding fish grew at

TABLE 8. THE EFFECT OF TEMPERATURE AND RATION SIZE ON GROWTH AND FOOD CONVERSION EFFICIENCIES OF THE WHITE SUCKER*

Temperature (C)	Ration sizes (% dry wt. food/ dry wt. fish/ day)	x̄ Initial wet wt. (g)	Specific growth rate (%/day)	Gross conversion efficiency (%)	Net conversion efficiency (%)
16.1	0	28.1	-0.25 ± .04		
16.1	1.55	30.4	0.05 ± .44	3.0	4.1
16.2	2.89(3.10)+	23.6	0.47 ± .13	16.2	18.8
16.0	3.05(4.51)	26.9	0.43 ± .20	14.1	16.2
19.0	0	30.1	-0.28 ± .09		
18.9	1.45	28.9	0.26 ± .11	17.9	32.4
19.0	2.96	23.4	0.66 ± .18	22.4	28.7
19.2	4.22(4.60)	27.6	0.72 ± .26	17.1	20.2
22.0	0	31.3	-0.34 ± .07		
22.0	1.55	31.6	0.24 ± .14	15.2	36.2
22.0	3.03	28.0	0.80 ± .20	26.4	37.6
22.1	4.65	26.5	0.89 ± .23	19.2	23.8
25.0	0	31.8	-0.53 ± .09		
24.9	1.46	30.6	0.16 ± .09	11.0	44.4
24.8	3.04	31.8	0.67 ± .12	21.9	34.3
25.0	4.63	25.4	1.02 ± .23	22.0	28.9
25.1	9.11(Excess)	25.6	1.38 ± .20	15.2	17.3
28.1	0	33.4	-0.62 ± .09		
28.1	1.52	32.3	0.12 ± .07	7.8	43.7
28.0	3.08	31.1	0.65 ± .20	21.0	35.4
27.8	4.50	28.4	0.81 ± .21	17.9	24.8
28.0	10.92(Excess)	25.2	0.91 ± .21	8.3	9.4

*A summer test at low light intensity. Fish were fed live tubificid worms.

+Ration sizes in parenthesis were the prescribed ration but were not fully consumed.

a rate of 0.385%/day. Therefore, this data point was smoothed out in subsequent plots.

Growth rate was plotted against ration for each temperature (Fig. 2), resulting in curves that described maintenance ration, optimum ration, and maximum ration. These growth parameters can be derived geometrically from the

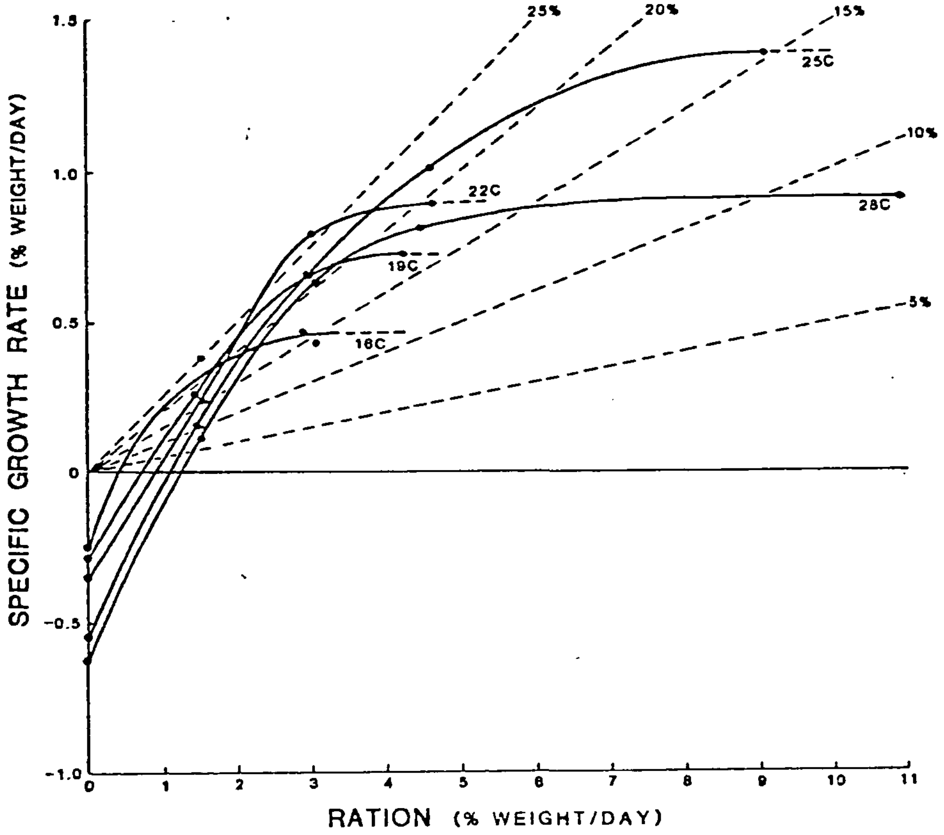

Figure 2. Relation of growth rate and ration at 5 temperatures for juvenile white suckers. Dashed lines indicate gross conversion efficiencies.

growth rate-ration size curve (Thompson 1941; Brett et al. 1969). The maintenance ration, the ration where fish maintains its weight without gain or loss, occurs where the line crosses the zero growth rate axis. The optimum ration, the ration where greatest growth occurs for the least intake, can be derived by drawing a tangent from the origin (0% growth rate and 0% ration) to the curve. The maximum ration, the ration that provides maximum growth, occurs at the asymptote of the curve.

The relation of maintenance, optimum and maximum ration to temperature for white suckers, derived from the procedure described above, are shown in Fig. 3. The rations describing these three growth parameters increased with an increase in temperature, but both maximum ration and optimum ration decreased at temperatures higher than 25°C. At 28°C, both the maximum and optimum ration decreased due to a lower efficiency of food conversion (Table 8).

The optimum temperature for growth decreased as the ration size decreased. Growth rate was plotted against temperature for each specific ration level (Fig. 4). Each curve describes the scope for growth for fish (25-30 g) on a prescribed ration during the summer and early fall. A greater growth potential would be expected in the spring. Maximum growth rate was at 25°C on excess rations and decreased to 19°C at a 1.5% ration level. Weight loss of unfed fish increased exponentially with increased temperatures. Zero growth limits of juvenile white sucker were estimated by graphical extrapolation. Lower and upper limits were 9 and 30°C, respectively, which were similar to those observed in larvae (McCormick et al. 1977). Broken lines were drawn by eye to these graphical limits.

Gross food conversion efficiency (E_g) provides a useful index of the efficiency of white suckers to convert food into fish flesh. With a common unit of dry weight, this index was calculated using the following equation:

$$E_g = \frac{G}{I} \times 100 \qquad (3)$$

where G = growth

I = food intake

Highest conversion efficiency for each temperature occurred in the area of most rapid change in curvature (Fig. 2). The maximum gross efficiency (26%) occurred at 22°C on a restricted ration of 3.0% (Table 8). Gross efficiency was generally less than 15% at all ration levels below 16°C and at lower and higher ration levels above 25°C.

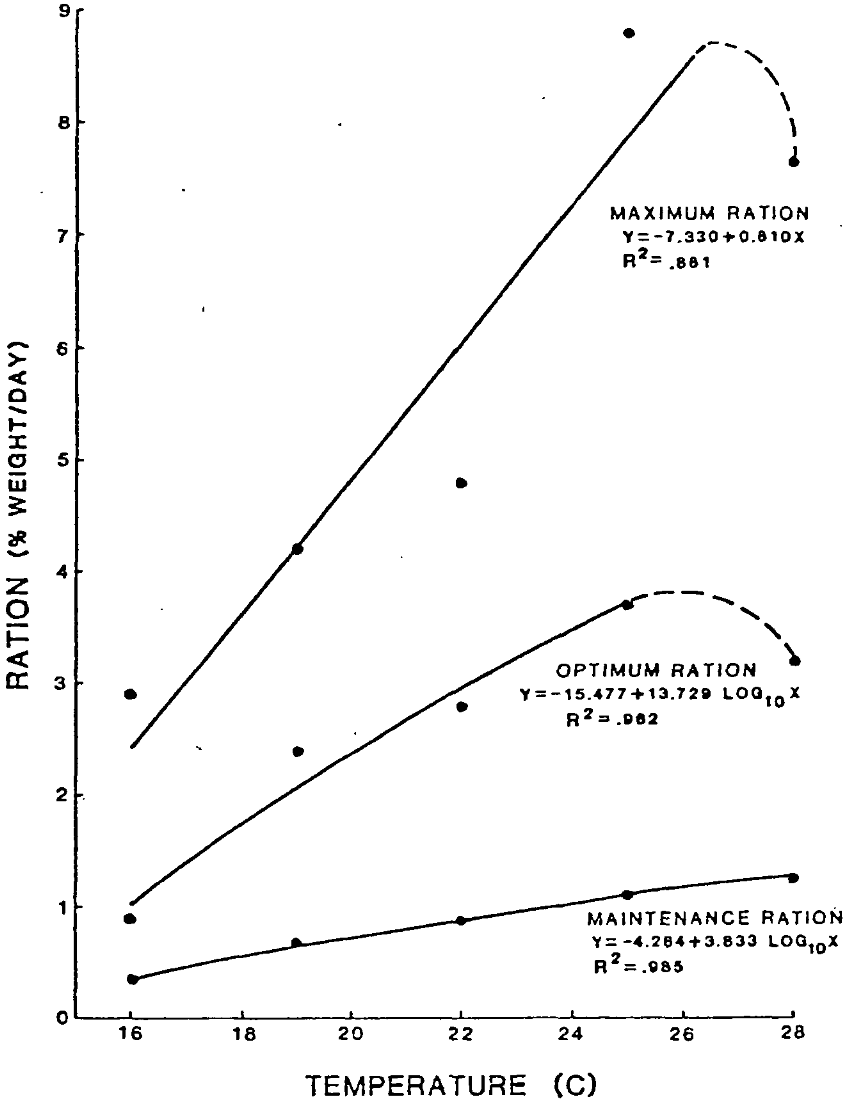

Figure 3. The relation of maintenance, optimum, and maximum rations to temperature for juvenile white suckers. Solid line fitted by regression equation, broken line fitted by eye.

The daily maintenance ration (M), obtained from Fig. 3, can be subtracted from the food intake to determine net conversion efficiency (E_n). This index measures the efficiency of utilization of the fraction of food available for growth and it can be derived with the following equation:

$$E_n = \frac{G}{I-M} \times 100 \qquad (4)$$

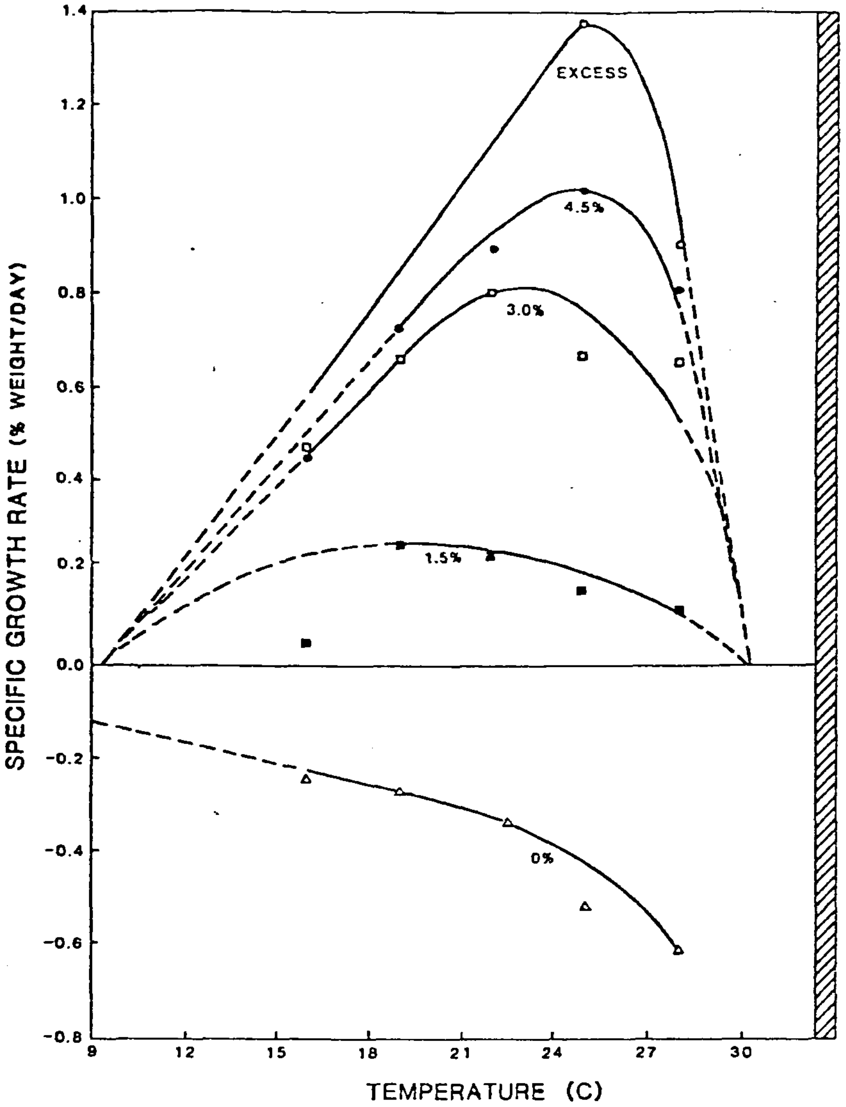

Figure 4. Temperature-growth relationships of white suckers at prescribed ration levels of live tubificids expressed as a percent of the fish dry body weight per day. Shaded area is the zone of thermal resistance in excess of the ultimate upper incipient lethal temperature of 32.5°C.

Highest net efficiency occurred at the combination of higher temperatures and lower rations. The maximum net efficiency (44.4%) occurred at a ration size of 1.46% at 25°C. In this example, the actual ration resulting in a growth rate above the maintenance level was 0.36% where fish grew at a rate of 0.160%/day.

BODY COMPOSITION

Changes in body composition were examined to determine how temperature and food intake influence the percentage of water, fat, and protein (Table 9). Samples of fish fed ration levels of live tubificids at 0, 1.5, and 3.0% were examined at the end of the test. No noticeable changes in protein and moisture contents were found between different temperatures and ration sizes. Fat content increased with an increase of food intake, particularly at temperatures of 19°C and below.

Fish that showed a high growth rate during the spring were also analyzed for body composition. These fish demonstrated a much greater food intake and growth potential during this time of year. These fish were compared to fish fed a ration of 3%/day which was close to the optimum ration level for their respective temperatures (Fig. 3). No change was noted in percentage protein and water, but fat content was significantly increased over summer fish ($P < 0.05$).

TABLE 9. THE EFFECT OF TEMPERATURE, RATION, AND SEASON ON BODY CONSTITUENTS OF JUVENILE WHITE SUCKERS FED LIVE TUBIFICID WORMS*

Ration (% dry weight)	Nominal Temperature (C)	$\bar{x}$ Water+ (%)	$\bar{x}$ Fat++ (%)	$\bar{x}$ Protein++ (%)
		SUMMER FISH+++		
0.0	16	75.2	4.8	11.9
0.0	19	78.2	2.3	13.4
0.0	22	78.0	2.3	13.5
0.0	25	78.2	2.2	13.0
0.0	28	76.8	2.4	12.3
1.5	16	77.8	3.0	14.0
1.5	19	76.1	3.9	14.3
1.5	22	76.5	3.8	14.7
1.5	25	77.7	3.0	14.0
1.5	28	76.2	3.1	14.2
3.0	16	76.3	4.6	14.3
3.0	19	76.5	4.5	14.2
3.0	22	76.4	4.0	15.0
3.0	25	75.5	3.7	14.3
3.0	28	76.4	3.6	13.7
		SPRING FISH#		
Maximum	24	75.0	7.4	12.8
Maximum	26	75.7	6.0	13.4
Maximum	28	75.9	6.6	13.2

*Tubificids contained 84.5% water, 2.3% fat, and 7.4% protein.

+N = 10.

++N = 5.

+++From ration size X temperature test (Table 8).

#From season X daylength test (Table 6); initial size 10 g.

SECTION 5

FACTORS INFLUENCING SURVIVAL

For many years the standardized procedure for determining the upper lethal temperature was to subject fish to a sharp increase in temperature, usually done by a direct transfer technique from an acclimation temperature to a series of upper lethal temperatures. Many field reports have shown fish to survive temperatures higher than the reported UILT determined in laboratory studies (K.E.F. Hokanson, U.S. EPA, Monticello, MN, personal communications; Wrenn and Forsythe, 1978). It was hypothesized that the direct transfer technique under estimates the UUILT because it does not maximize the acclimation temperature and provides additional stress to the fish from handling. Theoretically, slow rates of thermal increase (< 1°C/day) that maximize acclimation temperature and minimize handling stress should give the highest estimate of the UUILT.

Upper lethal temperatures were determined by both the direct transfer technique and the slow temperature rise for white suckers of different sizes (Table 10). The UUILT for smaller juveniles (19.7-34.5 g) was 32.2 to 32.5°C and was 31.3 to 31.7°C for larger juveniles (168-192 g) and adults. White suckers exposed to a slower rise in temperature experienced death (50%) at a temperature that is approximately 2°C higher than suckers tested with the direct transfer technique and by Brett (1944), and 3°C higher than the previously reported UILT by Hart (1947).

TABLE 10. UPPER LETHAL TEMPERATURES OF WHITE SUCKERS OF DIFFERENT SIZES MEASURED BY SLOW ACCLIMATION AND DIRECT TRANSFER METHODS*

$\bar{x}$ wet wt. (g)	Acclimation temperature (C)	Upper lethal temperature (C)	Source
	Ultimate Upper Incipient Lethal Temperature +		
26.7	26.1	32.4	Present study
19.7	28.0	32.2	" "
34.5	26.0	32.5	" "
30.9	28.0	32.3	" "
191.8	26.1	31.3	" "
168.7	28.0	31.7	" "
1000	23.0	31.5	" "
	Upper Incipient Lethal Temperature ++		
12-15	12.0	28.6	" "
12-15	16.1	30.3	" "
12-15	20.2	30.5	" "
12-15	24.1	30.5 (96-h)	" "
2-20	25	29.3 (133-h)	Hart, 1947
juvenile	25-26	31.2 (12-h)	Brett, 1944

*Tests conducted in summer at low light intensity

+Initial acclimation temperature increased 0.5C/day until death. Fish not handled before test as routinely done in direct transfer technique. Fish were not fed above 30°C.

++Direct transfer of fish from an acclimation tank to a series of lethal temperature baths.

SECTION 6

IMPLICATIONS FOR THERMAL CRITERIA

The physiological or growth optimum and UUILT of a species are used directly in derivation of summer limiting temperatures for aquatic life (U.S. EPA, 1976). These thermal criteria endpoints can be modified by several variables which greatly influence bioassay results and thermal responsiveness under field conditions. The light intensity threshold must be carefully controlled to provide optimal culture conditions and enhance the scope for growth for nocturnal organisms. Slower rates of temperature increase that minimize fish handling and maximize acclimation temperature give the highest UUILT. Therefore, laboratory methodology must be critically appraised before thermal criteria values are proposed or used. For some fish species, the growth optima and UUILT may be underestimated and should be revised by first recognizing sources of error as demonstrated herein.

Maximum growth of juvenile white suckers occurred over a wide temperature range of 19 to 26°C, depending upon several variables. Ration level and diet quality had the greatest influence on specific growth rate and optimum temperatures, whereas season and light intensity had a lesser but significant influence on these growth responses. Body size primarily influenced maximum specific growth rate and daylength primarily influenced acclimation time to test conditions. Sucker larvae showed a similar growth response with an optimum temperature range of 23.9 to 26.9°C (McCormick et al. 1979). The best culture conditions produced an optimum near 26°C in this species. Lower growth optima would most likely be observed in nature where ration size is usually restricted.

Maximum growth at optimum temperatures decreased nearly four-fold over a size range of 12 to 175 g. Optimum temperature for growth was not influenced over this fish size range. The slope for the summer maximum growth rate-body weight relationship was -0.452. The determined slope value compares favorably with salmonid growth-body weight relationships. Brett and Shelbourn (1975) found that juvenile sockeye salmon (Oncorhyncus nerka) displayed a similar slope of -0.416, but with higher intercept for a weight range of 2-40 g. Their comparison with other investigations showed that the slope value of -0.4 ± 0.04 appeared to characterize the salmonid family. The slope value declined to -0.168 by inclusion of larval white suckers in the spring growth rate-body weight relationship. This suggests that these weight correction factors are constant only for a limited size range and/or life history period.

Season had a marked effect on maximum growth of the white sucker independent of daylength changes. White sucker of a common size had a two-fold increase in maximum growth rate in spring compared to other seasons. Maximum growth rate in summer occurred at 26°C and at 24°C in winter and spring tests. There was no difference in growth rate between summer and winter fish under a constant 15h L-9h D photoperiod. Swift (1955) found that growth of hatchery brown trout, Salmo trutta, increased in the spring while temperatures were still cold and decreased in autumn when temperatures were still warm. These changes occurred despite the fact that they were fed to satiation. The increase in growth in the spring has been correlated with increasing daylength which stimulates endocrine activity including the production of growth hormones (STH), while decrease in growth in autumn was related to gonadal maturation (Brett 1979). Hogman (1968) also noted that seasonal changes in growth rate of lake whitefish, Coregonus clupeaformis, was more closely related to daylength than to changes in partially controlled water temperature.

Daylength changes itself did not influence maximum growth rate or optimum temperatures in the white sucker. This is consistent with the observation that low light intensity stimulates feeding and growth in this nocturnal species. Reduced daylength, however, increased acclimation time to test conditions which has important implications in the design of "aseasonal" growth studies. Clarke et al. (1978) observed that sensitivity of salmonid fry to photoperiod varied seasonally. Gross et al. (1963) found photoperiod to affect growth of green sunfish, Lepomis cyanellus, but also noted that prior photoperiod history was important. Brett (1979) stated that for freshwater fish, that long daylength, especially increasing daylength applied over a number of months in the right season, is stimulating to growth. The observed effects on growth are not large. Decreasing daylengths have an inhibiting effect on some freshwater fish. Growth of nocturnal species such as walleye, Stizostedion vitreum, is relatively more temperature dependent, while growth of diurnal species such as yellow perch, Perca flavescens, is relatively more photoperiod-dependent (Huh et al. 1976). The lack of greater induced response by photoperiod, compared with natural seasonal effects on normal populations (independent of temperature effects), suggests the evidence for an endogenous annual rhythm which is not subject to displacement by artificial control of daylength.

The loss of condition of winter fish and endogenous hormonal cycles may stimulate increased feeding to restore body food reserves. The growth rate of white sucker increased in spring due to a large increase in food consumption. Starvation alone is a normal endogenous stimulus to feeding activity. Therefore, it is possible for suckers to increase their growth rate without appreciable changes in food conversion efficiency or even with a possible decrease in efficiency. Wurtsbaugh and Davis (1977) indicated that rainbow trout, Salmo gairdneri, were less efficient in food utilization for growth in the spring. The increased growth in spring in suckers, consisted of a large increase in relative fat content compared to other seasons. Fat deposition of accumulation can occur rapidly in fish in response to enhanced feeding activity, and can also be rapidly depleted on demand by other metabolic processes and by overwintering (Shulman 1974). Although no fat analyses were done on fish prior to testing, it was observed that fish at this time of year were in relatively poorer condition at the start of the study than at other times of the year.

The specific growth rate of the white sucker of a given size and season is dependent mainly on the quantity of food consumed and temperature. Increasing temperatures markedly increased the maximum ration, optimum ration, and maintenance ration, but at temperatures above 26°C, both the optimum ration and maximum ration decreased. This decrease was probably due to a lack of appetite and the increase in maintenance requirements, and lower food conversion efficiency. Maximum gross food conversion efficiency for white suckers was 26% at 22°C and 3% ration level which compares favorably with salmonids. Increasing temperatures also reduced gross efficiencies at low ration levels (1.5%), while little effect was noted at higher ration levels. This pattern was also found for rainbow trout (Wurtsbaugh and Davis 1977) and for sockeye salmon (Brett et al. 1969).

Slow increases in temperature that maximize acclimation temperature without handling fish has significantly increased previous estimates of the UUILT. Juvenile and adult suckers tolerated temperatures 32.5° and 31.5°C, respectively. The UILT for juvenile white suckers in this 96-h summer test was 30.5°C. Brett (1944) reported an UILT of 31.2°C in a shorter 12-h summer test. A time period of at least 72-h is required to measure an UILT (Brett 1970). Hart (1947) measured an UILT of 29.3°C for juvenile suckers acclimated to 25°C in a winter test. The UILT of newly hatched and free-swimming larvae were 28.2 and 30.5°C, respectively (McCormick et al. 1977). These previously reported limits were based on tests where fish were subjected to a very quick temperature change. When fish were exposed to a slower temperature increase, an UUILT endpoint that was 2-3°C higher than the UILT was attained for juvenile fish. This method avoids handling stress and maximizes acclimation temperature. This method gives a more realistic upper lethal limit when compared to field situations where fish have been observed at temperatures higher than the upper lethal temperatures previously reported in the literature.

REFERENCES

American Public Health Association, American Water Works Association, Water Pollution Control Federation. 1971. Standard Methods for the Examination of Water and Wastewater. 13th ed. APHA, Washington, D.C. 874 pp.

Brett, J.R. 1944. Some lethal temperature relations of Algonquin Park fishes. Univ. Toronto Stud. Biol. Ser. No. 52, Publ. Ontario Fish. Res. Lab. No. 63, 49 pp.

Brett, J.R. 1970. Temperature. Animals. Fishes. pp. 515-560. In: O. Kinne (ed.). Marine Ecology. Vol. I. Environmental factors. Wiley-Interscience, New York.

Brett, J.R. 1971a. Satiation time, appetite and maximum food intake of sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Canada 28: 409-415.

Brett, J.R. 1971b. Growth responses of young sockeye salmon (Oncorhynchus nerka) to different diets and planes of nutrition. J. Fish. Res. Bd. Canada 28: 1635-1643.

Brett, J.R. 1979. Environmental factors and growth. pp. 599-675. In: W.S. Hoar, D.J. Randall, and J.R. Brett (eds.). Fish physiology. Vol VIII. Bioenergetics and growth. Academic Press, New York.

Brett, J.R. and J.E. Shelbourn. 1975. Growth rate of young sockeye salmon, Oncorhynchus nerka, in relation to fish size and ration level. J. Fish. Res. Bd. Canada 32: 2103-2110.

Brett, J.R., J.E. Shelbourn, and C.T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, Oncorhynchus nerka, in relation to temperature and ration size. J. Fish. Res. Bd. Canada 26: 2363-2394.

Brown, M.E. 1946. The growth of brown trout (Salmo trutta Linn.) II. Growth of two-year-old trout at a constant temperature of 11.5°C. J. Exp. Biol. 22: 145-155.

Campbell, K.P. 1971. Influence of light and dark periods of spatial distribution and activity of the white sucker, Catostomus commersoni. Trans. Am. Fish. Soc. 100: 353-355.

Clarke, W.C., J.E. Shelbourn, and J.R. Brett. 1978. Growth and adaptation to sea water in underyearling sockeye (Oncorhynchus nerka) and coho (O. Kisutch) salmon subjected to regimes of constant or changing temperature and daylength. Can. J. Zool. 56: 2413-2421.

Cocking, A.W. 1959. The effects of high temperatures on roach (Rutilus rutilus). II. The effects of temperature increasing at a known constant rate. J. Exp. Biol. 36: 217-226.

Committee on Methods for Toxicity Tests with Aquatic Organisms. 1975. Methods for acute toxicity tests with fish, macroinvertebrates, and amphibians. Ecol. Res. Ser. No. EPA-660 3-75-009. U.S. EPA, Corvallis, OR. 61 pp.

Eisler, T. 1957. The influence of light on the early growth of chinook salmon. Growth 21: 197-203.

Elliot, J.M. 1975. The growth rate of brown trout (Salmo trutta L.) fed on reduced rations. J. Animal Ecol. 44: 823-842.

Fry, F.E.J. 1947. Effects of the environment on animal activity. Univ. of Toronto Stud. Biol. Ser. No. 55, Publ. Ont. Fish. Res. Lab. No. 68. 62 pp.

Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. Pp. 1-98. In: W.S. Hoar and D.J. Randall (eds.) Fish physiology. Vol. VI. Environmental relations and behavior. Academic Press, New York.

Gross, W.L., P.O. Fromm, and E.W. Roelofs. 1963. Relationship between thyroid and growth in green sunfish, Lepomis cyanellus (Rafinesque). Trans. Am. Fish. Soc. 92: 401-408.

Hart, J.S. 1947. Lethal temperature relations of certain fish of the Toronto region. Trans. Roy. Soc. Canada, Sec. V: Biol. Sci. 41: 57-71.

Hogman, W.J. 1968. Annulus formation on scales of four species of coregonids reared under artificial conditions. J. Fish. Res. Bd. Canada 25: 2111-2112.

Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Bd. Canada 34: 1524-1550.

Huh, H.T., H.E. Calbert, and D.A. Stuiber. 1976. Effects of temperature and light on growth of yellow perch and walleye using formulated feed. Trans. Amer. Fish. Soc. 105: 254-258.

McCormick, J.H., B.R. Jones, and K.E.F. Hokanson. 1977. White sucker (Catostomus commersoni) embryo development, and early growth and survival at different temperatures. J. Fish. Res. Bd. Canada 34: 1019-1025.

Shelbourn, J.E., J.R. Brett, and S. Shirahata. 1973. Effect of temperature and feeding regime on the specific growth rate of sockeye salmon fry (Oncorhynchus nerka), with a consideration of size effect. J. Fish. Res. Bd. Canada 30: 1191-1194.

Shulman, G.E. 1974. Life cycles of fish: physiology and biochemistry. John Wiley and Sons, Inc., New York. 258 pp.

Smith, L.L., Jr. and W.M. Koenst. 1975. Temperature effects of eggs and fry of percoid fishes. Ecol. Res. Ser. No. EPA-660/3-75-017. U.S. EPA, Duluth, MN. 91 pp.

Smith, L.L., Jr., D.M. Oseid, G.L. Kimball, and S.G. El-Kandelgy. 1976. Toxicity of hydrogen sulfide to various life history stages of bluegill (Lepomis macrochirus). Trans. Am. Fish. Soc. 105: 442-449.

Spoor, W.A. and C.L. Schloemer. 1938. Diurnal activity of the common sucker, Catostomus commersoni (Lacepede), and the rock bass, Ambloplites rupestris (Rafinesque), in Muskellunge Lake. Trans. Am. Fish. Soc. 68: 211-220.

Steel, R.G.D. and J.H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, New York. 481 pp.

Stewart, N.H. 1926. Development, growth, and food habits of the white sucker, Catostomus commersoni Le Sueur. Bull. Bur. Fish. 42(1007): 147-184.

Swift, D.R. 1955. Seasonal variations in the growth rate, thyroid gland activity, and food reserves of brown trout (Salmo trutta Linn.). J. Exp. Biol. 32: 751-764.

Thompson, D.H. 1941. The fish production of inland streams and lakes. Pp. 206-217. Symp. Hydrobiol., Univ. Wisc. Press, Madison, WI.

U.S. Environmental Protection Agency. 1976. Quality criteria for water. EPA-440/9-76-023, Washington, D.C. 501 pp.

Wrenn, W.B. and T.D. Forsythe. 1978. Effects of temperature on production and yield of juvenile walleyes in experimental ecosystems. Am. Fish. Soc. Spec. Publ. 11: 66-73.

Wurtsbaugh, W.A. and G.E. Davis. 1977. Effects of temperature and ration level on the growth and food conversion efficiency of Salmo gairdneri, Richardson. J. Fish. Biol. 11: 87-98.

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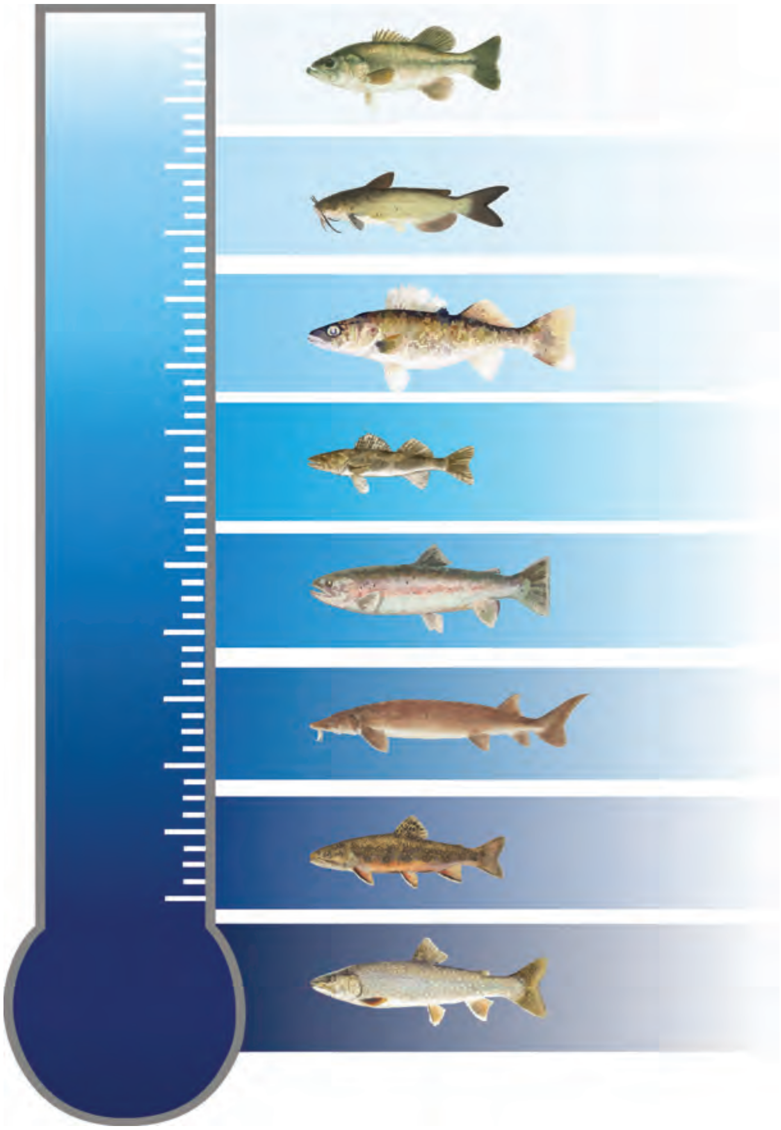
Dr. Kenneth E.F. Hokanson is the EPA Project Officer and can be contacted for information about this report or the EPA thermal program.

17

CLIMATE
CHANGE
RESEARCH
REPORT
CCRR-17

Key Ecological Temperature Metrics for Canadian Freshwater Fishes



Responding to
Climate Change
Through Partnership

Ministry of Natural Resources
Natural. Valued. Protected.

Ontario

Climate Change and MNR: A Program-Level Strategy and Action Plan

The following describes how the Ministry of Natural Resources works to contribute to the Ontario Government's commitment to reduce the rate of global warming and the impacts associated with climate change. The framework contains strategies and sub-strategies organized according to the need to understand climate change, mitigate the impacts of rapid climate change, and help Ontarians adapt to climate change:

Theme 1: Understand Climate Change

Strategy #1: Gather and use knowledge in support of informed decision-making about climate change. Data and information gathering and management programs (e.g., research, inventory, monitoring, and assessment) that advances our knowledge of ecospheric function and related factors and forces such as climate change are critical to informed decision-making. Accordingly, MNR will work to:

- Strategy 1.A: Develop a provincial capability to describe, predict, and assess the important short- (0-5 years), medium- (5-20 years), and long-term (20+ years) impacts of climate change on the province's ecosystems and natural resources.
- Strategy 1.B: Model the carbon cycle.

Strategy #2: Use meaningful spatial and temporal frameworks to manage for climate change. A meaningful spatial and temporal context in which to manage human activity in the ecosphere and address climate change issues requires that MNR continue to define and describe Ontario's ecosystems in-space and time. In addition, MNR will use the administrative and thematic spatial units required to manage climate change issues.

Theme 2: Mitigate the Impacts of Climate Change

Strategy #3: Gather information about natural and cultural heritage values and ensure that this knowledge is used as part of the decision-making process established to manage for climate change impacts. MNR will continue to subscribe to a rational philosophy and corresponding suite of societal values that equip natural resource managers to take effective action in combating global warming and to help Ontarians adapt to the impacts of climate change.

Strategy #4: Use partnership to marshal a coordinated response to climate change. A comprehensive climate change program involves all sectors of society as partners and participants in decision-making processes. The Ministry of Natural Resources will work to ensure that its clients and partners are engaged.

Strategy #5: Ensure corporate culture and function work in support of efforts to combat rapid climate change. Institutional culture and function provide a "place" for natural resource managers to develop and/or sponsor proactive and integrated programs. The Ministry of Natural Resources will continue to provide a "home place" for the people engaged in the management of climate change issues.

Strategy #6: Establish on-site management programs designed to plan ecologically, manage carbon sinks, reduce greenhouse gas emissions, and develop tools and techniques that help mitigate the impacts of rapid climate change. On-site land use planning and management techniques must be designed to protect the ecological and social pieces, patterns, and processes. Accordingly, MNR will work to:

- Strategy 6.A: Plan ecologically.
- Strategy 6.B: Manage carbon sinks.
- Strategy 6.C: Reduce emissions.
- Strategy 6.D: Develop tools and techniques to mitigate the impacts of rapid climate change.

Theme 3: Help Ontarians Adapt

Strategy #7: Think and plan strategically to prepare for natural disasters and develop and implement adaptation strategies. MNR will sponsor strategic thinking and planning to identify, establish, and modify short- and long-term direction on a regular basis. Accordingly, MNR will work to:

- Strategy 7.A: Sponsor strategic management of climate change issues.
- Strategy 7.B: Maintain and enhance an emergency response capability.
- Strategy 7.C: Develop and implement adaptation strategies for water management and wetlands.
- Strategy 7.D: Develop and implement adaptation strategies for human health.
- Strategy 7.E: Develop and implement adaptation strategies for ecosystem health, including biodiversity.
- Strategy 7.F: Develop and implement adaptation strategies for parks and protected areas for natural resource-related recreational opportunities and activities that are pursued outside of parks and protected areas.
- Strategy 7.G: Develop and implement adaptation strategies for forested ecosystems.

Strategy #8: Ensure policy and legislation respond to climate change challenges. Policy, legislation, and regulation guide development and use of the programs needed to combat climate change. MNR will work to ensure that its policies are proactive, balanced and realistic, and responsive to changing societal values and environmental conditions.

Strategy #9: Communicate. Ontarians must understand global warming, climate change, and the known and potential impacts in order to effectively and consistently participate in management programs and decision-making processes. Knowledge dissemination through life-long learning opportunities that are accessible and current is critical to this requirement. MNR will raise public understanding and awareness of climate change through education, extension, and training programs.

Key Ecological Temperature Metrics for Canadian Freshwater Fishes

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Abstract

Habitat temperature is a major determinant of performance and activity in fish. We examined the relationship between six temperature metrics describing the growth (optimal growth temperature and final temperature preferendum), survival (upper incipient lethal temperature and critical thermal maximum), and reproduction (optimum spawning temperature and optimum egg development temperature) requirements of 87 Canadian freshwater fish species. Our results suggest that all metrics were highly correlated, especially those within each life process. Values for different metrics fell into distinct groups that were associated with thermal preference classes, reproductive guilds, and spawning season. These results suggest that it may be possible to estimate missing metric values using known values. This compilation of metrics provides easy access to information for a broad range of fish species common to North America and should foster more extensive use of this information in fish ecology.

Résumé

Principales mesures de température écologiques pour les poisons d'eaux douce canadiens

La température de l'habitat du poisson est un facteur déterminant de sa performance et de son activité. Nous avons examiné la relation entre six mesures de température correspondant aux exigences de croissance (température de croissance optimale et préférendum de température finale), de survie (température létale initiale et température maximale critique), de reproduction (température de fraie maximale et température optimale pour le développement des œufs) de 87 espèces canadiennes de poissons d'eau douce. Les résultats démontrent que toutes les mesures étaient étroitement corrélées, surtout celles d'un même processus vital. Les valeurs de différentes mesures se regroupaient dans des catégories distinctes associées aux préférences thermales, aux guildes reproductives et aux saisons de fraie. Les résultats laissent croire qu'il pourrait être possible d'estimer les valeurs manquantes à partir des valeurs connues. Cette compilation de mesures permet d'accéder facilement aux données d'une large gamme d'espèces de poissons communes en Amérique du Nord et devrait favoriser l'utilisation de ces données en ce qui a trait à l'écologie du poisson.

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Contents

Introduction

Temperature is one of the most important abiotic factors influencing fish survival and performance (Brett 1971, Christie and Regier 1988). According to the thermal primacy paradigm developed by Brett (1956), the fundamental requirement for fishes is "an external temperature most suitable to internal temperature". Fry (1947) noted that the survival and growth of fish depend on relationships between external environmental factors and internal metabolic processes. As fish are obligate poikilothermic ectotherms, their body temperatures are equal to or within a few fractions of a degree of the surrounding water temperature (Wood and McDonald 1997, Beitinger et al. 2000). Therefore, they are highly dependent on water temperature to maintain important biochemical, physiological, and life history processes (Wood and McDonald 1997, Beitinger et al. 2000). Previous studies have shown that the reaction rates for many critical processes "rise slowly as the preferred temperature is approached from below, and drop rapidly after it is exceeded until reaching zero at the lethal temperature"(Kling et al. 2003). This indicates that physiological performance is maximized within a narrow temperature range and that, depending on the species, optimal temperatures for many processes centre around a specific value (Brett 1971, Hokanson 1977, Beitinger and Fitzpatrick 1979, Jobling 1994).

Environmental thermal conditions are also important determinants of reproductive success. Processes such as spawning and egg development require specific thermal conditions and are sensitive to water temperature perturbations (Van der Kraak and Pankhurst 1997). Increases in temperature of only 2 Cº above normal can result in eggs with abnormal cleavage patterns leading to decreased hatching success (Van der Kraak and Pankhurst 1997). High temperatures have been shown to also arrest development, causing damage to both previtellogenic and mature oocytes (Chimlevsky 1999). In addition, changes in temperature can shift the balance between oxygen availability in the environment and oxygen demand by internal metabolic processes, in ways that lead directly to mortality among eggs and/or embryos (Alderdice et al. 1958, Rombough 1997, Evans 2007).

Given the importance of water temperature for fish physiological and reproductive activities, it is important to assess the relationships among the various metrics that characterize fish thermal requirements. The objectives of this study were twofold: (1) to compile a comprehensive database summarizing the available data on temperature metrics for growth, reproduction, and survival of Canadian freshwater fish species, and (2) to identify correlations and groupings among those metrics.

In this study, we compared two metrics for each of the three processes: growth, survival, and reproduction. For growth, we compiled optimum growth and final temperature preferenda. For survival, we compiled upper incipient lethal temperatures and critical thermal maxima, and for reproduction, we compiled optimal spawning and egg development temperatures.

We predicted that due to similarities in temperature requirements for processes within each stage, measures within a stage would be more positively correlated with one another than with other measures. We also expected values for each metric to co-vary with life history characteristics such as temperature preference class, reproductive guild, and spawning season.

Methods

Data collection

Metric values were compiled for 87 Canadian freshwater fish species. Only freshwater fish species occurring in Canada were considered. Species were evaluated only when data were available for one or more thermal metrics and information was not collected for extinct or extirpated species, or for hybrid forms. A complete list of the species for which data were compiled (with scientific names) is provided in the Appendix (Tables A1-3) along with the sources for the metric values.

For each species, the following thermal metrics and life history characteristics were compiled: optimum growth temperature, final temperature preferendum, upper incipient lethal limit, critical thermal maximum, spawning temperature, egg development temperature, temperature preference class, spawning season, and reproductive guild. A list of temperature metrics and life history characteristics for each species is provided in the Appendix. All metric estimates were derived using adult members of each species.

Species-specific temperature metrics were first compiled from secondary literature sources. The main texts used were:

- *Freshwater Fishes of Canada* (Scott and Crossman 1987)
- *Morphological and Ecological Characteristics of Canadian Freshwater Fishes* (Coker et al. 2001)
- *Temperature Relationships of Great Lakes Fishes: A Data Compilation* (Wismer and Christie 1987)
- *Temperature Requirements of Fishes from Eastern Lake Erie and the Upper Niagara River: A Review of Literature* (Spotila et al. 1979)
- *Temperature Tolerances and the Final Temperature Preferenda for the Assessment of Optimum Growth Temperature* (Jobling 1981)
- *Acute and Final Temperature Preferenda as Predictors of Lake St. Clair Fish Catchability* (Danzman et al. 1991)
- *Temperature Tolerances of North American Freshwater Fishes Exposed to Dynamic Changes in Temperature* (Beitinger et al. 2000)

Information from these sources was supplemented by species-specific primary and secondary literature cited in these references and primary literature sources published between 1980 and 2009, gathered through a literature search based on the ISI Web of Knowledge (http://isiwebofknowledge.com/). Only peer-reviewed sources and government publications were considered.

Thermal metrics

(i) Growth

Optimum growth temperature (OGT): The optimum growth temperature is that which supports the highest growth rate in an experiment where separate groups of fish are exposed to one of a set of constant temperatures under *ad libitum* feeding conditions. The range of these constant temperatures is chosen so that reduced growth is observed at both extremes (McCauley and Casselman 1980 cited in Wismer and Christie 1987, Jobling 1981).

Final temperature preferendum (FTP): Final temperature preferendum is that towards which fish gravitate when exposed to an 'infinite' temperature range (Giattina and Garton 1982 cited in Wismer and Christie 1987). Two methods are used to determine FTP: the gravitation method and the acclimation method (Jobling 1981). The gravitation method involves exposing fish to a temperature gradient until they gravitate towards a specific temperature. The acclimation method extends the gravitation method by carrying out repeated 'gravitation trials' with fish acclimated to progressively higher temperatures. The preferred temperature exhibited in each trial is then plotted against the acclimation temperature and the FTP is the temperature at which the best fit line for these data crosses the line of equality (Jobling 1981). An informal survey of a subset of the original sources indicated that most estimates were determined via the gravitation method. FTP estimates obtained using both methods were compiled in the database.

Thermal preference class: For each species, thermal preference class was determined based on Coker et al.'s (2001) classification, which uses preferred summer water temperature to classify species as follows: *warm* – >25°C, *cool* – 19 to 25°C, and *cold* – <19°C. A species could occupy one of two intermediate classes, i.e., *cool/cold* or *warm/cool* if their preferred termperature overlaps classes.

(ii) Survival

Upper incipient lethal temperature (UILT): The upper incipient lethal temperature is that at which 50% of the fish in an experimental trial survive for an extended period (Spotila et al. 1979, Jobling 1981, Wismer and Christie 1987). Testing for UILT involves placing groups of fish in separate baths, each held at a different constant temperature, using a sufficiently wide range of constant temperatures that rapid mortality is observed in some baths whereas slow incomplete mortality occurs in others (Spotila et al. 1979).

Critical thermal maximum (CTMax): The critical thermal maximum is an indicator of 'thermal resistance' and is defined as the temperature at which a fish loses its ability to maintain a 'normal' upright posture in the water (loss of equilibrium; Jobling 1981). It is determined by exposing fish in a tank to steadily increasing water temperatures (typically at a rate of 1 C° min^{-1}) and noting the temperature at which the fish exhibit spasms and loss of equilibrium (Jobling 1981, Wismer and Christie 1987). Remaining at, or above, CTMax results in mortality (Jobling 1981, Wismer and Christie 1987).

(iii) Reproduction

Optimal spawning temperature (OS): The optimum spawning temperature is that at which spawning reaches its peak (Wismer and Christie 1987).

Optimum egg development temperature (OE): The optimum egg development temperature is that at which the rate of successful egg development is highest (Wismer and Christie 1987).

Spawning season: Each species was designated as either a spring or fall spawner using the spawning data cited in Scott and Crossman (1973). Spring spawners were those species that spawn between early April and late June, while fall spawners were species that spawn from early September to late October.

Reproductive guild: The reproductive guild groups fish species by their spawning behaviour. All 87 species were assigned to a reproductive guild based on Coker et al.'s (2001) application of Balon's (1975, 1981) classification system:

A.1 = broadcast spawners pelagophils
A.2 = broadcast spawners lithophils
B.1 = brood hiders lithophils
B.2 = brood hiders aeropsammophils

Quality control

We did not attempt to assess the validity of the methods used to estimate each value for each metric. However, for FTP and UILT, intra-specific replication of estimates was sometimes high enough to identify clearly aberrant values. In these cases, we examined the original references to assess the reliability of the methods used to generate the estimates and we flagged those values (see Table A1 in the Appendix; 7 FTP values are flagged) where the methods did not match the requirements specified for the metric. These values were not included in the species-specific mean values used in the analyses described below. Although a similar assessment would have been ideal for the other metrics as well, typically the degree of intra-specific replication was insufficient to reliably identify apparently aberrant values.

Statistical analyses

For each fish species, means and standard deviations were calculated from the individual estimates for each metric. If a range (instead of a single value) was specified for a metric estimate then the mid-point of that range was used in mean and standard deviation calculations. If only one estimate was available for a metric, this value was taken as the mean (Table 1). Once species-specific mean values for each metric were compiled, covariation between these metric means was assessed using the Pearson correlation coefficient and the Spearman rank correlation coefficient. For each metric, box and whisker plots were used to compare observed variation across temperature preference classes, reproductive guilds, and spawning season groups.

For families represented by at least 5 species, family mean, family minimum and family maximum values were determined from the appropriate species mean values. All statistical analyses were performed using R statistical software (R Development Core Team 2008).

Results

Of the 87 species listed in the database, growth, survival, and reproduction metric data were complete for 32 (Table 1). For growth metrics, complete FTP and OGT data were available for 52 species. Thermal preference class data were available for all species but survival metrics were complete for only 45 species. Complete data for reproduction metrics, OS and OE, were available for only 48 species but reproductive guild data were complete for all species.

Table 1. *Mean optimum growth temperature (OGT), final temperature preferendum (FTP), upper incipient lethal temperature (UILT), critical thermal maxima (CTMax),optimal spawning temperature (OS), and optimum egg development temperature (OE) data for 87 Ontario freshwater fish species. A dash (-) indicates that no data were found. Species are arranged alphabetically within families. References are listed in Table A1 in the Appendix.*

Family	Common Name	**Scientific Name**	Temperature °C					
			OGT	FTP	UILT	CTMax	OS	OE
Ascipenseridae	Lake Sturgeon	*Ascipenser fulvescens*	-	11.0	-	-	15	14.5
Amiidae	Bowfin	*Amia calva*	-	30.3	-	37.0	-	-
Anguillidae	American Eel	Anguilla rostrata	25.0	19.9	-	-	-	-
Catostomidae	Bigmouth Buffalo	*Ictiobus cyprinellus*	-	19.8	-	-	16.95	20.5
	Longnose Sucker	*Catostomus catostomus*	-	11.1	26.8	-	10	12.5
	Northern Hog Sucker	*Hypentelium nigricans*	25.6	27.0	29.8	30.8	17.5	17.4
	Quillback	*Carpoides cyprinus*	-	20.5	-	37.2	-	-
	Spotted Sucker	*Minytrema melanops*	-	21.8	-	31.0	-	-
	White Sucker	*Catostomus commersoni*	25.5	23.4	27.8	31.6	15.83	15
Centrarchidae	Black Crappie	*Pomoxis nigromaculatus*	18.0	23.4	33.3	34.9	19.2	18.15
	Bluegill	*Lepomis macrochirus*	29.2	30.2	32.2	40.2	25	23
	Green Sunfish	*Lepomis cyanellus*	28.0	25.4	40.0	36.0	21.9	29.1
	Largemouth Bass	*Micropterus salmoides*	26.6	28.6	31.9	38.4	19.15	20
	Pumpkinseed	*Lepomis gibbosus*	25.0	27.7	31.7	37.6	26	28
	Rock Bass	*Ambloplites rupestris*	28.4	24.9	33.9	36.0	-	-
	Smallmouth Bass	*Micropterus dolomieui*	26.0	25.0	36.0	36.3	18	21
	White Crappie	*Pomoxis annularis*	22.5	19.1	-	32.8	17	19.15
Clupeidae	Alewife	*Alosa pseudoharengus*	20.1	16.9	23.1	31.3	13.75	17.8
	Gizzard Shad	*Dorosoma cependianum*	17.0	20.7	35.5	31.7	22	22.2
Cottidae	Deepwater Sculpin	*Myoxocephalus thompsoni*	-	5.0	-	-	-	-
	Fourhorn Sculpin	*Myoxocephalus quadricornis*	-	5.0	-	-	-	-
	Mottled Sculpin	*Cottus biardii*	-	16.2	24.3	30.9	11.4	12.55
	Slimy Sculpin	Cottus cognatus	-	11.0	22.8	26.1	-	-
	Spoonhead Sculpin	*Cottus ricei*	-	6.0	-	-	-	-
Cyprinidae	Blackchin Shiner	*Notropis heterodon*	-	-	38.0	32.8	-	-
	Blacknose Dace	*Rhinichthys atratulus*	-	19.6	28.6	30.2	-	-
	Bluntnose Minnow	*Pimephales notatus*	26.2	24.1	31.5	29.9	-	-
	Carp	*Cyprinus carpio*	27.3	27.7	34.5	39.0	24	21
	Central Stoneroller	*Campostoma anomalum*	24.8	23.9	31.0	34.3	-	-
	Common Shiner	*Notropis cornutus*	22.0	21.9	30.4	31.2	-	-
	Creek Chub	*Semotilus atromaculatus*	-	24.9	29.1	33.0	-	-
	Emerald Shiner	*Notropis atherinoides*	25.7	19.3	27.4	28.6	24	23.9
	Fallfish	*Semotilus coropralis*	-	22.0	-	-	-	-

Family	Common Name	**Scientific Name**	Temperature °C					
			OGT	FTP	UILT	CTMax	OS	OE
	Fathead Minnow	*Pimephales promelas*	25.8	26.6	31.3	34.1	19.48	25
	Finescale Dace	*Chrosomus neogaeus*	-	24.1	30.3	32.2	18.5	20
	Golden Shiner	*Notemigonus crysoleucas*	25.0	21.8	32.0	33.4	20.25	20
	Goldfish	*Carassius auratus*	26.6	27.4	34.9	35.8	21.08	16.95
	Longnose Dace	*Rhinichthys cataractae*	-	15.3	-	31.4	11.7	15.6
	Northern Redbelly Dace	*Chrosomus eos*	-	25.3	29.2	29.0	-	-
	Pugnose Shiner	*Notropis anogenus*	-	16.5	-	-	-	-
	Rosyface Shiner	*Notropis rubellus*	25.5	25.3	33.0	33.6	24.3	21.1
	Spotfin Shiner	*Cyprinella spiloptera*	28.9	27.5	36.0	-	-	-
	Spottail Shiner	Notropis hudsonius	27.3	16.6	33.0	33.2	19	20
Cyprinodontidae	Banded Killifish	*Fundulus diaphanus*	-	23.0	31.7	-	23	24.35
	Mummichog	*Fundulus heteroclitus*	24.3	25.0	27.6	39.8	-	-
Esocidae	Grass Pickerel	*Esox americanus vermiculatus*	-	25.7		-	9.45	8.35
	Muskellunge	*Esox masquinongy*	25.1	25.4	32.2	32.0	12.8	13.5
	Northern Pike	*Esox lucius*	23.0	20.7	31.0	-	11.5	12.05
Gadidae	Burbot	*Lota lota*	16.6	13.2	23.3	-	1.15	7.5
Gasterosteidae	Brook Stickleback	*Culaea inconstans*	-	21.3	30.6	-	13.13	18.3
	Ninespine Stickleback	*Pungitius pungitius*	-	16.5	-	-	-	-
	Threespine Stickleback	*Gasterosteus aculeatus*	17.1	12.5	27.2	28.7	12.5	19
Hiodontidae	Mooneye	*Hiodon tergisus*	-	28.0	-	-	-	-
Ictaluridae	Black Bullhead	*Ictalurus melas*	-	-	35.4	37.5	-	-
	Brown Bullhead	*Ameiurus nebulosus*	30.0	26.2	33.4	37.9	21.1	22.8
	Channel Catfish	*Ictalurus punctatus*	29.5	27.3	32.9	36.7	-	-
	Stonecat	*Noturus flavus*	-	15.3	-	29.0	-	-
	Yellow Bullhead	*Ictalurus natalis*	-	28.2	-	36.4	-	-
Lepisosteidae	Longnose Gar	*Lepisosteus osseus*	26.4	27.4	-	-	-	-
	Spotted Gar	*Lepisosteus oculatus*	-	16.0	-	-	-	-
Moronidae	White Bass	*Morone chrysops*	-	27.3	33.5	35.3	15.5	17.45
	White Perch	*Morone americana*	28.5	29.8	36.0	-	17.5	19.95
Percichthyidae	Striped Bass	Morone saxatilis	-	-	28.8	25.9	-	-
Percidae	Eastern Sand Darter	*Ammocrypta pellucida*	-	24.6	-	-	-	-
	Rainbow Darter	*Ethestoma carolineum*	-	19.9	-	32.1	-	-
	Sauger	*Stizostedion canadense*	22.0	19.6	-	-	10.33	13.5
	Walleye	*Stizostedion vitreum*	22.1	22.5	29.7	23.4	7.73	12.2
	Yellow Perch	*Perca flavescens*	25.4	17.6	25.6	35.0	9.13	15
Percopsidae	Trout-Perch	*Percopsis omniscomaycus*	-	13.4	-	22.9	-	-
Petromyzontidae	Sea Lamprey	*Petromyzon marinus*	17.5	10.3	31.4	-	15.35	18.5
Salmonidae	Atlantic Salmon	*Salmo salar*	13.6	15.3	27.6	32.8	-	-
	Bloater	*Coregonus hoyi*	18.6	8.5	26.5	-	-	-
	Brook Trout	*Salvelinus fontinalis*	14.2	14.8	24.9	29.3	10.7	6.1
	Brown Trout	*Salmo trutta*	12.6	15.7	25.0	28.3	7.8	7.5
	Chinook Salmon	*Oncorhynchus tshawytscha*	14.3	13.8	23.5	25.1	-	-
	Chum Salmon	*Oncorhynchus keta*	13.0	14.1	-	-	-	-
	Coho Salmon	*Oncorhynchus kisutch*	13.6	14.4	21.8	27.6	6.05	7.15
	Cutthroat Trout	*Oncorhynchus clarkii*	16.5	14.9	21.9	28.0	-	-
	Lake Herring, Cisco	*Coregonus artedii*	18.1	12.4	23.9	-	3.3	5.6
	Lake Trout	*Salvelinus namaycush*	10.0	11.8	24.3	-	-	-
	Lake Whitefish	*Coregonus clupeaformis*	14.7	12.7	23.9	-	3.05	4.95
	Pink Salmon	*Oncorhynchus gorbuscha*	15.5	13.0	-	-	10	7.25
	Rainbow Trout	Oncorhynchus mykiss	15.7	15.5	25.0	22.1	7	8.9
	Round Whitefish	*Proposium cylindraceum*	-	8.3	-	-	3.75	3
	Sockeye Salmon	*Oncorhynchus nerka*	15.0	13.7	21.5	-	8.63	8.25
Sciaenidae	Freshwater Drum	*Aplodinotus grunniens*	22.0	24.6	32.8	34.0	21	23.9
Umbridae	Central Mudminnow	*Umbra limi*	-	-	33.5	-	-	-

Of all the metrics, FTP was the most complete, with information available for 83 of 87 species (Table 2). These data also had the most within-species replication, with a median of 10.5 estimates per species. Forty-seven species had four or more values for FTP, the most among all metrics. The reproduction metrics (OS and OE) had the least amount of data available and the least amount of intra-specific replication, with neither metric having more than three estimates per species. Spawning season data were available for all but one species, American eel (*Anguilla rostrata*), which spawns in the Sargasso Sea (Scott and Crossman 1973). This species was disregarded in any further analyses involving spawning season.

Where sufficient replication was available to evaluate it, intra-specific variation among the estimates for a single metric was relatively similar for the four metrics: standard deviations ranged from 2.3 C° for OGT and CTmax to 3.7 C° for FTP (Table 2). Replication within families was moderately high: six families had five or more species with values for at least one metric (Table 3).

Pair-wise correlation analysis revealed high covariation among metrics (correlation values>0.6; Figure 1). The highest correlation was found between the reproductive metrics, OS and OE, and the growth metrics, FTP and OGT, with Pearson correlation values of 0.8398 and 0.9098, respectively. Metrics FTP and OE exhibited the lowest Pearson correlation (0.6225).

Temperature metrics were also clearly grouped by temperature preference class, reproductive guild, and spawning season with very little overlap. For temperature preference class, OGT, FTP, and ULIT data were well clustered within each class and increased progressively from *cold* to *warm* (Figure 2). All metrics were also distinctly grouped by reproductive guild, with a prominent clustering of low temperature values for guild A.2. Grouping by spawning season was also observed, with metric values clustered at lower temperature values for fall spawners and higher ones for spring spawners (Figure 3). Fall spawners exhibited a narrower range of values for their temperature metrics than spring spawners.

Table 2. *Summary statistics for growth, survival, and reproduction metric data for 87 Ontario freshwater fish species. A dash (-) indicates that no data were found.*

Summary Statistics	Growth		Survival		Reproduction	
	OGT[1]	FTP[2]	UILT[3]	CTMax[4]	OS[5]	OE[6]
Total number of species present	52	83	60	55	48	48
Median number of values present per species	3.5	10.5	9.5	4.5	2.5	2
Total number of species with n≥4 values	7	47	27	11	-	-
Median standard deviation with n≥4 values	2.3	3.7	2.8	2.3	-	-

[1] OGT: Optimum growth temperature [2] FTP: Final temperature preferendum [3] UILT: Upper incipient lethal temperature [4] CTMax: Critical thermal maximum
[5] OS: Optimum spawning temperature [6] OE: Optimum egg development temperature

Table 3. *Mean, minimum, and maximum temperature (°C) values for the growth, survival,and reproduction metrics for taxonomic families (n>5, data available across all metrics).*

Family Name	Temperature (°C)	Growth		Survival		Reproduction	
		OGT[1]	FTP[2]	ULIT[3]	CTMax[4]	OS[5]	OE[6]
Catostomidae	mean	25.3	20.6	28.1	32.7	15.1	16.4
	minimum	25.0	11.1	26.8	30.8	10.0	12.5
	maximum	25.6	23.4	30.9	37.2	17.5	20.5
Centrarchidae	mean	25.5	25.5	34.1	36.5	20.9	22.6
	minimum	19.2	19.1	31.9	32.8	17.0	18.2
	maximum	30.1	30.6	40.0	40.2	26.0	28.0
Cyprinidae	mean	25.9	22.8	31.9	32.6	20.3	20.4
	minimum	22.0	15.3	27.8	28.6	11.7	15.6
	maximum	28.9	27.9	38.0	39.0	24.3	25.0
Ictaluridae	mean	29.8	24.3	33.9	35.5	21.1	22.8
	minimum	29.4	18.6	33.2	29.0	21.1	22.8
	maximum	30.0	28.3	35.4	37.9	21.1	22.8
Percidae	mean	22.1	21.7	29.3	27.1	9.0	12.9
	minimum	22.3	17.8	25.6	23.4	7.7	12.2
	maximum	25.4	24.6	30.5	35.0	10.3	15.0
Salmonidae	mean	14.8	13.0	29.0	27.6	7.4	7.7
	minimum	10.0	8.3	21.9	22.1	3.1	3.0
	maximum	18.6	15.7	31.4	32.8	15.4	18.5

[1] OGT: Optimum growth temperature [2] FTP: Final temperature preferendum [3] UILT: Upper incipient lethal temperature [4] CTMax: Critical thermal maximum

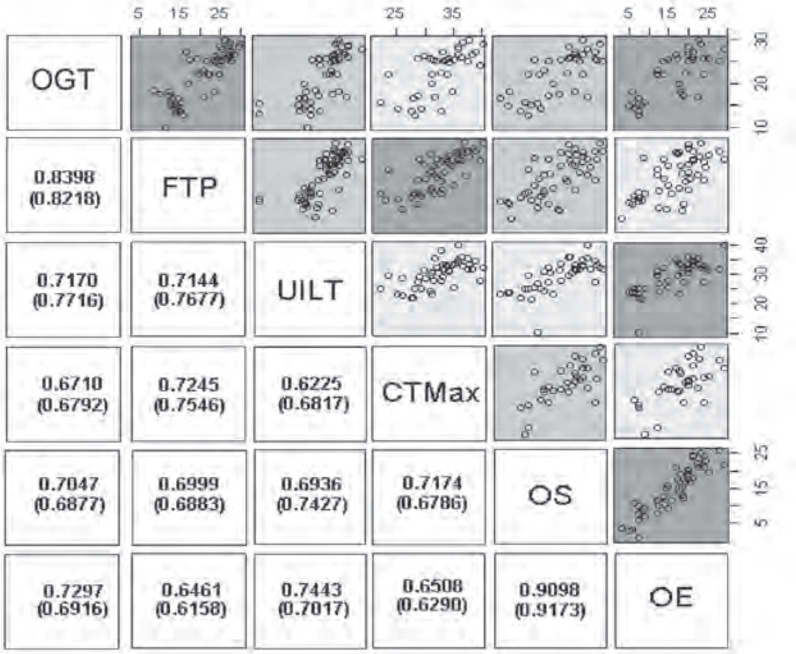

Figure 1. *A scatterplot matrix showing the relationships among growth (optimum growth temperature [OGT] and final temperature preferendum [FTP]), survival (upper incipient lethal temperature [UILT] and critical thermal maximum [CTMax]) and reproduction metrics (optimum spawning temperature [OS] and optimum egg development temperature [OE]). Correlation increases with colour intensity (dark gray>0.72, medium gray 0.72-0.69, light gray<0.69). For each relationship, Pearson and Spearman (in parentheses) correlation coefficients are also provided. All correlations were statistically significant (p<0.01).*

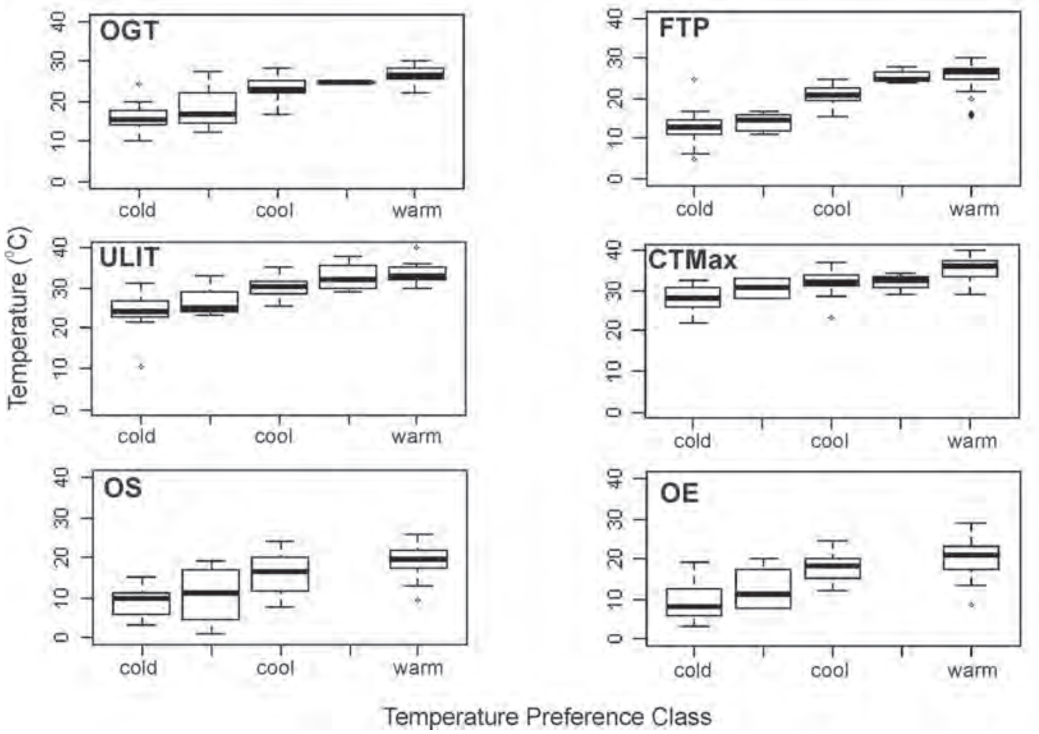

Figure 2. *Growth (OGT and FTP), survival (UILT and CTMax), and reproduction (OS and OE) metric distributions across five temperature preference classes: cold (<19°C, n=24), cold/cool (n=4), cool (19-25°C, n=24), cool/warm (n=6) and warm (>25°C, n=28).*

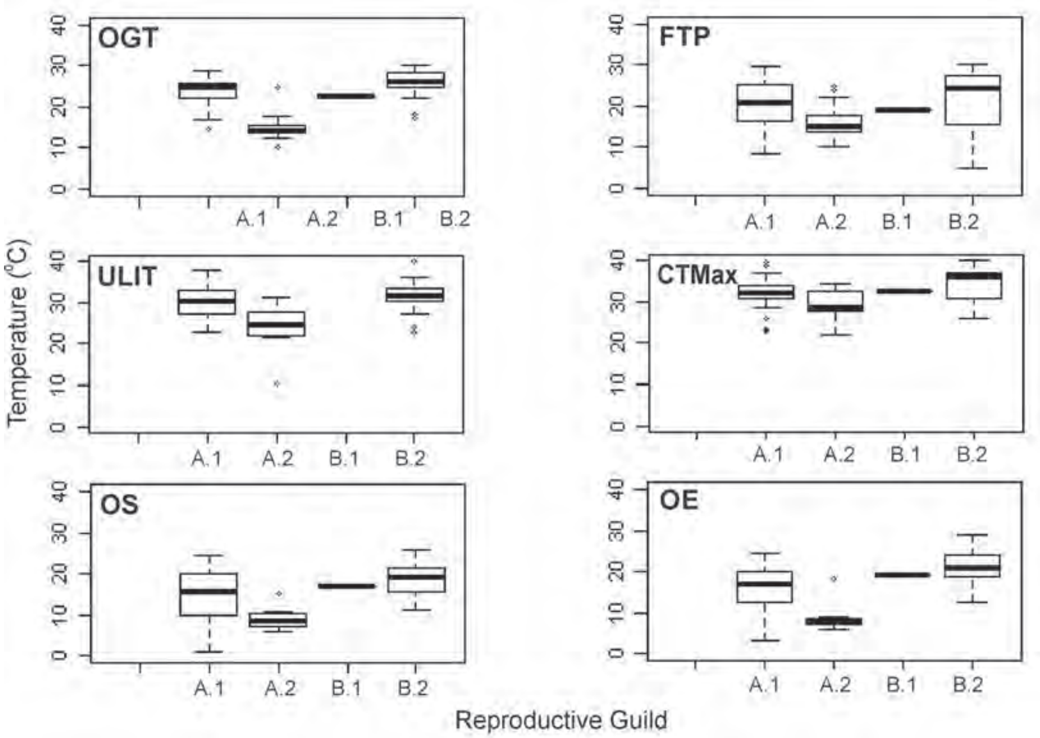

Figure 3. *Growth (OGT and FTP), survival (UIT and CTMax), and reproduction (OS and OE) metric distributions across four reproductive guild categories; A.1 (broadcast spawners pelagophils, n=47), A.2 (broadcast spawners lithiophils, n=16), B.1 (brood hiders lithiophils, n=1) and B.2 (brood hiders aeropsammophils, n=23).*

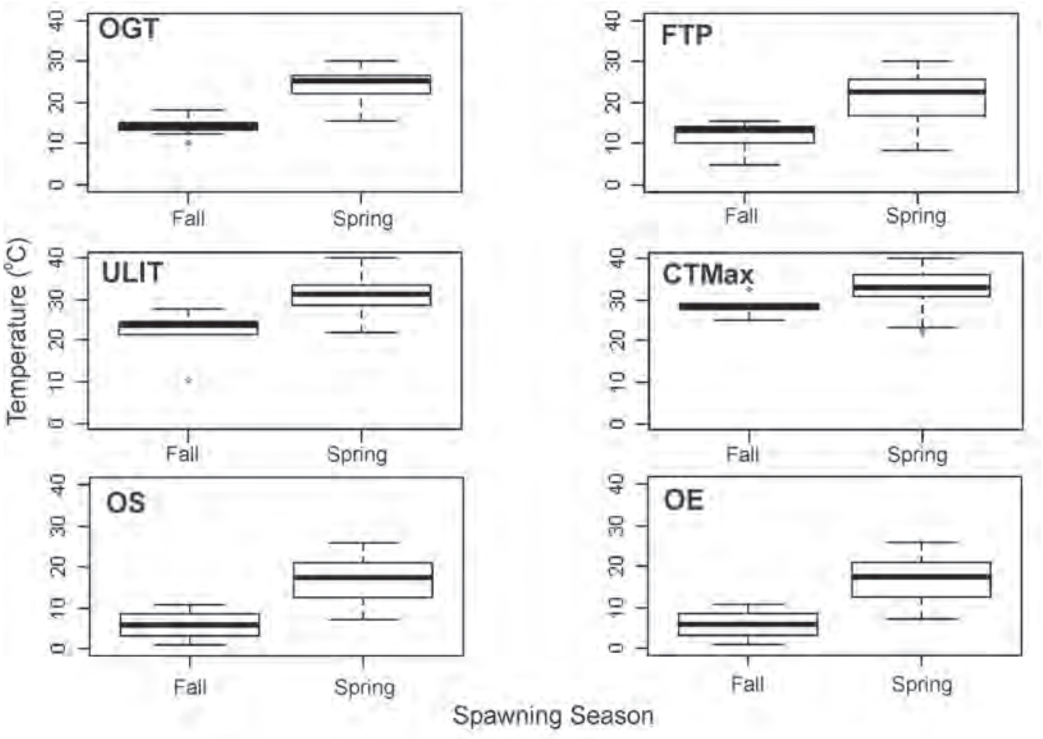

Figure 4. *Growth (OGT and FTP), survival (ULIT and CTMax), and reproduction (OS and OE) metric distributions for two spawning seasons; fall (September to early November, n=17); spring (April to late June, n=70).*

Discussion

The significant positive correlations observed between all metrics confirm (for a larger sample size) the results of similar studies by Jobling (1981) and Beitinger et al. (2000). In addition, we examined reproductive metrics along with growth and survival metrics and found that metrics associated with all three processes were positively correlated. These strong correlations suggest that growth, survival and reproductive metrics are interdependent across species and this interdependence provides the empirical basis for estimating the value of an unknown metric from the value of a known metric.

The strong associations between growth, survival, and reproduction metrics on the one hand and three life history characteristics (i.e., temperature preference class, reproductive guild and spawning season) on the other, also indicate that a species' life history characteristics shape and are shaped by its thermal preferences and limits. These results also indicate that the temperature preference classification system developed by Coker et al. (2000), with limited metric data, holds true for a larger data set. In addition, the results point to the possibility of a thermal association with the seasonal timing of spawning, and with reproductive behaviour itself, as categorized by Balon's (1975, 1981) reproductive guild concept.

Our compilation of estimates for six thermal metrics, reveals a number of biases in the thermal ecology literature for Canadian freshwater fish. For example:

- Numerous FTP estimates for many species contrast with few OS and OE estimates, suggesting a need for further work to characterize inter-specific differences in the thermal ecology of reproduction.
- Most metric estimates focus on a single life stage (young-of-year, juvenile, or adult), suggesting the need for further work to evaluate the intra-specific stability of thermal metrics across life stages. This is re-inforced by, for example, the compilation of metric estimates by Wismer and Christie (1987) in which adult growth metric estimates can differ by more than ±2C° from those for younger life stages of the same species.
- Many metric estimates are derived from test fish acclimated to a single temperature. Given the sensitivity of growth and survival metrics to acclimation temperature, estimates based on only one acclimation temperature may suggest a narrower temperature range for survival and growth than is actually the case (Beitinger et al. 2000).

Potential Applications

Potential applications for growth temperature, survival, and reproduction metrics are numerous. Some examples for each are:

Growth Metrics

- Values for the optimum growth and final temperature preferendum can be used to establish the thermal niche habitable by a particular fish species (Magnuson et al. 1979, Christie and Regier 1988). Combined with lake volume and temperature profile data, the thermal niche can then be used to determine the productive capacity for the population of a particular species, resident in a given lake (Christie and Regier 1988).
- Given lake temperature data, and values for optimum growth and final temperature preferendum, species-specific thermal habitat dynamics can be derived and used to predict population performance and suitable habitat area (Chu et al. 2004).

Survival Metrics

- Values for the upper incipient lethal and critical thermal maximum temperatures can be used to identify the potential southern limit of the zoogeographical distribution of a species (Meisner 1990a).
- Survival metrics coupled with species diversity in a given lake can provide a basis for regulating heated discharge from power plants (Coutant and Talmadge 1977).
- Seasonal temperature maxima exhibited by streams during spring and summer can be detrimental to fish species limited by low survival threshold temperatures. Survival metrics can be used to identify affected species and determine thermal avoidance migration patterns (Meisner 1990b).

Reproduction Metrics

- Species-specific spawning and egg development temperatures can be used to identify spawning sites (Rejwan et al. 1997).
- Coupled with lake temperature data, reproduction metrics can be used to determine species specific spawning times (Shuter and Post 1990).

References

Alderdice, D., W. Wickett and J. Brett. 1958. Some effects of temporary exposure to low dissolved oxygen levels on Pacific salmon eggs. J. Fish. Res. Board Can. 15: 229-249.

Balon, E. 1975. Reproductive guilds of fishes: a proposal and definition. J. Fish. Res. Board Can. 32: 821-864.

Balon, E. 1981. Additions and amendments to the classification of reproductive styles in fishes. Env. Biol. Fish. 6(3/4): 377-389.

Beitinger, T.L., W.A. Bennett and R.W. McCauley. 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Env. Biol. Fish. 58: 237-275.

Beitinger, T.L. and L.C. Fitzpatrick. 1979. Physiological and ecological correlates of preferred temperature in fish. Am. Zool. 19: 319-329.

Brett, J.R .1956. Some principles in the thermal requirements of fishes. Quart. Rev. Biol. 31: 75-87.

Brett J.R. 1971. Energetic responses of salmon to temperature: A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. 11: 99-113.

Chimlevsky, D. 1999. Effect of extreme temperature on oogenesis in tilapia and rainbow trout. P. 316 *in* Norberg, B., O. Kjesbu, G. Taranger, E. Anderson and S. Stefansson (eds.). Proceedings of the 6th International Symposium on the Reproductive Physiology of Fish. Institute of Marine Research and University of Bergen, Bergen, Norway.

Christie, G.C. and H.A. Regier.1988. Measures of optimal thermal habitat and their relationship to yields for 4 commercial fish species. Can. J. Fish. Aquat. Sci. 45: 301-314.

Chu, C., C.K. Minns, J.E. Moore and E.S. Millard. 2004. Impact of oligotrophication, temperature, and water levels on walleye habitat in the Bay of Quinte, Lake Ontario. Tran. Am. Fish. Soc. 133 (4): 868-879.

Coker, G.A., C.B. Portt and C.K. Minns. (2001, January). Morphological and ecological characteristics of Canadian freshwater fishes. Can. Dept. Fish. Oceans, Ottawa, ON. Canadian Manuscript Report of Fisheries and Aquatic Sciences, 2554. 86 p.

Danzman, R.G., G.S. MacLennan, D.G. Hector, P.D.N. Hebert and J. Kolasa. 1991. Acute and final temperature preferenda as predictors of Lake St. Clair catchability. Can. J. Fish. Aquat. Sci. 48: 1408-1418.

Evans, D.O. 2007. Effects of hypoxia on scope-for-activity and power capacity of Lake Trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. 64: 345-361.

Fry, F.E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Press, Toronto, ON. Publication of the Ontario Fisheries Research Laboratory 68. 62 p.

Giattinna, J.D. and R.R. Garton. 1982. Graphical model of thermoregulatory behaviour by fishes with a new measure of eurythermality. Can. J. Fish. Aquat. Sci. 39: 524-528.

Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board Can. 34: 1524-1550.

Jobling, M. 1981. Temperature tolerance and the final preferendum -- rapid methods for the assessment of optimum growth temperatures. J. Fish Biol. 19: 439-455.

Jobling, M. 1994. Fish Bioenergetics. Chapman and Hall, London, UK.

Kling, G.W., K Hayhoe, L.B. Johnson, J.J. Magnuson, S. Polasky, S.K Robinson, B.J. Shuter, M.M. Wander, D.J. Wuebbles and D.R. Zack. 2003. Confronting climate change in the Great Lakes Region. The Union of Concerned Scientists, Cambridge, MA and the Ecological Society of America, Washington, DC. 92 p.

Magnuson, J.J., L.B. Crowder and P.A. Medvic. 1979. Temperature as an ecological resource. Am. Zool. 19: 331-343.

McCauley, R.W. and J.M. Casselman 1980. The final preferendum as an index of the temperature for optimum growth in fish. Pp 83-93 *In* United Nations Food and Agriculture Organization, European Inland Fisheries Advisory Commission, Symposium 80/E76, Rome, Italy.

Meisner, J. D. 1990a. Effect of climatic warming on the southern margins of the native range of brook trout, Salvelinus fontinalis. Can. J. Fish. Aquat. Sci. 47: 1065-1070.

Meisner, J.D. 1990b. Potential loss of thermal habitat for brook trout, due to climatic warming in two southern Ontario streams. Trans. Am Fish Soc. 119: 282-291.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rejwan, C., B.J. Shuter, M.S. Ridgway and N.C. Collins. 1997. Spatial and temporal distributions of smallmouth bass (*Micropterus dolomieu*) nests in Lake Opeongo, Ontario. Can. J. Fish. Aquat. Sci. 54: 2007-2013.

Rombough, P. 1997. The effects of temperature on embryonic and larval development. Pp. 177-224 *in* Wood, C. and D. McDonald (eds.). Global Warming: Implications for Freshwater and Marine Species. Society for Experimental Biology, Seminar Series 61. Cambridge Univ. Press, Cambridge, UK.

Scott, W. and E. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can., Ottawa, ON. Bulletin 184.

Shuter, B.J. and J.R. Post. 1990. Climate, population viability and the zoogeography of temperate fishes. Tran. Am. Fish. Soc. 119: 314-336.

Spotila, J.R., K.N. Terpin, R.R. Koons and R.L. Bonati. 1979. Temperature requirements of fishes from eastern Lake Erie and the upper Niagara River: A review of the literature. Env. Biol. Fish. 4: 281-307.

Van der Kraak, G. and N. Pankhurst.1997. Temperature effects on the reproductive performance of fish. Pp. 159-176 *in* Wood, C. and D. McDonald (eds.). Global Warming: Implications for Freshwater and Marine Species. Society for Experimental Biology, Seminar Series 61. Cambridge Univ. Press, Cambridge, UK.

Wismer, D.A. and A.E. Christie. 1987. Temperature relationships of Great Lakes fishes: A data compilation. Great Lakes Fishery Commission, Ann Arbor, MI. Spec. Publ. 87-3. 196 p.

Wood, C.M. and D.G. McDonald (eds.). 1997. Global Warming: Implications for Freshwater and Marine Fish. Society for Experimental Biology, Seminar Series 61. Cambridge Univ. Press, Cambridge, UK.

Appendix

Table A1. *Optimum growth temperature (OGT), final temperature preferendum (FTP), upper incipient lethal temperature (UILT), and critical thermal maximum (CTMax) data for 87 Canadian freshwater species. Species are arranged alphabetically within families. All temperatures are recorded in °C. Asterisks (**) indicate temperature values not included in statistical analyses due to procedural discrepancies. References are provided in an Appendix reference list that follows the tables.*

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
Acsipenseridae									
Lake Sturgeon	*Ascipenser fulvescens*			11.0	E(2009)				
Amiidae									
Bowfin	*Amia calva*			30.5	WC(1987)			37.0	WC(1987)
				28.0-32.0	E(2009)				
Anguillidae									
American Eel	*Anguilla rostrata*	25.0	WC (1987)	16.7	WC(1987)				
				20.5	WC(1987)				
				24.9	WG(1991)				
				16.0-19.0	E(2009)				
Catostomidae									
Bigmouth Buffalo	*Ictiobus cyprinellus*			6.0-24.0	WC(1987)				
				18.0-26.0	WC(1987)				
				22.0-23.0	WC(1987)				
Longnose Sucker	*Catostomus catostomus*			8.0-17.0	E(2009)	26.5	WC(1987)		
				11-11.6	WC(1987)	27.0	WC(1987)		
				8.0-17.0	WC(1987)				
				8.0	WC(1987)				
Northern Hog Sucker	*Hypentelium nigricans*	25.8	J(1981)	26.0	J(1981)	30-34	R(2000)	30.9	S(1979)
		25.3	J(1981)	26.6	E(2009)	33.0	WC(1987)		
				29.2	WC(1987)	27.0	WC(1987)		
				25.2	WC(1987)	30.0	WC(1987)		
				28.6	J(1998)	19.0-27.0	E(2009)		
				26-27	S(1974)	34.0	WC(1987)		
Quillback	*Carpoides cyprinus*			22.1	WC(1987)			37.2	S(1979)
				26.3	WC(1987)				
				10.0-16.0	WC(1987)				
Spotted Sucker	*Minytrema melanops*			25.0-27.0	WC(1987)	31.0	WC (1987)		

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				16.0-19.0	WC(1987)				
White Sucker	*Catostomus commersoni*	27.0	J(1981)	24.0	J(1981)	26.3	S(1979)	31.6	WC (1987)
		24.0	WC(1987)	18.3-26.7	D(1991)	27.7	S(1979)		
				22.4	WC(1987)	29.3	S(1979)		
				14.1-18.3	WC(1987)				
				23.9	WC(1987)				
				25-27	WC(1987)				
				16.0-49.0	WC(1987)				
				19.0-21.0	WC(1987)				
				24.1	WC(1987)				
				26.7	WC(1987)				
				14.4	WC(1987)				
				22-26	E(2009)				
				27.1	J(1998)				
Centrarchidae									
Black Crappie	*Poxomis negromaculatus*	9.0-17.0	WC(1987)	27.8-29.8	J(1998)	34.0	WC (1987)	34.9	S(1979)
		22-25	WC(1987)	24.0-29.8	J(1998)	32.5	WC (1987)		
				20.5	WC(1987)				
				21.0	WC(1987)				
				21.7	WC(1987)				
				22.2	WC(1987)				
				24.0	WC(1987)				
				24.6	WC(1987)				
				21.3	WC(1987)				
				21.0-25.0	E(2009)				
Bluegill	*Lepomis macrochirus*	30.1	J(1981)	32.0	J(1981)	31.0	WC(1987)	37.8	S(1979)
		31.0	J(1981)	31.2	J(1981)	32.0	WC(1987)	40.0	S(1979)
		29-30	J(1981)	31.0	J(1981)	33.0	WC(1987)	43.4	S(1979)
		30.0	WC(1987)	32.0	J(1981)	34.0	WC(1987)	38.3	S(1979)
		24-27	WC(1987)	30.9	J(1981)	35.5	WC(1987)	41.5	WC(1987)
		27.0	WC(1987)	30.7	J(1998)	30.7	S(1979)		
		31.2	WC(1987)	31.4	J(1998)	31.7	S(1979)		
				30.9-32.3	D (1991)	33.8	S(1979)		
				24.6-32.0	D(1991)	28.5	S(1979)		
				27.4	WC(1987)				
				24.0-30.0	E(2009)				

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
Green Sunfish	*Lepomis cyanellus*	28.0	WC(1987)	30.3	J(1998)	40.0	WG(1991)	36.0	WC(1987)
				15.9	WC(1987)				
				22.7	WC(1987)				
				30.6	WC(1987)				
				26.8	WC(1987)				
				27.0-31.0	E(2009)				
Largemouth Bass	*Micropterus salmoides*	27.5	J(1981)	30.0-32.0	J(1981)	29.0	WC(1987)	36.7	S(1979)
		27.0	J(1981)	30.0	J(1981)	30.0	WC(1987)	40.1	S(1979)
		25.0	J(1981)	30.2	J(1981)	32.5	S(1979)		
		26.0-28.0	J(1981)	28.5	J(1981)	34.5	S(1979)		
				32.2	J(1998)	36.4	S(1979)		
				28.5-32.0	J(1981)	28.9	S(1979)		
				26.6-32.0	J(1981)				
				29.0	J(1981)				
				28.0	WC(1987)				
				27.0-32.0	WC(1987)				
				29.5	WC(1987)				
				27.1	WC(1987)				
				27.0	WC(1987)				
				30.4	WC(1987)				
				21.3	WC(1987)				
				27.0	WC(1987)				
				26.0-30.0	E(2009)				
Pumpkinseed	*Lepomis gibbous*	25.0	WC (1987)	31.0	J(1981)	28.0	S(1979)	37.6	S(1979)
				26.0	J(1981)	30.0	S(1979)		
				31.3	J(1998)	34.5	S(1979)		
				26.0-32.0	D (1991)	27.7-28.3	WC(1987)		
				26.0	J(1981)	32.3-32.9	WC(1987)		
				28.5	WC(1987)	35.2-35.3	WC(1987)		
				31.7	WC(1987)	28.5	WC(1987)		
				31.5	WC(1987)	31.6	WC(1987)		
				28.4	WC(1987)	31.9	WC(1987)		
				22.9	WC(1987)	33.5	WC(1987)		
				25.3	WC(1987)	31.7	WC(1987)		
				26.9	WC(1987)	37.0	WC(1987)		
				27.0	WC(1987)	24.5	WC(1987)		

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				23.2	WC(1987)	36.6	WC(1987)		
				25.5	WC(1987)	34.8	WC(1987)		
				28.8	WC(1987)				
				29.5	WC(1987)				
				25.6	WC(1987)				
				28.1	WC(1987)				
				30.3	WC(1987)				
				24.2	WC(1987)				
				27.7	WC(1987)				
				22.0-30.0	E(2009)				
Rock Bass	*Ambloplites rupestris*	27.7	J(1981)	28.0	J(1981)	35.0	WC(1987)	36.0	S(1979)
		29.0	J(1981)	30.6	J(1998)	32.8	S(1979)		
				21-30	D(1991)				
				29.0	J(1981)				
				21.3	WC(1987)				
				20.7	WC(1987)				
				27.0-27.8	WC(1987)				
				26.8-28.3	WC(1987)				
				26.2	WC(1987)				
				28.8	WC(1987)				
				21.6	WC(1987)				
				20.5	WC(1987)				
				22.8	WC(1987)				
				27.5	WC(1987)				
				27.4	WC(1987)				
				30.0	WC(1987)				
				19.6	WC(1987)				
				20.2	WC(1987)				
				18.7	WC(1987)				
				21.0-26.0	E(2009)				
Smallmouth bass	*Micropterus dolomieui*	26.0	J(1981)	28.0	J(1981)	37.0	WC(1987)	36.3	S(1979)
				31.3	J(1981)	35.0	WC(1987)		
				30.3	J(1981)				
				21.3-31.3	D(1991)				
				12.0-13.0	WC(1987)				
				15.0-16.0	WC(1987)				

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				30.0	WC(1987)				
				21.0-23.0	WC(1987)				
				30.0-31.0	WC(1987)				
				26.6	WC(1987)				
				20.0	WC(1987)				
				20-26	E(2009)				
				28.5	J(1981)				
White Crappie	*Poxomis annularis*	24.0	B(2007)	19.8	WC(1987)			32.8	S(1979)
		18-24	HA(1996)	18.3	WC(1987)				
				10.4	WC(1987)				
				19.4	WC(1987)				
				23.0	WC(1987)				
				23-24	WC(1987)				
				19.4	E(2009)				
Clupeidae									
Alewife	*Alosa pseudoharengus*	20.1	GLFC(2009)	16-21	E(2009)	28.5	WC(1987)	31.0-34.0	WC(1987)
				19.6	WC(1987)	8.5	WC(1987)	28.6	WC(1987)
				12.0	WC(1987)	7.0	WC(1987)	30.6	WC(1987)
				21.0	WC(1987)	31.0-34.0	WC(1987)	32.6	WC(1987)
				19.0	WC(1987)	2.0	WC(1987)	32.0	WG(1991)
				16.0	WC(1987)	22.8	WC(1987)		
				11.0	WC(1987)	33.3	WC(1987)		
				11.0-14.0	WC(1987)	31.4	WC(1987)		
				13.0-16.0	WC(1987)	23.2	WC(1987)		
				25.0	WG(1991)	29.7	GLFC(2009)		
						23.5	S(1979)		
						24.5	S(1979)		
						33.0	WG(1991)		
						23.0	WG(1991)		
Gizzard Shad	*Dorosoma cependianum*	16.0-18.0	WC (1987)	19.0	WC(1987)	34.0	S(1979)	31.7	WC(1987)
				20.5	WC(1987)	36.0	S(1979)		
				23.0	WC(1987)	36.5	S(1979)		
				26.0-34.0	WC(1987)				
				10.0-12.0	WC(1987)				
				12.0	WC(1987)				
				4.0-10.0	WC(1987)				

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				28.5-31.0	WC(1987)				
Cottidae									
Deepwater Sculpin	*Myoxocephalus thompsoni*			5.0	WC(1987)				
				2.0-10.0	WC(1987)				
				2.0-6.0	WC(1987)				
Fourhorn Sculpin	*Myoxocephalus quadricornis*			1.0-9.0	E(2009)				
Mottled Sculpin	*Cottus biardii*			16.5	WC(1987)	24.3	Wh(1999)	30.9	S(1979)
				16.7	WC(1987)				
				13.0-18.0	E(2009)				
Slimy Sculpin	*Cottus cognatus*			6.0-8.0	WC(1987)	26.5	WC(1987)	22.7	WC(1987)
				4.0-6.0	WC(1987)	18.5	WC(1987)	24.8	WC(1987)
				9.0	WC(1987)	22.5	WC(1987)	26.3	WC(1987)
				12.0	WC(1987)	23.5	WC(1987)	29.4	WC(1987)
				10.0	WC(1987)			24.0	WC(1987)
				13.0	WC(1987)			25.1	WC(1987)
				9.0-14.0	E(2009)			27.3	WC(1987)
				10.7	WG(1991)			29.4	WC(1987)
Spoonhead Sculpin	*Cottus ricei*			4.0-8.0	E(2009)				
Cyprinidae									
Blackchin Shiner	*Notropis heterodon*					38.0	WC(1987)	32.8	WC(1987)
Blacknose Dace	*Rhinichthys atratulus*			19.6	WG(1991)	25.0	WC(1987)	29.5	WC(1987)
						27.0	WC(1987)	29.3	WC(1987)
						29.3	WC(1987)	31.9	WC(1987)
						26.5	WC(1987)		
						28.8	WC(1987)		
						29.6	WC(1987)		
						31.7	WC(1987)		
						29.9	WC(1987)		
						30.0	WC(1987)		
Bluntnose Minnow	*Pimephales notatus*	27.4	J(1981)	29.0	J(1981)	32.0	WC(1987)	27.8	S(1979)
		24.0	J(1981)	28.1	J(1981)	28.3	WC(1987)	31.9	S(1979)
		27.2	J(1981)	20-27.2	S(1974)	26.0	S(1979)		
				15.7	S(1979)	28-28.3	S(1979)		
				17.2	S(1979)	30.6	S(1979)		
				20.5	S(1979)	31.7-32.0	S(1979)		

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				20.4	S(1979)	33.3	S(1979)		
				21.5	S(1979)	34.8	S(1979)		
				22.8	S(1979)	31.7	WC(1987)		
				25.7	S(1979)	38.0	WC (1987)		
				28.9	S(1979)				
				29.0	S(1979)				
				28.4	S(1979)				
				21.0	S(1979)				
				26.3	E(2009)				
				29.0	WC(1987)				
Carp	*Cyprinus carpio*	30.0	J(1981)	32.6	J(1998)	31.0-34.0	S(1979)	39.0	S(1979)
		32.0	J(1981)	32.0	J(1981)	35.7	S(1979)		
		27.0	WC(1987)	31.5	J(1981)	35.4	S(1979)		
		20.0-25.0	WC(1987)	29.3-31.9	D(1991)	31-34	S(1979)		
		23.0-27.0	WC(1987)	28.2-31.9	D(1991)	35.7	S(1979)		
				29.0	J(1981)				
				27.4	WC(1987)				
				29.7	WC(1987)				
				25.0-30.0	WC(1987)				
				26.0-34.0	WC(1987)				
				16.0-20.0	WC(1987)				
				5.0-16.0	WC(1987)				
				28-32	E(2009)				
Central Stoneroller	*Campostoma anomalum*	26.6	J(1981)	29.0	J(1998)	31.0	WC (1987)	28.8	B(2000)
		23.0	J(1981)	26.6	J(1998)			35.8	B(2000)
				28.6	J(1981)			37.7	B(2000)
				26.2	J(1981)			37.2	B(2000)
				29.0	WC(1987)			31.8	B(2000)
				28.5	WC(1987)				
				26.2	WC(1987)				
				20-27	S(1974)				
				13.4	WC(1987)				
				15.2	WC(1987)				
				20.7	WC(1987)				

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				21.7	WC(1987)				
				22.3	WC(1987)				
				23.6	WC(1987)				
				25.3	WC(1987)				
				27.5	WG(1991)				
Common Shiner	*Notropis cornutus*	22.0	NJFW(2009)	21.9	E(2009)	32.0	S(1979)	30.6	S(1979)
						26.7-27.0	WC(1987)	31.9	S(1979)
						28.6-29.0	WC(1987)	31.0	WG(1991)
						30.3	WC(1987)		
						31.0-32.3	WC(1987)		
						33.5	WC(1987)		
						29.0	WC(1987)		
						30.5	WC(1987)		
						26.7	WC(1987)		
						28.6	WC(1987)		
						30.3	WC(1987)		
						31.0	WC(1987)		
						30.6	WC(1987)		
						31.1	WC(1987)		
Creek Chub	*Semotilus atromaculatus*			28.0	E(2009)	24.7	WC(1987)	30.3	WC(1987)
				21.8	WG(1991)	27.0	WC(1987)	35.7	B(2000)
						30.1-30.5	WC (1987)		
						30.0	WC (1987)		
						31.8	WC (1987)		
						32.1	WC (1987)		
						32.6	WC (1987)		
						24.7	WC (1987)		
						27.3	WC (1987)		
						30.3	WG(1991)		
						29.3	WC (1987)		
Emerald Shiner	*Notropis atherinoides*	27.0	J(1981)	27.8	J(1981)	23.2	S(1979)	28.6	WC (1987)
		24-28.9	WC (1987)	25.1	J(1981)	26.7	S(1979)		
				8.3	WC (1987)	28.9	S(1979)		
				9.0-23.0	E(2009)	30.7	S(1979)		

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
Fallfish	*Semotilus coropralis*			22.0	E(2009)				
Fathead Minnow	*Pimephales promelas*	26.0	J(1981)	26.2	J(1998)	33.2	WC (1987)	32.4	B(2000)
		25.5	J(1981)	23.4	J(1981)	28.0	WC (1987)	34.0	B(2000)
				28.5	J(1981)	32.3	WC (1987)	33.2	B(2000)
				29.0	J(1981)	33.0	WC (1987)	35.1	B(2000)
				26.6	J(1981)	28.2	WC (1987)	34.8	B(2000)
				23.0-29.0	E(2009)	31.7	WC (1987)	34.9	B(2000)
								33.1	B(2000)
								36.8	B(2000)
								36.2	B(2000)
								36.7	B(2000)
								34.4	B(2000)
								28.6	B(2000)
								30.7	B(2000)
								36.4	B(2000)
								40.4	B(2000)
								25.9	B(2000)
								36.5	B(2000)
Finescale Dace	*Chrosomus neogaeus*			24.1	WG(1991)	27.0	WC (1987)	32.2	WG(1991)
						28.0	WC (1987)		
						31.0	WC (1987)		
						30.3	WC (1987)		
						32.2	WC (1987)		
						31.3	WC (1987)		
						32.2	WC (1987)		
Golden Shiner	*Notemigonus crysoleucas*	26.0	M(2008)	16.8	WC (1987)	29.3	WC (1987)	30.5	WC (1987)
		23.9	M(2008)	23.7	WC (1987)	30.5	WC (1987)	36.4	B(2000)
				22.3	WC (1987)	31.8	WC (1987)	33.4	B(2000)
				21.0	WC (1987)	33.2	WC (1987)		
				23.9-28.9	WC (1987)	34.7	WC (1987)		
				24.0	WC (1987)	30.3	WC (1987)		
				16.8-23.7	CSJ(1984)	33.5	WC (1987)		

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				17.0-24.0	E(2009)	33.4	WC (1987)		
						32.8	WC (1987)		
						31.6	WC (1987)		
						30.4	WC (1987)		
						31-31.6	WC (1987)		
						32.7	WC (1987)		
						27.0-35.0	WC (1987)		
Goldfish	*Carassius auratus*	25.0	J(1981)	30.0	J(1981)	40.0	WC (1987)	36.6	S(1979)
		28.1	WC (1987)	28.0	J(1981)	29-38.6	WC (1987)	35.0	S(1979)
				27.0	WC (1987)	29.9-41	WC (1987)		
				24.0	WC (1987)	29.0	S(1979)		
				27.9	WC (1987)	30.8	S(1979)		
						32.8	S(1979)		
						34.8	S(1979)		
						36.6	S(1979)		
						38.6	S(1979)		
						29.9	S(1979)		
						31.5	S(1979)		
						33.0	S(1979)		
						35.0	S(1979)		
						37.5	S(1979)		
						39.0	S(1979)		
						41.0	S(1979)		
Longnose Dace	*Rhinichthys cataractae*			10.0-19.7	WC (1987)			31.4	S(1979)
				8.0-14.0	WC (1987)				
				10.0-22.7	WC (1987)				
				13.0-21.0	E(2009)				
				7.2-14.7	WC (1987)				
				20.9	WG(1991)				
				10.0-22.9	WG(1991)				

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
Northern Redbelly Dace	*Chrosomus eos*			25.3	WG(1991)	33.1	WC (1987)	29.0	WC (1987)
						28.0	WC (1987)		
						21.5	WC (1987)		
						26.5	WC (1987)		
						30.0	WC (1987)		
						31.0	WC (1987)		
						28.0	WC (1987)		
						31.5	WC (1987)		
						29.5	WC (1987)		
						32.7	WC (1987)		
Pugnose Shiner	*Notropis anogenus*			15.0-18.0	WC (1987)				
Rosyface Shiner	*Notropis rubellus*	25.7	J(1981)	27.6	J(1998)	33.0	WC (1987)	31.8	B(2000)
		25.3	J(1981)	26.1	J(1998)			35.3	B(2000)
				26.8	WC (1987)				
				20.8	WC (1987)				
				21.7	WC (1987)				
				22.2	WC (1987)				
				22.5	WC (1987)				
				25.8	WC (1987)				
				28.1	WC (1987)				
				28.0	WC (1987)				
				27.7	WC (1987)				
				26.0	WC (1987)				
Spotfin Shiner	*Cyprinella spiloptera*	28.6	J(1981)	31.0	J(1998)	36.0	WC (1987)		
		29.2	J(1981)	29.5	WC (1987)				
				29.4	WC (1987)				
				21.4	WC (1987)				
				21.8	WC (1987)				
				24.1	WC (1987)				
				26.4	WC (1987)				
				27.3	WC (1987)				

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				30.6	WC (1987)				
				31.8	WC (1987)				
				29.2	WC (1987)				
Spottail Shiner	*Notropis hudsonius*	27.3	WG(1991)	10.2**	WC (1987)	30.6	WC (1987)	32.80	WC (1987)
				17.0-20.0	WC (1987)	31.1	WC (1987)	33.50	WG(1991)
				19.0-20.0	WC (1987)	35.0	WC (1987)		
				17.0-18.0	WC (1987)	35.2	WG(1991)		
				13.0-22.0	E(2009)				
Esocidae									
Grass Pickerel	*Esox americanus vermiculatus*			26.0	WC(1987)				
				25.5	WC(1987)				
				25.6	WC(1987)				
Muskellunge	*Esox masquinongy*	24.0	J(1981)	24.0	J(1981)	32.2	SC(1973)	28.8	S(1979)
		26.6	J(1981)	25.1	J(1981)			31.9	S(1979)
		25.6	GLFC(2009)	22.0-26.0	E(2009)			34.5	S(1979)
								29.9-35.6	S(1979)
Northern Pike	*Exos lucius*	26.0	J(1981)	23.0-24.0	J(1981)	32.0	WC (1987)		
		19.0-21.0	J(1981)	19.0-20.0	D (1991)	31.6-31.7	WC (1987)		
				17.0-21.0	E(2009)	34.0	WC (1987)		
						28.4	WC (1987)		
						30.8	S(1979)		
						29.4	SC(1973)		
Cyprinodontidae									
Banded Killifish	*Fundulus diaphanus*			19.3	WC (1987)	27.50	WC (1987)		
				21.0	E(2009)	38.30	WC (1987)		
				28.6	M (1980)	34.50	WC (1987)		
						26.50	WC (1987)		
Mummichog	*Fundulus heteroclitus*	24.3	J(1981)	25.0	J(1981)	18.6-36.3	GCYK (1972)	34.3	B(2000)
								36.2	B(2000)
								41.0	B(2000)
								42.4	B(2000)
								43.1	B(2000)

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
								44.1	B(2000)
								32.2	B(2000)
								36.2	B(2000)
								38.5	B(2000)
								39.0	B(2000)
								40.5	B(2000)
								42.4	B(2000)
								43.1	B(2000)
								43.6	B(2000)
Gadidae									
Burbot	*Lota lota*	15.6-18.3	WC (1987)	21.2	WC (1987)	23.3	WC (1987)		
				11.4	WC(1987)				
				8.0-17.0	WC(1987)				
				6.0-11.0	WC(1987)				
				7.0-18.0	E(2009)				
Gasterosteidae									
Brook Stickleback	*Culaea inconstans*			21.3	E(2009)	30.6	WC (1987)		
Ninespine stickleback	*Pungitius pungitius*			17.0-24.0	WC(1987)				
				5.0-6.0**	WC(1987)				
				9.0-16.0	E(2009)				
				13.0-14.0**	WC(1987)				
Threespine Stickleback	*Gasterosteus aculeatus*	12.8	J(1981)	7.5-10.0	J(1981)	28.5	WC (1987)	28.7	B(2000)
		19.3	J(1981)	16.0	J(1981)	25.8	WC (1987)		
		19.1	J(1981)	4.0-8.0**	WC(1987)				
				10.0	WC(1987)				
				9.0-12.0	E(2009)				
				16.0-18.0	J(1981)				
Hiodontidae									
Mooneye	*Hiodon tergisus*			27.0-29.0	E(2009)				
Ictaluridae									
Black Bullhead	*Ictalurus melas*					35.7	WC (1987)	37.5	WC (1987)
						35.0	S(1979)		

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
Brown Bullhead	*Ameiurus nebulosus*	32.0	WC (1987)	27.3-31.0	D(1991)	36.1	WC (1987)	37.80	S(1979)
		28.2	J(1981)	11.9**	WC(1987)	28.6-29	WC (1987)	38.00	WC (1987)
		29.9	J(1981)	23.5	WC (1987)	30-30.2	WC (1987)		
				24.9	WC (1987)	33-33.4	WC (1987)		
				23.6	WC (1987)	35.5	WC (1987)		
				29.0-31.0	WC (1987)	36.5-37	WC (1987)		
				27.3	WC (1987)	37.5	WC (1987)		
				26.0	WC (1987)	37.2	WC (1987)		
				26-30	E(2009)	29.0	WC (1987)		
				10.9**	WC (1987)	32.3	WC (1987)		
				22.4	WC (1987)	33.7	WC (1987)		
						34.7	WC (1987)		
						29.9	WC (1987)		
						31.5	WC (1987)		
						33.0	WC (1987)		
						35.0	WC (1987)		
						39.0	WC (1987)		
						41.0	WC (1987)		
						29.1-32.6	WC (1987)		
						33.2-35.5	WC (1987)		
						32.9	WC (1987)		
						27.8	WC (1987)		
						31.0	WC (1987)		
						32.5	WC (1987)		
						33.8	WC (1987)		
						34.8	WC (1987)		
						28.0	WC (1987)		
						36.5	J(1981)		
Channel Catfish	*Ictalurus punctatus*	29.0	J(1981)	30.5	J(1981)	30.3	WC (1987)	34.5	S(1979)
		30.0	J(1981)	30.0	WC(1987)	32.8	WC (1987)	34.2	S(1979)
		28.0-30.0	J(1981)	25.2	WC (1987)	33.5	WC (1987)	35.5	S(1979)

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				25.3	WC (1987)	35.0	WC (1987)	37.5	S(1979)
				26.6-27.2	S(1974)	30.4	WC (1987)	39.2	S(1979)
				32.0	WC (1987)	32.8	WC (1987)	41.0	S(1979)
				18.9	WC (1987)	35.0	WC (1987)	38.0	S(1979)
				20.4	WC (1987)	32.8	WC (1987)	33.5	WC (1987)
				19.9	WC (1987)				
				21.7	WC (1987)				
				22.9	WC (1987)				
				26.1	WC (1987)				
				29.4	WC (1987)				
				29.5	WC (1987)				
				17.0	WC (1987)				
				21.0	WC (1987)				
				22.0	WC (1987)				
				28.0	WC (1987)				
				26.0	WC (1987)				
				15.2**	WC (1987)				
				27-31	E(2009)				
				30.3	S(1979)				
				32.8	S(1979)				
				33.5	S(1979)				
				36.6	S(1979)				
				37.3	S(1979)				
				37.8	S(1979)				
Stonecat	*Noturus flavus*			5.5	WC(1987)			29.0	S(1979)
				25.1	WC(1987)				
Yellow Bullhead	*Ictalurus natalis*			28.3	WC(1987)			36.4	S(1979)
				28.8	WC(1987)				
				27.6	WC(1987)				
Lepisosteidae									
Longnose Gar	*Lepisosteus osseus*	26.4	WC (1987)	30.0-31.8	WC (1987)				
				25.3	WC (1987)				
				33.1	WC (1987)				

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				30.0-34.0	WC (1987)				
				24.0-28.0	WC (1987)				
				12.0-16.0	WC (1987)				
				33.0-35.0	WC (1987)				
				34.0	WC (1987)				
Spotted Gar	*Lepisosteus oculatus*			15.0-17.0	WC (1987)				
Moronidae									
White Bass	*Morone chrysops*			29.4-34.4	D(1991)	33.5	S(1979)	35.3	S(1979)
				12.0-17.0	WC (1987)				
				28-30	WC (1987)				
				16.0-17.0	WC (1987)				
				29.0	WC (1987)				
				33.9-34.3	WC (1987)				
				30.0-34.0	WC (1987)				
				27.8	WC (1987)				
				28.0-32.0	E(2009)				
				27.8	WG(1991)				
White Perch	*Morone americana*	28.5	WC (1987)	29.8	WG(1991)	36.0	WG(1991)		
				26.0-30.0	E(2009)				
Percichthyidae									
Striped Bass	*Morone saxatilis*					24.4	C(2006)	25.3	C(2006)
						27.2	C(2006)	26.0	C(2006)
						29.7	C(2006)	26.5	C(2006)
						31.1	C(2006)		
						31.8	C(2006)		
						33.9	C(2006)		
Percidae									
Eastern Sand Darter	*Ammocrypta pellucida*	24.0	WC (1987)						
		25.0	WC (1987)						
		24.0-25.5	E(2009)						
Rainbow Darter	*Ethestoma carolineum*			19.8	E(2009)			32.1	WC (1987)
				20.0	WC (1987)				
Sauger	*Stizostedion canadense*	22.0	J(1981)	22.6	J(1981)				
				21.3	J(1981)				

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				27.0-29.0	WC (1987)				
				14-21	WC (1987)				
				8.0-11.0	WC (1987)				
				26-28	WC (1987)				
				7.2	WC (1987)				
				21.1	WC (1987)				
				20.0	WC (1987)				
				20.0-24.0	E(2009)				
Walleye	*Stizostedion vitreum*	22.1	J(1981)	20.6-32.2	D(1991)	28.9	WC (1987)	23.4	WC (1987)
				23.0	J(1981)	31.0	WC (1987)		
				22.0	WC (1987)	27.0-31.6	S(1979)		
				20.0	WC (1987)	30.5	WC (1987)		
				19.0-23.0	E(2009)				
Yellow Perch	*Perca flavescens*	23.0	J(1981)	24.2	J(1981)	21.0	WC (1987)	35.0	WC(1987)
		28.0	J(1981)	20.1	J(1981)	25.0	S(1979)		
		23.0-24.0	J(1981)	23.3	J(1981)	28.0	WC (1987)		
		26.0-30.0	WC (1987)	23.0	J(1981)	32.3	WC (1987)		
			WC (1987)	21.4	J(1981)	30.9	WC (1987)		
				20.2	J(1981)	21.3	S(1979)		
				18.0-21.1	D(1991)	27.7	S(1979)		
				20.1-23.0	D(1991)	29.0	S(1979)		
				21.0	J(1981)	18.0	S(1979)		
				7.0-12.0	WC (1987)	22.0-24.0	S(1979)		
				13-16	WC (1987)				
				27.0	WC (1987)				
				22-25	WC (1987)				
				14.1	WC (1987)				
				20.9	WC (1987)				
				19.9	WC (1987)				
				18-20	WC (1987)				
				12.3-13.8	WC (1987)				
				13.5-18.8	WC (1987)				
				17.6-20.2	WC (1987)				
				16.1-24.2	WC (1987)				

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				25.0	WC (1987)				
				17.0	WC (1987)				
				6.3	WC (1987)				
				8.0	WC (1987)				
				22.0	WC (1987)				
				5.4	WC (1987)				
				6.3	WC (1987)				
				7.0-8.0	WC (1987)				
				11.0-17.0	WC (1987)				
				14.0-19.0	WC (1987)				
				18.0-21.0	WC (1987)				
				20.0-24.0	E(2009)				
Percopsidae									
Trout-Perch	*Percopsis omniscomaycus*			16.0-18.0	WC(1987)			22.9	WC (1987)
				15.0-16.0	WC(1987)				
				7.0-16.0	WC(1987)				
				7.0-8.0	WC(1987)				
				10.0-16.0	E(2009)				
				16.0	WG(1991)				
Petromyzontidae									
Sea Lamprey	*Petromyzon marinus*	15.0	WC(1987)	14.3	WC(1987)	31.40	WG(1991)		
		20.0	WC(1987)	6.0-15.0	WC(1987)				
				6.0	WC(1987)				
Salmonidae									
Atlantic Salmon	Salmo salar	15.1	J(1981)	14.0	J(1981)	27.8	P(1993)	32.9	B(2000)
		12.1	J(1981)	18.0	J(1981)	27.5	G(1973)	32.6	B(2000)
				12.0-16.0	E(2009)			32.8	B(2000)
								32.7	B(2000)
Bloater	*Coregonus hoyi*	18.6	EF(1997)	7.0-10.0	WC(1987)	26.0-27.0	WC(1987)		
Brook Trout	*Salvelinus fontinalis*	13.0	J(1981)	13.8	J(1981)	25.3	WW(2007)	28.70	WC(1987)
		14.0	J(1981)	15.7	WC(1987)	24.5	WW(2007)	29.80	WC(1987)

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
		16.1	J(1981)	14.8	WC(1987)				
		15.4	WC(1987)	13.0-17.0	E(2009)				
		10.0-15.0	WC(1987)						
Brown Trout	*Salmo trutta*	10.0	J(1981)	17.6	J(1981)	24.7	WW(2007)	25.0	WC(1987)
		15.5	J(1981)	14.3	J(1981)	25.3	WW(2007)	26.0	WC(1987)
		12.0	J(1981)	12.2	J(1981)			29.0	B(2000)
		12.8	J(1981)	17.4	J(1998)			29.8	B(2000)
				15.0-18.0	E(2009)			29.9	B(2000)
								30.00	B(2000)
Chinook Salmon	*Oncorhynchus tshawytscha*	12.0	WC(1987)	11.7	J(1981)	21-22	WC(1987)	25.1	S(1979)
		15.5	WC(1987)	17.3	WC(1987)	21.5	S(1979)		
				12.0-16.0	E(2009)	24.3	S(1979)		
				12.3	J(1998)	25.0	S(1979)		
						25.1	S(1979)		
Chum Salmon	*Oncorhynchus keta*	13.0	J(1981)	14.0	J(1998)	-	W(1995)		
				14.1	J(1981)				
Coho Salmon	*Oncorhynchus kisutch*	14.8	J(1981)	15.0	J(1981)	9.4	W(1995)	25.0	BG(1979)
		17.0	WC(1987)	11.4	WC(1987)	26.0	S(1979)	24.8	BG(1979)
				16.6	WC(1987)	22.9	S(1979)	25.3	BG(1979)
				13.0-15.0	WC(1987)	23.1	S(1979)	25.9	BG(1979)
				20.0	WC(1987)	24.3	S(1979)	25.8	BG(1979)
				8.0	WC(1987)	25.0	S(1979)	27.7	BG(1979)
				12.0-16.0	WC(1987)			28.1	BG(1979)
				15.6	WC(1987)			28.7	BG(1979)
				14.3	WC(1987)			29.2	BG(1979)
				16.6	WC(1987)			29.6	BG(1979)
				11.0-17.0	E(2009)			27.5	B(2000)
				13.0	J(1981)			29.7	B(2000)
								28.2	B(2000)
								29.2	B(2000)
								29.1	B(2000)
								27.6	B(2000)
								27.9	B(2000)

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
Cutthroat Trout	*Oncorhynchus clarkii*	22.0	W(2009)	14.8-14.9	Mc(2006)	24.0	W(2009)	27.6	B(2000)
		13.4	Mc(2006)			19.7	B(2005)	29.1	B(2000)
		14.2	Mc(2006)					29.9	B(2000)
								25.5	B(2000)
Lake Herring, Cisco	*Corengus artedii*	18.1	J(1981)	18.5	J(1981)	19.8	S(1979)		
				13.7	J(1998)	21.2	S(1979)		
				9.9	J(1981)	24.3	S(1979)		
				10.0	WC(1987)	26.8	S(1979)		
				7.2	WC(1987)	25.8	S(1979)		
				13.0	WC(1987)	26.0	WG(1991)		
				13.0-18.0	WC(1987)				
				9.0-14.0	WC(1987)				
				16.5	WG(1991)				
				7.0-10.0	E(2009)				
Lake Trout	*Salvelinus namaycush*	10.0	J(2001)	11.8	WC(1987)	23.5	NSFA(2007)		
		5.0-15.0	J(2001)	12.0	WC(1987)	25.1	WC(1987)		
				10.0	WC (1987)				
				14.0	WC (1987)				
				9.0-13.0	E(2009)				
Lake Whitefish	*Coregonus clupeaformis*	13.5	J(1981)	12.7	J(1981)	20.6	S(1979)		
		15.8	J(1981)	12.0-16.0	J(1981)	22.7	S(1979)		
				8.0-14.0	E(2009)	25.8	S(1979)		
				13.0	WC (1987)	26.6	S(1979)		
Pink Salmon	*Oncorhynchus gorbuscha*	15.5	J(1981)	11.7	J(1981)	-	W(1995)		
				13.0-17.0	E(2009)				
				11.7-12.8	J(1981)				
Rainbow Trout	*Oncorhynchus mykiss*	17.2	WC (1987)	13.6	J(1998)	21.50	WC(1987)	17.50	WC(1987)
		16.5	WC (1987)	18.7	J(1998)	26.60	WW(2007)	26.70	WG(1991)
		17.0	WC (1987)	19.7	J(1998)	25.60	WW(2007)		
		12.0	WC (1987)	18.9-21.7	WC (1987)	26.20	WW(2007)		
				13.0	WC (1987)				
				16.5	WC (1987)				
				11.3	WC (1987)				

Common Name	**Scientific Name**	OGT	Reference	FTP	Reference	UILT	Reference	CTMax	Reference
				14.0	WC (1987)				
				15.8	WC (1987)				
				17.5	WC (1987)				
				22.0	WC (1987)				
				11.6	WC (1987)				
				12.6	WC (1987)				
				5.0-17.0	WC (1987)				
				12.0-18.0	E(2009)				
Round Whitefish	*Proposium cylindraceum*			17.5	WC (1987)				
				3-5.8	WC (1987)				
				2.1-3.6	WC (1987)				
Sockeye Salmon	*Oncorhynchus nerka*	15.0	J(1981)	14.1	J(1981)	8.9	W(1995)		
				10.0-15.0	WC (1987)	26.8	USBR(2007)		
				14.4	J(1998)	28.8	USBR(2007)		
Sciaenidae									
Freshwater Drum	*Aplodinotus grunniens*	22.0	WC (1987)	21.0-31.0	D(1991)	32.8	S(1979)	34.0	S(1979)
				26.5	WC (1987)				
				19.6	WC (1987)				
				21.1-26.1	WC (1987)				
				22.0	WC (1987)				
				29.0-31.0	WC (1987)				
				22.0-30.0	WC (1987)				
				6.0-11.00	WC (1987)				
				24.0-28.0	E(2009)				
Umbirdae									
Central Mudminnow	*Umbra limi*			28.9	WC (1987)				
				38.0	WC(1987)				

Table A2. *Reproductive thermal data (optimum spawning temperature [OS] and optimum egg development temperature [OE]) for 87 Canadian freshwater fish species. Values for events (e.g. hatching) and life stages (eg. embryo survival) other than spawning are taken to be representative of egg development. A dash (-) indicates that no data were found. Species are arranged alphabetically within families. All temperatures are recorded in °C. References are provided in an Appendix reference list that follows the tables.*

Common Name	**Scientific Name**	Event	Optimum Temperature	Temperature Range	References
Acsipenseridae					
Lake Sturgeon	*Ascipenser fulvescens*	embryo survival	12.0-17.0	-	W (1985)
		spawning	14.0-16.0	-	WC (1987)
Amiidae					
Bowfin	*Amia calva*		-	-	-
Anguillidae					
American Eel	*Anguilla rostrata*		-	-	-
Catostomidae					
Bigmouth Buffalo	*Ictiobus cyprinellus*	spawning	15.5-18.3	-	SC(1973)
		spawning	17.0	-	WC (1987)
		hatching	-	14-27	WC(1987)
Longnose Sucker	*Catostomus catostomus*	spawning	-	5.0	SC(1973)
		hatching	-	10.0-15.0	SC(1973)
		spawning	-	15.0	-
		spawning	-	12.0-23.0	WC(1987)
		hatching	-	17.4	WC(1987)
Quillback	*Carpoides cyprinus*		-	-	-
Spotted Sucker	*Minytrema melanops*		-	-	-
White Sucker	*Catostomus commersoni*	spawning	10.0	-	WC(1987)
		incubation/hatch	15.0	-	WC(1987)
		spawning	17.8	-	WC(1987)
		spawning	11.2	-	WC(1987)
		spawning	23.4	-	WC(1987)
		spawning	16.8	-	WC(1987)
Centrarchidae					
Black Crappie	*Pomoxis nigromaculatus*	spawning	19.0-20.0	-	SC(1973)
		spawning	17.8-20	-	WC(1987)
		hatching	18.3	-	WC(1987)
Bluegill	*Lepomis macrochirus*	spawning	-	-	WC(1987)
		hatching	22.2-23.9	-	S(1979)
		spawning	25.0	-	WC(1987)
		hatching	22.0-24.0	-	WC(1987)
Green Sunfish	*Lepomis cyanellus*	spawning	-	15.6-28.0	WC(1987)
		spawning	-	20.0-24.0	WC(1987)
		hatching	29.1	-	WC(1987)
Largemouth Bass	*Micropterus salmoides*	spawning	15.6-21.0	-	-
		hatching	20.0	-	-
		spawning	-	-	-
		spawning	20.0	-	-

Common Name	**Scientific Name**	Event	Optimum Temperature	Temperature Range	References
Pumpkinseed	*Lepomis gibbosus*	spawning	-	-	-
		spawning	28.0	-	WC(1987)
		spawning	24.0	-	WC(1987)
		hatching	28.0	-	WC(1987)
Rock Bass	*Ambloplites rupestris*		-	-	-
Smallmouth Bass	*Micropterus dolomieui*	spawning	18.0	-	WC(1987)
		spawning	-	-	WC(1987)
		spawning	-	-	WC(1987)
		egg/larval development	21.0	-	WC(1987)
White Crappie	*Pomoxis annularis*	spawning	18.0-20.0	-	WC(1987)
		spawning		-	WC(1987)
		spawning	16.0-20.0	-	WC(1987)
		hatching		18.3-20.0	WC(1987)
		spawning	14.0-16.0	-	WC(1987)
Clupeidae					
Alewife	*Alosa pseudoharengus*	spawning	12.9-13.1	-	WC(1987)
		spawning	13.0-16.0	-	WC(1987)
		embryo development	17.8	-	WC(1987)
Gizzard Shad	*Dorosoma cependianum*	spawning	22.0	-	WC(1987)
		hatch	22.2	-	WC(1987)
Cottidae					
Deepwater Sculpin	*Myoxocephalus thompsoni*		-	-	-
Fourhorn Sculpin	*Myoxocephalus quadricornis*		-	-	-
Mottled Sculpin	*Cottus biardii*	spawning	12.8	-	WC(1987)
		hatching	-	-	WC(1987)
		spawning	10.0	-	SC(1973)
Slimy Sculpin	*Cottus cognatus*		-	-	-
Spoonhead Sculpin	*Cottus ricei*		-	-	-
Cyprinidae					
Blackchin Shiner	*Notropis heterodon*		-	-	-
Blacknose Dace	*Rhinichthys atratulus*		-	-	-
Bluntnose Minnow	*Pimephales notatus*		-	-	-
Carp	*Cyprinus carpio*	spawning	19.0-23.0	-	WC(1987)
		hatching	23.4	-	WC(1987)
		spawning	27.0	-	WC(1987)
Central Stoneroller	*Campostoma anomalum*		-	-	-
Common Shiner	*Notropis cornutus*		-	-	-
Creek Chub	*Semotilus atromaculatus*		-	-	-
Emerald Shiner	*Notropis atherinoides*	spawning	24.0	-	SC(1973)
		hatch	23.9	-	WC(1987)
Fallfish	*Semotilus coropralis*		-	-	-
Fathead Minnow	*Pimephales promelas*	spawning	-	15.6-17.8	SC(1973)
		hatching	25.0	-	SC(1973)
		spawning		15.6-28.9	WC(1987)
Finescale Dace	*Chrosomus neogaeus*	spawning	-	-	WC(1987)

Common Name	**Scientific Name**	Event	Optimum Temperature	Temperature Range	References
		hatching	20.0	-	WC(1987)
		Spawning	-	15.0-22.0	WC(1987)
Golden Shiner	*Notemigonus crysoleucas*	spawning	20.0	-	SC(1973)
		spawning	20.0-21.0	-	WC(1987)
		hatching	20.0	-	R(1997)
Goldfish	*Carassius auratus*	spawning	-	18.4-24.9	SC(1973)
		hatching	-	15.5-18.4	WC(1987)
		spawning	-	17.0-24.0	WC(1987)
Longnose Dace	*Rhinichthys cataractae*	spawning	11.7	-	SC(1973)
		hatching	15.6	-	SC(1973)
Northern Redbelly Dace	*Chrosomus eos*		-	-	-
Pugnose Shiner	*Notropis anogenus*		-	-	-
Rosyface Shiner	*Notropis rubellus*	spawning	-	26.1-28.9	SC(1973)
		spawning	-	20.0-22.2	SC(1973)
		hatching	21.1	-	SC(1973)
Spotfin Shiner	*Cyprinella spiloptera*		-	-	-
Spottail Shiner	*Notropis hudsonius*	spawning	20.0	-	WC(1987)
		hatching	20.0	-	WC(1987)
		spawning	18.0	-	WC(1987)
Esocidae			-	-	-
Grass Pickerel	*Esox americanus vermiculatus*	spawning	7.2-11.7	-	SC(1973)
		hatching	7.8-8.9	-	SC(1973)
Muskellunge	*Esox masquinongy*	hatching & development	-	8.0-19.0	WC(1987)
		spawning	12.8	-	SC(1973)
Northern Pike	*Esox lucius*	spawning	-	4.0-19.0	WC(1987)
		hatch	6.4-17.7		S(1979)
Fundulidae			-	-	-
Banded Killifish	*Fundulus diaphanus*	spawning	23.0	-	SC(1973)
		hatching	-	22.0-26.7	SC(1973)
Mummichog	*Fundulus heteroclitus*		-	-	-
Gadidae					
Burbot	*Lota lota*	spawning	0.6-1.7	-	SC(1973)
		hatching	8.0-10.0	-	-
Gasterosteidae					
Brook Stickleback	*Culaea inconstans*	spawning	-	8.0-19.0	SC(1973)
		hatching	18.3		SC(1973)
		spawning	-	4.5-21.0	WC(1987)
Ninespine Stickleback	*Pungitius pungitius*		-	-	-
Threespine Stickleback	*Gasterosteus aculeatus*	hatching	19.0	-	SC(1973)
		spawning		5.0-20.0	WC(1987)
Hiodontidae					
Mooneye	*Hiodon tergisus*		-	-	-

Common Name	**Scientific Name**	Event	Optimum Temperature	Temperature Range	References
Ictaluridae					
Black Bullhead	*Ictalurus melas*		-	-	-
Brown Bullhead	*Ameiurus nebulosus*	spawning	21.1	-	SC(1973)
		hatching	-	20.6-25.0	WC(1987)
Channel Catfish	*Ictalurus punctatus*	spawning	26.7	-	SC(1973)
		hatching	-	15.6-27.8	SC(1973)
		spawning	23.9	-	WC(1987)
		hatching	-	23.9-22.8	WC(1987)
		spawning	27.0	-	WC(1987)
		hatch		18.0-29.0	WC(1987)
Stonecat	*Noturus flavus*		-	-	-
Yellow Bullhead	*Ictalurus natalis*		-	-	-
Lepistosteridae					
Longnose Gar	*Lepisosteus osseus*		-	-	-
Spotted Gar	*Lepisosteus oculatus*		-	-	-
Moronidae					
White Bass	*Morone chrysops*	eggs	-	11.0-23.9	WC(1987)
		spawning	14.7-16.3	-	WC(1987)
White Perch	*Morone Americana*	spawning	15.6-19.4	-	WC(1987)
		eggs	19.0-20.9	-	WC(1987)
Percichthyidae					
Striped Bass	*Morone saxatilis*		-	-	-
Percidae					
Eastern Sand Darter	*Ammocrypta pellucida*		-	-	-
Rainbow Darter	*Ethestoma carolineum*		-	-	-
Sauger	*Stizostedion canadense*	spawning	9.0-15.0	-	WC(1987)
		spawning	9.0	-	WC(1987)
		spawning	10.0	-	WC(1987)
		incubation/hatch	12.0-15.0	-	WC(1987)
Walleye	*Stizostedion vitreum*	spawning	8.0	-	WC(1987)
		hatching	9.0-15.0	-	WC(1987)
		spawning	6.0-12.0	-	WC(1987)
		hatching	17.8-19.4	-	WC(1987)
		spawning	6.1-8.3	-	WC(1987)
		spawning	3.4-10	-	WC(1987)
Yellow Perch	*Perca flavescens*	spawning	12.0	-	WC(1987)
		incubation/hatch	10.0-20.0	-	WC(1987)
		spawning	7.8-12.2	-	WC(1987)
		spawning	5.0-6.0	-	WC(1987)
		spawning	6.0-12.0	-	WC(1987)
Percopsidae					
Trout-Perch	*Percopsis omniscomaycus*		-	-	-
Petromyzontidae					
Sea Lamprey	*Petromyzon marinus*	spawning	14.4-15.6	-	SC(1973)
		spawning	15.7	-	WC(1987)
		eggs	18.5	-	WC(1987)

Common Name	**Scientific Name**	Event	Optimum Temperature	Temperature Range	References
Salmonidae					
Atlantic Salmon	*Salmo salar*		-	-	-
Bloater	*Coregonus hoyi*		-	-	-
Brook Trout	*Salvelinus fontinalis*	embryo	6.1	-	estimated from R(1997)
		spawning	10.7	-	WC(1987)
Brown Trout	*Salmo trutta*	spawning	-	6.7-8.9	SC(1973)
		embryo	-	0.0-15.0	WC(1987)
Chinook Salmon	*Oncorhynchus tshawytscha*		-	-	-
Chum Salmon	*Oncorhynchus keta*		-	-	-
Coho Salmon	*Oncorhynchus kisutch*	spawning	-	4.4-7.7	WC(1987)
		embryo	0.9-13.4	-	R (1997)
Cutthroat Trout	*Oncorhynchus clarkii*			-	
Lake Herring, Cisco	*Coregonus artedii*	spawning	3.3	-	SC(1973)
		incubation	5.6	-	SC(1973)
Lake Trout	*Salvelinus namaycush*		-	-	-
Lake Whitefish	*Coregonus clupeaformis*	spawning	-	0.5-9.4	WC(1987)
		hatching	-	-	S(1979)
		hatching	2.2-7.7	-	R(1997)
Pink Salmon	*Oncorhynchus gorbuscha*	spawning	10.0	-	SC(1973)
		embryo	1.0-13.5	-	R(1997)
Rainbow Trout	*Oncorhynchus mykiss*	spawning	6.0-8.0		WC(1987)
		egg development	5-6-12.2		WC(1987)
Round Whitefish	*Proposium cylindraceum*	spawning	4.5		SC(1973)
		egg survival	1.0-5.0		WC(1987)
		spawning	3.0		WC(1987)
Sockeye Salmon	*Oncorhynchus nerka*	spawning		5.0-10.5	SC(1973)
		embryo	1.0-15.5		R(1997)
		spawning		7.0-12.0	WC(1987)
Sciaenidae					
Freshwater Drum	*Aplodinotus grunniens*	spawning	21.0		WC(1987)
		hatching	23.9		WC(1987)
		spawning	21.0		WC(1987)
Umbridae					
Central Mudminnow	*Umbra limi*	-	-	-	-

Table A3. *Spawning season, reproductive guild, and temperature preference class data for 87 Canadian freshwater fish species. Species are arranged alphabetically within families. References are provided in an Appendix reference list that follows the tables.*

Family	Common Name	**Scientific Names**	Spawning Season	Reference	Reproductive Guild	Temperature Preference Class	Reference
Ascipenseridae	Lake Sturgeon	*Ascipenser fulvescens*	Spring	SC(1973)	A.1.2	cold/cool	C(2001)
Amiidae	Bowfin	*Amia calva*	Spring	SC(1973)	B.2.5	warm	C(2001)
Anguillidae	American Eel	*Anguilla rostrata*	N/A*	SC(1973)	A.1.1	cool	C(2001)
Catostomidae	Bigmouth Buffalo	*Ictiobus cyprinellus*	Spring	SC(1973)	A.1.5	warm	C(2001)
	Longnose Sucker	*Catostomus catostomus*	Spring	SC(1973)	A.1.3	cold	C(2001)
	Northern Hog Sucker	*Hypentelium nigricans*	Spring	SC(1973)	A.1.3	warm	C(2001)
	Quillback	*Carpoides cyprinus*	Spring	SC(1973)	A.1.6	cool	C(2001)
	Spotted Sucker	*Minytrema melanops*	Spring	SC(1973)	A.1.3	warm	C(2001)
	White Sucker	*Catostomus commersoni*	Spring	SC(1973)	A.1.3	cool	C(2001)
Centrarchidae	Black Crappie	*Pomoxis nigromaculatus*	Spring	SC(1973)	B.2.5	cool	C(2001)
	Bluegill	*Lepomis macrochirus*	Spring	SC(1973)	B.2.3	warm	C(2001)
	Green Sunfish	*Lepomis cyanellus*	Spring	SC(1973)	B.2.3	warm	C(2001)
	Largemouth Bass	*Micropterus salmoides*	Spring	SC(1973)	B.2.5	warm	C(2001)
	Pumpkinseed	*Lepomis gibbosus*	Spring	SC(1973)	B.2.2	warm	C(2001)
	Rock Bass	*Ambloplites rupestris*	Spring	SC(1973)	B.2.3	cool	C(2001)
	Smallmouth Bass	*Micropterus dolomieui*	Spring	SC(1973)	B.2.3	warm	C(2001)
	White Crappie	*Pomoxis annularis*	Spring	SC(1973)	B.1.4	cool	C(2001)
Clupeidae	Alewife	*Alosa pseudoharengus*	Spring	SC(1973)	A.1.4	cold	C(2001)
	Gizzard Shad	*Dorosoma cependianum*	Spring	SC(1973)	A.1.2	cool	C(2001)
Cottidae	Deepwater Sculpin	*Myoxocephalus quadricornis*	Fall	SC(1973)	B.2.3	cold	C(2001)
	Fourhorn Sculpin	*Myoxocephalus quadricornis*	Fall	SC(1973)	B.2.3	cold	C(2001)
	Mottled Sculpin	*Cottus biardii*	Spring	SC(1973)	B.2.7	cold	C(2001)
	Slimy Sculpin	*Cottus cognatus*	Spring	SC(1973)	B.2.7	cold	C(2001)
	Spoonhead Sculpin	*Cottus ricei*	Fall	SC(1973)	B.2.7	cold	C(2001)
Cyprinidae	Blackchin Shiner	*Notropis heterodon*	Spring	SC(1973)	A.1.5	cool/warm	C(2001)
	Blacknose Dace	*Rhinichthys atratulus*	Spring	SC(1973)	A.1.3	cool	C(2001)
	Bluntnose Minnow	*Pimephales notatus*	Spring	SC(1973)	B.2.7	warm	C(2001)
	Carp	*Cyprinus carpio*	Spring	SC(1973)	A.1.5	warm	C(2001)
	Central Stoneroller	*Campostoma anomalum*	Spring	SC(1973)	A.2.3	cool/warm	C(2001)
	Common Shiner	*Notropis cornutus*	Spring	SC(1973)	B.2.3	cool	C(2001)
	Creek Chub	*Semotilus atromaculatus*	Spring	SC(1973)	A.2.3	cool	C(2001)
	Emerald Shiner	*Notropis atherinoides*	Spring	SC(1973)	A.1.1	cool	C(2001)

Family	Common Name	**Scientific Names**	Spawning Season	Reference	Reproductive Guild	Temperature Preference Class	Reference
	Fallfish	*Semotilus coropralis*	Spring	SC(1973)	A.2.3	cool	C(2001)
	Fathead Minnow	*Pimephales promelas*	Spring	SC(1973)	B.2.7	warm	C(2001)
	Finescale Dace	*Chrosomus neogaeus*	Spring	SC(1973)	A.1.4	cool	C(2001)
	Golden Shiner	*Notemigonus crysoleucas*	Spring	SC(1973)	A.1.5	cool	C(2001)
	Goldfish	*Carassius auratus*	Spring	SC(1973)	A.1.5	warm	C(2001)
	Longnose Dace	*Rhinichthys cataractae*	Spring	SC(1973)	A.1.3	cool	C(2001)
	Northern Redbelly Dace	*Chrosomus eos*	Spring	SC(1973)	A.1.5	cool/warm	C(2001)
	Pugnose Shiner	*Notropis anogenus*	Spring	SC(1973)	A.1.3	cool	C(2001)
	Rosyface Shiner	*Notropis rubellus*	Spring	SC(1973)	A.1.3	warm	C(2001)
	Spotfin Shiner	*Cyprinella spiloptera*	Spring	SC(1973)	A.1.4	warm	C(2001)
	Spottail Shiner	*Notropis hudsonius*	Spring	SC(1973)	A.1.6	cold/cool	C(2001)
Esocidae	Grass Pickerel	*Esox americanus vermiculatus*	Spring	SC(1973)	A.1.5	warm	C(2001)
	Muskellunge	*Esox masquinongy*	Spring	SC(1973)	A.1.5	warm	C(2001)
	Northern Pike	*Esox lucius*	Spring	SC(1973)	A.1.5	cool	C(2001)
	Banded Killifish	*Fundulus diaphanus*	Spring	SC(1973)	A.1.5	cool	C(2001)
	Mummichog	*Fundulus heteroclitus*	Spring	SC(1973)	A.1.4	cold	C(2001)
Gadidae	Burbot	*Lota lota*	Fall	SC(1973)	A.1.2	cold/cool	C(2001)
Gasterosteidae	Brook Stickleback	*Culaea inconstans*	Spring	SC(1973)	B.2.4	cool	C(2001)
	Ninespine Stickleback	*Pungitius pungitius*	Spring	SC(1973)	A.1.3	warm	C(2001)
	Threespine Stickleback	*Gasterosteus aculeatus*	Spring	SC(1973)	B.2.4	cold	C(2001)
Hiodontidae	Mooneye	*Hiodon tergisus*	Spring	SC(1973)	A.1.2	cool/warm	C(2001)
Ictaluridae	Black Bullhead	*Ictalurus melas*	Spring	SC(1973)	B.2.3	warm	C(2001)
	Brown Bullhead	*Ameiurus nebulosus*	Spring	SC(1973)	B.2.7	warm	C(2001)
	Channel Catfish	*Ictalurus punctatus*	Spring	SC(1973)	B.2.7	warm	C(2001)
	Stonecat	*Noturus flavus*	Spring	SC(1973)	B.2.7	warm	C(2001)
	Yellow Bullhead	*Ictalurus natalis*	Spring	SC(1973)	B.2.7	warm	C(2001)
Lepisosteidae	Longnose Gar	*Lepisosteus osseus*	Spring	SC(1973)	A.1.5	warm	C(2001)
	Spotted Gar	*Lepisosteus oculatus*	Spring	SC(1973)	A.1.5	warm	C(2001)
Moronidae	White Bass	*Morone chrysops*	Spring	SC(1973)	A.1.4	warm	C(2001)
	White Perch	*Morone americana*	Spring	SC(1973)	A.1.4	warm	C(2001)
Percichthyidae	Striped Bass	*Morone saxatilis*	Spring	SC(1973)	A.1.2	cold	C(2001)
Percidae	Eastern Sand Darter	*Ammocrypta pellucida*	Spring	SC(1973)	A.1.6	cool/warm	C(2001)
	Rainbow Darter	*Ethestoma carolineum*	Spring	SC(1973)	A.2.3	cool	C(2001)
	Sauger	*Stizostedion canadense*	Spring	SC(1973)	A.1.3	cool	C(2001)

Family	Common Name	**Scientific Names**	Spawning Season	Reference	Reproductive Guild	Temperature Preference Class	Reference
	Walleye	*Stizostedion vitreum*	Spring	SC(1973)	A.1.2	cool	C(2001)
	Yellow Perch	*Perca flavescens*	Spring	SC(1973)	A.1.4	cool	C(2001)
Percopsidae	Trout-Perch	*Percopsis omniscomaycus*	Spring	SC(1973)	A.1.3	cold	C(2001)
Petromyzontidae	Sea Lamprey	*Petromyzon marinus*	Spring	SC(1973)	A.2.3	cold	C(2001)
Salmonidae	Atlantic Salmon	*Salmo salar*	Fall	SC(1973)	A.2.3	cold	C(2001)
	Bloater	*Coregonus hoyi*	Spring	SC(1973)	A.1.2	cold	C(2001)
	Brook Trout	*Salvelinus fontinalis*	Fall	SC(1973)	A.2.3	cold	C(2001)
	Brown Trout	*Salmo trutta*	Fall	SC(1973)	A.2.3	cold/cool	C(2001)
	Chinook Salmon	*Oncorhynchus tshawytscha*	Fall	SC(1973)	A.2.3	cold	C(2001)
	Chum Salmon	*Oncorhynchus keta*	Fall	SC(1973)	A.2.3	cold	C(2001)
	Coho Salmon	*Oncorhynchus kisutch*	Fall	SC(1973)	A.2.3	cold	C(2001)
	Cutthroat Trout	*Oncorhynchus clarkii*	Spring	SC(1973)	A.2.3	cold	C(2001)
	Lake Herring, Cisco	*Coregonus artedii*	Fall	SC(1973)	A.1.2	cold	C(2001)
	Lake Trout	*Salvelinus namaycush*	Fall	SC(1973)	A.2.3	cold	C(2001)
	Lake Whitefish	*Coregonus clupeaformis*	Fall	SC(1973)	A.1.3	cold	C(2001)
	Pink Salmon	*Oncorhynchus gorbuscha*	Fall	SC(1973)	A.2.3	cold	C(2001)
	Rainbow Trout	*Oncorhynchus mykiss*	Spring	SC(1973)	A.2.3	cold	C(2001)
	Round Whitefish	*Proposium cylindraceum*	Fall	SC(1973)	A.1.3	cold	C(2001)
	Sockeye Salmon	*Oncorhynchus nerka*	Fall	SC(1973)	A.2.3	cold	C(2001)
Sciaenidae	Freshwater Drum	*Aplodinotus grunniens*	Spring	SC(1973)	A.1.1	warm	C(2001)
Umbridae	Central Mudminnow	*Umbra limi*	Spring	SC(1973)	A.1.5	cool/warm	C(2001)

Appendix References

Bajer, P.G., J.J. Millpaugh and R.S. Hayward. 2007. Application of discrete choice models to predict white crappie temperature selection in two Missouri impoundments. Trans. Amer. Fish. Soc. 136: 889-901. B(2007).

Bear, B.A., T.E. McMahon and A.V. Zale. 2005. Thermal requirements of westslope cutthroat trout. Final report to the Wild Fish Habitat Initiative, Montana Water Center at Montana State University-Bozeman and Partners for Fish and Wildlife Program, U.S. Fish and Wildlife Service. (Available at: http://wildfish.montana.edu) B(2005).

Beitinger TL., W.A. Bennett and R.W. McCauley. 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Env. Biol. Fish. 58: 237-275. B(2000).

Becker, C.D. and T.G. Genoway. 1979. Evaluation of the critical thermal maximum for determining thermal tolerance of freshwater fish. Env. Biol. Fish. 4: 245-256. BG(1979).

Cincotta, D.A. and J.R. Stauffer, Jr. 1984. Temperature preference and avoidance studies of six North American freshwater fish species. Hydrobiol. 190: 173-177. CSJ(1984).

Coker, G.A., C.B Portt and C.K. Minns. 2001. Morphological and ecological characteristics of Canadian freshwater fishes. Can. Dept. Fish. Oceans, Ottawa, ON. Canadian Manuscript Report of Fisheries and Aquatic Sciences, 2554. 86 p. C(2001).

Cook, A.M., J. Dunston and R.G. Bradford. 2006. Thermal tolerance of a northern population of striped bass *Morone saxitalis*. J. Fish Biol. 69: 1482-1490. C(2006).

Danzman, R.G., G.S. MacLennan, D.G. Hector, P.D.N Hebert and J. Kolasa. 1991. Acute and final temperature preferenda as predictors of Lake St. Clair catchability. Can. J. Fish. Aquat. Sci. 48: 1408-1418. D(1991).

Eakins, R.J. 2009. Ontario Freshwater Fishes Life History Database. Version 3.75. On-line database. (www.fishdb.ca), accessed 30 September 2009 E(2009).

Edsall, T.A. and A.M. Frank. 1997. The effect of temperature on growth of juvenile bloater. J. Great. Lakes. Res. 23 (4): 468-471. EF(1997).

Garside, E.T. 1973. Ultimate upper lethal temperature of Atlantic Salmon *Salmo Salar L.* Can. J. Zool. 51: 898-900. G(1973).

Garside, E.T. and Z.K. Chin-Yuen-Kee. 1972. Influence of osmotic stress on upper lethal temperatures in the cyprinodontid fish *Fundulus heteroclitus* (L.). Can. J. Zool. 50: 787-791. GCYK(1972).

Great Lakes Fisheries Commission. 2009. Fish habitat database. Ann Arbor, MI. (http://www.glfc.org/fishmgmt/habitat/contents.htm; accessed October 16th 2009) GLFC(2009).

Jobling, M. 1981. Temperature tolerance and the final preferendum--rapid methods for the assessment of optimum growth temperatures. J. Fish Biol. 19: 439-455. J(1981).

Johnson, J.A. and S.W. Kelsch. 1998. Effects of evolutionary thermal environment on temperature-preference relationships in fishes. Env. Biol. Fish. 53: 447-448. J(1998).

McMahon, T.E., B.A. Bear and A.V. Zale. 2006. Comparative thermal preferences of Westslope Cutthroat Trout and Rainbow Trout. Montana State Univ., Bozemon, MT. Final Report to the Wild Fish Habitat Initiative-Montana Water Centre. 20 p. Mc(2006).

Melandri, M., N. Stone and R. Lochmann. 2008. Effects of temperature on the growth of Golden Shiners in Aquaria. N. Am. J. Aquacult. 70: 452-458. M(2008).

Melisky, E., J.R. Stauffer and C.H. Hocutt. 1980. Temperature preference of Banded Killifish, *Fundulus disphanus*, from southwestern Pennsylvania. Copeia 2: 346-349.

New Jersey Division of Fish and Wildlife. 2009. Common Shiner. New Jersey Department for the Environment. (http://www.state.nj.us/dep/fgw/fishfact.htm; accessed October 29 2009) NJFW(2009).

Nova Scotia Fisheries and Aquaculture. 2007. Lake Trout (*Salvelinus namaycush*). (http://www.gov.ns.ca/fish/sportfishing/species/lktrout.shtml; accessed October 16 2009) NSFA (2007).

Power, G. 1993. Estimating production, food supplies and consumption by Juvenile Atlantic Salmon (*Salmo salar*). Pp. 163-172 *in* Gibson, J.R and R.E Cutting (eds.) Production of Juvenile Atlantic Salmon, *Salmo salar*, in Natural Waters. Natl. Res. Coun. Can., Montreal, QC. Canadian Special Publication of Fisheries and Aquatic Sciences 118. P(1993).

Reash, R.J., G.L. Seegert and W.L. Goodfellow. 2000. Experimentally-derived upper thermal tolerances for Redhorse Suckers: revised 316(A) variance conditions at two generating facilities in Ohio. Env. Sci. Pol. 3: 191-196. R(2000).

Rombough, P. 1997. The effects of temperature on embryonic and larval development. Pp.177-224 *in* C. Wood and D. McDonald (eds.). Global Warming: Implications for Freshwater and Marine Species. Cambridge University Press. Cambridge, UK. R(1997).

Scott, W. and E. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Ottawa, ON. Bulletin 184. SC(1973).

Spotila, J.R., K.N. Terpin, R.R. Koons and R.L. Bonati. 1979. Temperature requirements of fishes from eastern Lake Erie and the upper Niagara River: A review of the literature. Env. Biol. Fish. 4: 281-307. S(1979).

United States Bureau of Reclamation. 2007. Assessment of Sockeye Salmon production potential in the Cle Elum River Basin, Storage Dam Fish Passage Study, Yakima Project, Washington. , U.S. Bureau of Reclamation, Boise, ID. Tech. Ser. No. PN-YDFP-008 USBR(2007).

Wang, Y., F. Binkowksi and S. Doroshov. 1985. Effect of temperature on early development of white and lake sturgeon, *Acipenser transmontanus* and *A. fulvescens.* Env. Biol. Fish. 14(1): 43-50. W(1985).

Wehrly, K.E. and L. Wang. 2007. Field-based estimates of thermal temperature tolerance limits for trout: Incorporating exposure time and temperature fluctuations. Trans. Am. Fish. Soc. 136: 365-374. WW(2007).

Welch, W.D., A.I. Chigirinsky and Y. Ishida. 1995. Upper thermal limits on the Oceanic Distribution of Pacific Salmon (*Oncorhynchus spp.*) in the spring. Can. J. Fish Aquat. Sci. 52(3): 489-503. W(1995).

Wichert, G.A. 1991. The fish associations of Toronto area waters, 1948-85: major changes and some causes. Dept. Zool., Univ. Toronto., Toronto, ON. M.Sc. thesis, WG(1991).

Williams, J.E., A.L. Haak, H.M. Neville and W.T. Colyer. 2009. Potential Consequences of Climate Change to Persistence of Cutthroat Trout Populations. N. Am. J. Fish. Manage. 29(3): 533-548. W(2009).

Wismer, D.A. and A.E. Christie. 1987. Temperature relationships of Great Lakes fishes: A data compilation. Great Lakes Fishery Commission, Ann Arbor, MI. Spec. Publ. 87-3. 196 p. WC(1987).

Climate Change Research Reports

CCRR-01 Wotton, M., K. Logan and R. McAlpine. 2005. **Climate Change and the Future Fire Environment in Ontario: Fire Occurrence and Fire Management Impacts in Ontario Under a Changing Climate**. Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-01. 23 p.

CCRR-02 Boivin, J., J.-N. Candau, J. Chen, S. Colombo and M. Ter-Mikaelian. 2005. **The Ontario Ministry of Natural Resources Large-Scale Forest Carbon Project: A Summary**. Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-02. 11 p.

CCRR-03 Colombo, S.J., W.C. Parker, N. Luckai, Q. Dang and T. Cai. 2005. **The Effects of Forest Management on Carbon Storage in Ontario's Forests.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-03. 113 p.

CCRR-04 Hunt, L.M. and J. Moore. 2006. **The Potential Impacts of Climate Change on Recreational Fishing in Northern Ontario.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-04. 32 p.

CCRR-05 Colombo, S.J., D.W. McKenney, K.M. Lawrence and P.A. Gray. 2007. **Climate Change Projections for Ontario: Practical Information for Policymakers and Planners.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-05. 37 p.

CCRR-06 Lemieux, C.J., D.J. Scott, P.A. Gray and R.G. Davis. 2007. **Climate Change and Ontario's Provincial Parks: Towards an Adaptation Strategy.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-06. 82 p.

CCRR-07 Carter, T., W. Gunter, M. Lazorek and R. Craig. 2007. **Geological Sequestration of Carbon Dioxide: A Technology Review and Analysis of Opportunities in Ontario.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-07. 24 p.

CCRR-08 Browne, S.A. and L.M Hunt. 2007. **Climate Change and Nature-based Tourism, Outdoor Recreation, and Forestry in Ontario: Potential Effects and Adaptation Strategies.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-08. 50 p.

CCRR-09 Varrin, R. J. Bowman and P.A. Gray. 2007. **The Known and Potential Effects of Climate Change on Biodiversity in Ontario's Terrestrial Ecosystems: Case Studies and Recommendations for Adaptation.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-09. 34 p + append.

CCRR-10 Dixon, R.L., J. Gleeson and K. Curren. (in prep.) **Climate Change and Renewable Energy in Ontario: Mitigation and Adaptation.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-10.

CCRR-11 Dove, D., I. Cameron and L. Demal. (in prep.) **Climate Change and Ontario's Water Resources: A Discussion of Potential Impacts and Water Resource Management Considerations.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-11.

CCRR-12 Colombo, S.J. 2008. **Ontario's Forests and Forestry in a Changing Climate.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-12. 21 p.

CCRR-13 Candau, J.-N. and R. Fleming. 2008. **Forecasting the Response to Climate Change of the Major Natural Biotic Disturbance Regime in Ontario's Forests: The Spruce Budworm.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-13. 14 p.

CCRR-14 Minns, C.K., B.J. Shuter and J.L. McDermid. 2009. **Regional Projects of Climate Change Effects on Ontario Lake Trout (Salvelinus namaycush) Populations.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-14. 11 p.

CCRR-15 Subedi, N., M. Sharma, and J. Parton. 2009. **An Evaluation of Site Index Models for Young Black Spruce and Jack Pine Plantations in a Changing Climate.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-15. 16 p.

CCRR-16 McKenney, D.W., J.H. Pedlar, K. Lawrence, P.A. Gray, S.J. Colombo and W.J. Crins. 2010. **Current and Projected Future Climatic Conditions for Ecoregions and Selected Natural Heritage Areas in Ontario.** Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-16. 24 p.

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An employee of the Lake Tahoe Resource Conservation District uses a high pressure hot water nozzle to remove adult mussels from the hull of a boat.

ANS Control Technology: Lethal Water Temperature—Pressurized Hot Water/ Steam Treatments and Hot Water Thermal Barrier

Targeted Species: Lethal water temperature is an effective control method for many types of organisms, and may be effective at preventing the transfer, via aquatic pathways, of all ANS of Concern – CAWS[1].

Selectivity: This technology was designed to manage the majority of aquatic organisms. It cannot selectively remove the specific ANS of Concern – CAWS. See *Brief Description* section for more details.

Developer/Manufacturer/Researcher: Research on this technology is currently being proposed by Bart De Stasio of Lawrence University (Appleton, WI).

Brief Description: There are two general types of thermal treatment, pressurized hot water/steam treatments and hot water thermal barrier. The pressurized hot water/steam treatment involves spraying pressurized hot water or steam onto ANS to kill and remove them from boats, pipes and structures. The hot water thermal barrier is a lethal zone created in a section of the waterway by mixing heated water throughout the water column, creating a kill zone for ANS that barrier area. Both strategies rely on the inability of ANS to adjust to changes in temperature that exceed their thermal tolerance.

The preferred, upper, and lower lethal temperature ranges for all aquatic life forms vary between and among species and are dependent on genetics, developmental stage and thermal histories (Beitinger et al. 2000). Free swimming aquatic organisms tend to gravitate to a narrow range of temperatures, referred to as a preferred temperature zone. See figure on page 2. In fish, avoidance will occur as water temperature exceeds the preferred temperature zone by 4-18 °F (1-10 °C) (Coutant 1977).

Aquatic nuisance species are susceptible to temperatures that exceed their thermal tolerance. Two types of upper lethal thermal limits exist: acute upper lethal temperatures, and chronic or incipient upper lethal temperatures. Acute upper lethal temperatures are the temperatures at which death occurs when water temperature is raised rapidly. Chronic or incipient upper lethal thermal limits involve continuous exposure of the target organism to constant lethal temperatures for a time period long enough to achieve significant mortality. The zone of resistance, within which there is a strong interaction between temperature and exposure time, lies outside the tolerance temperatures.

The upper boundary of the resistance zone is represented by the acute upper lethal temperature. Susceptibility of an organism to the upper lethal thermal limit is dependent upon the acclimation

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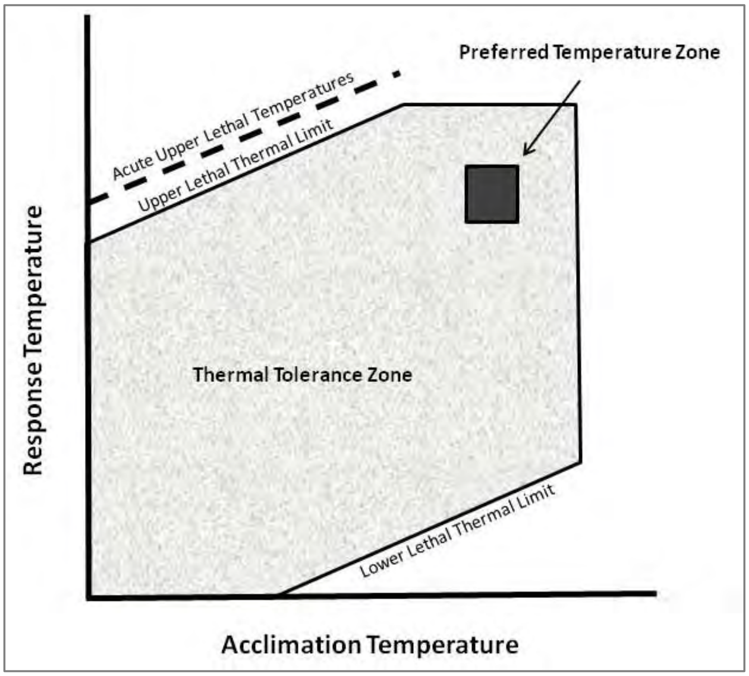
[1] For a complete list of the 39 specific ANS of Concern – CAWS, please see Table 1 of the main report.

temperature and the previous thermal history of the organism (Reynolds & Casterlin 1979; Jobling 1981).



Adapted from: Journal of Fish Biology: 19 439-455, Jobling, M.

Diagram showing temperature relations of fish

Operationally, this implies that, to achieve lethal temperatures in the CAWS, there is a need for hotter water in the summer than in the winter. Lower thermal limits are not discussed in this fact sheet because they are unachievable in the CAWS due to widespread thermal inputs during the winter months.

Hot water can be used to achieve acute upper lethal temperatures for a variety of species..

Thermal Tolerance of Various Non-native Species in the Great Lakes and Mississippi River Basins

		Temperature			
Species	**Size or Age**	**Acute Upper Lethal**	**Upper Avoidance**	**Preferred**	**Reference**
Alewife (*Alosa psuedoharengus*)	Large	-	71.6 °F (22 °C)	-	Coutant
coho salmon (*Oncorhynchus kisutch*)	Adult	-	-	57.2 - 62.6 °F (14 - 17 °C)	Brown
common carp (*Cyprinus carpio*)	Large	-	94.1 °F (34.5 °C)	84.4 - 89.4 °F (29.1 - 31.9	Gammon
grass carp (*Ctenopharyngodon idella*)	Adult	100 °F (38 °C)	-	-	Federenko & Fraser
skipjack herring (*Alosa chrysochloris*)	Adult	-	84.2 °F (29 °C)	78.8 - 83.3 °F (26 - 28.5 °C)	Gammon
spiny waterflea (*Bythotrephes longimanus*)	Adult	110 °F (43 °C)	-	-	Beyer et al.
zebra mussel (*Dreissena polymorpha*)	Adult	104 °F (40 °C)	-	-	McMahon et al.

Beyer et al. (2011) found that a water temperature of 110 °F (43 °C) was necessary to kill the spiny waterflea (*Bythotrephes longimanus)*. Grass carp, a close relative of the silver, bighead, and black carps, cannot tolerate temperatures greater than 100 °F (38 °C) (Federenko & Fraser 1978). Zebra mussel mortality occurs at 104 °F (40 °C) (McMahon et al. 1995).

Thermal shock can occur under natural conditions, however it is most frequently observed as a result of changes in thermal effluents from power generation and production industries and at various water control projects. Thermal shock can occur when aquatic organisms are rapidly subjected to temperature changes greater than 18 °F (10 °C) of acclimation temperature (Coutant 1977; Donaldson et al. 2008). Depending upon the degree of shock, the organism may react with instantaneous or delayed mortality. Thermal shock is a potential threat only to those fish resident and acclimated to temperatures in the thermal plume, and has no effect on fish outside of the plume, including those migrating through the system (USEPA 2008).

Prior Applications:

Pressurized Hot Water/ Steam Treatments – There are a variety of application methods for applying hot water to control ANS. The most direct is to spray heated water or steam directly onto the species of concern using a pressure nozzle. This technique is commonly used to kill zebra and quagga mussels at municipal and industrial facilities. High pressure hot water spray is used to clean ANS off of recreational boats at cleaning stations by the Tahoe Resource Conservation District (Jonelle Bright, Tahoe Resource Conservation District, telephone communication, 2011). Hot water and steam are commonly used in the food and medication industry to sterilize equipment (autoclaving), purify water (boiling), and preserve foods (pasteurization) to destroy harmful microorganisms. These methods are intended to treat small objects, equipment, and structures but are impractical for treating flowing waters.

Hot Water Thermal Barrier – This type of control has been proposed for the CAWs because of the availability of existing sources of heated industrial water in the vicinity. The United States Environmental Protection Agency (USEPA) commissioned a study of the existing conditions of water temperature in the CAWS and their effect on non-indigenous species. The report concluded that current thermal conditions in the CAWS present a very small obstacle (1-12%) to passage of approximately half of the non-indigenous species considered. Warm temperatures which would impede movement occur only in the summer months, leaving nine (9) months for completely unimpeded passage. The report identified the Lockport region with the highest water temperatures and thus the greatest temperature barrier to fish movement (USEPA 2008). A hot water thermal barrier would also require downstream cooling to restrict the length of the heat zone.

General Effectiveness: Lethal water temperature can be 100% effective in preventing ANS transfer when ANS are exposed to the correct temperatures for the appropriate duration. Sub-lethal water temperatures are an attractant to many species, particularly in the fall, winter, and spring.

Pressurized Hot Water/ Steam Treatments – This Control is very effective for treating small objects, equipment, and structures.

Hot Water Thermal Barrier – This method was previously examined by a report from Midwest Generation in the CAWS (USEPA 2008). Most industrial sources would find it difficult to generate a thermal load to the receiving water that would ensure that t lethal zone would be maintained to allow sufficient exposure time. For some industrial facilities, it may be possible to establish a thermal barrier in the summer, but for most it would be impossible in the winter due to the increase in thermal load that would be necessary to result in lethal water temperatures. Where ANS are mobile and able to preferentially avoid or seek a thermal plume, this control will not have the desired effect and ANS could pass the barrier in the winter months.

Operating Constraints: The temperatures necessary to create lethal zones in the waterbody would also be at levels that would represent significant danger to human health. Establishing a zone of lethal impact with sufficient exposure time would require initial temperatures well in excess of those that could cause 3rd degree burns within seconds on human skin. Additionally, temperatures that would be sustained in order to kill invasive species (around 110 °F) can cause second degree burns in approximately 10 minutes.

Controls that kill plants, algae, and other microorganisms have the potential to greatly alter downstream food webs through increased biological oxygen demand, elimination of the base food chain, and can result in significant changes to the quantity and quality of aquatic food resources for macro-invertebrates and fishes. The downstream impact will depend upon the severity, duration, and frequency of alteration to these important resources for each Control.

Maintaining temperature and exposure time in the CAWS would be a significant challenge due to: widely fluctuating flow velocities driven by wet vs. dry weather, inconsistent flow direction, including reverse flows, driven by storm surges, density currents, and flat gradients; and sporadic and significant re-suspension of dissolved oxygen demanding sediments, due to watercraft activity and abrupt changes in flow velocity.

Hot water from industrial sources would need to be supplied on a continuous basis and be adequately mixed throughout the water column. The thermal tolerance of all life stages of an organism must also be considered; many aquatic plants can tolerate a wide range of temperatures, especially in the seed stage (Lacoul & Freedman 2006). Regulatory agencies would need to be contacted to determine an approach to conduct this activity in accordance with regulatory requirements.

Cost Considerations:

Implementation: Implementation costs for this Control would vary depending on the system implemented. Each system would require a means of heating water or a source of hot water, such as a neighboring industrial source. A distribution and mixing component would also be necessary to ensure the required temperature is reached throughout the water column.

Planning and design activities in the implementation phase may include research and development of this Control, modeling, site selection, site-specific regulatory approval, plans and specifications, and real estate acquisition. Design will also include analysis of this Control's impact to existing waterway uses including, but not limited to, flood risk management, natural resources, navigation, recreation, water users and dischargers, and required mitigation measures.

Operations and Maintenance: Operations and maintenance costs would vary with the technique selected for heating and mixing water. An effectiveness monitoring program would be required.

Mitigation: Design and cost for mitigation measures required to address impacts as a result of implementation of this Control cannot be determined at this time. Mitigation factors will be based on site-specific and project-specific requirements that will be addressed in subsequent, more detailed, evaluations.

Citations:

Beitinger, T. L., Bennett, W. A. & McCauley, R. W. 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. *Environmental Biology of Fishes* vol. 58, pp. 237–275.

Beyer J, P., P. B. Moy, & B. De Stasio. 2011. Acute upper thermal limits of three aquatic invasive invertebrates: hot water treatment to prevent upstream transport of invasive species. *Environmental Management*, vol. 47(1), pp. 67-76

Bright, J. November 21, 2011. Telephone communication. Tahoe Resource Conservation District, Watercraft Inspection Program. jbright@tahoercd.org) (530) 543-1501 ext 112.

Brown, H.W. 1974. Handbook of the Effects of Temperature on Some North American Fishes. American Electric Power Service Corp., Canton, OH. 524 pp.

Coutant, C.C. 1977. Compilation of temperature preference data. Journal of the Fisheries Research Board of Canada vol. 34:739-745.

Cranshaw, L.I. 1977. Physiological and behavioral reactions of fishes to temperature change. Journal of the Fisheries Research Board of Canada, vol. 24 pp 730-734.

Donaldson, M.R., S.J. Cooke, D.A. Patterson, & J.S. Macdonald. 2008. Review paper, cold shock and fish. Journal of Fish Biology, vol. 73, pp 1491-1530

Federenko, A, and F.J. Fraser. 1978. Review of grass carp biology. Interagency Committee on Transplants and Introductions of Fish and Aquatic Invertebrates in British Columbia. British Columbia, Department of Fisheries and Environment, Fisheries and Marine Service. Technical Report 786. 15pp

Gammon, J. R., 1973. The effects of thermal inputs on the populations of fish and macroinvertebrates in the Wabash River. Purdue University, Indiana Water Resources Research Center, Technical Reports. Paper 32.

Jobling, M. 1981. Temperature tolerance and the final preferendum-rapid methods for the assessment of optimum growth temperatures. *Journal of Fish Biology*, vol. 19, pp 439-455

Lacoul, P. & B. Freedman. 2006. Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews.* vol. 14, pp. 89-136

McMahon, R.F., M.A. Matthews, T. A. Ussery, R. Chase, & M. Clarke. 1995. Studies of heat tolerance of zebra mussels: effects of temperature acclimation and chronic exposure to lethal temperatures. U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, MS.

Reynolds, W.W. & M.E. Casterlin. 1979. Behavioral thermoregulation and the “Final Preferndum” paradigm. *American Zoologist*, vol. 19 (1), pp 211-224

U.S. Environmental Protection Agency (USEPA). 2008. Non-indigenous species migration through the Chicago Area Waterways (CAWS): Comparative Risk of Water Quality Criteria. U.S. EPA Office of Science and Technology, Washington D.C.

Wismer, D.A. and A.E. Christie. 1987. Temperature relationships of Great Lakes fishes: a data compilation. Great Lakes Fisheries Commission Special Publication 87-3. 165 p.

Environmental Biology of Fishes Vol. 12, No. 4, pp. 309–314, 1985
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Temperature preference and tolerance of hybrid carp (female grass carp, *Ctenopharyngodon idella* × male bighead, *Aristichthys nobilis*)

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Keywords: Thermal gradient, Acclimation temperature, Thermal preferendum, Gravitate, Exploratory behavior, Ultimate upper incipient lethal temperature

Synopsis

Hybrid carp, acclimated at three temperatures, were tested for temperature preference in a laboratory gradient tank. There was no relationship between the acclimation and acute preferred temperatures. After a 10-day period of exploration, irrespective of acclimation temperature, all the hybrids gravitated to a final thermal preferendum of 29° C. In the temperature tolerance test the ultimate upper incipient lethal temperature, (TL50), was estimated as 39.2° C.

Introduction

Temperature is a very important ecological factor influencing various life processes of fish. A knowledge of interaction between fish and their thermal environment enhances our understanding of fish distribution, metabolism and growth. This knowledge is essential if one is interested in introducing a fish species into new habitat and even more so if the species in question is an artificially produced hybrid. Recently an intergeneric triploid hybrid was developed by crossing female grass carp, *Ctenopharyngodon idella* and male bighead carp, *Aristichthys* (*Hypophthalmichthys*) *nobilis* (Marian & Krasznai 1978). This hybrid is currently produced on a large scale basis in Arkansas for use as a biological weed control agent. Little is known of the ecology of this fish with the exception of food habits (Kilambi & Zdinak 1980, 1982, Cassani 1981) and early developmental stages (Kilambi & Zdinak 1981). This paper reports on the temperature preference and ultimate upper incipient lethal temperature of the hybrid carp.

Materials and methods

The temperature preferendum experiment was conducted in a horizontal gradient tank (673 cm long × 66 cm wide × 36 cm deep) filled with 666 l of water. The gradient tank was divided into six compartments by plexiglass partitions with each partition having an opening (15.5 × 13.5 cm) that could be closed by a sliding plexiglass plate. The thermal gradient was static, and was maintained by the placement of a variable number of 150 and 200 watt immersion heaters in the compartments and a cooling coil at one end of the tank. Each compartment was aerated by air stones to supply oxygen and to prevent thermal stratification. Preliminary observations indicated that a relatively uniform gradient existed in each compartment except occasionally in the area in or immediately adjacent to the intercompartmental openings. Changes in air temperature, water level fluctions, or deposit build-up on the immersion heaters could change conditions such that a steep gradient could develop temporarily in an intercompartmental opening. Water temperatures were measured at least 4 cm away from the openings when determining the mean water temperature of each compartment.

The triploid hybrids used in this study were obtained from Malone's Fish Hatchery, Lonoke, Arkansas in April and were maintained under a 12-h photoperiod by flourescent lights during the course of the study. Twenty-one juvenile fish (average total length and weight, 186.8 mm; 59.7 g) were individually marked by numbered anchor tags over one month prior to testing in the gradient. Three groups of six, seven, and eight hybrids were acclimated for two weeks at 31° C, 27° C, and 22° C in three compartments of the gradient tank that were separated by wire screens over the intercompartmental openings. At the end of the acclimation period, on 11 July 1982, the wire screens were removed to allow free movement of the hybrids in the gradient tank. At 24-h intervals around 1500 CST, the openings in the intercompartmental partitions were covered and the presence of fish and water temperatures in each of the compartments were recorded. The temperature preferendum experiment was conducted for 22 days employing the gravitational method. Due to the extended length of the study period, each of the compartments was provided daily with approximately 100 g of water cress, *Nasturtium* sp., as a surplus ration for the

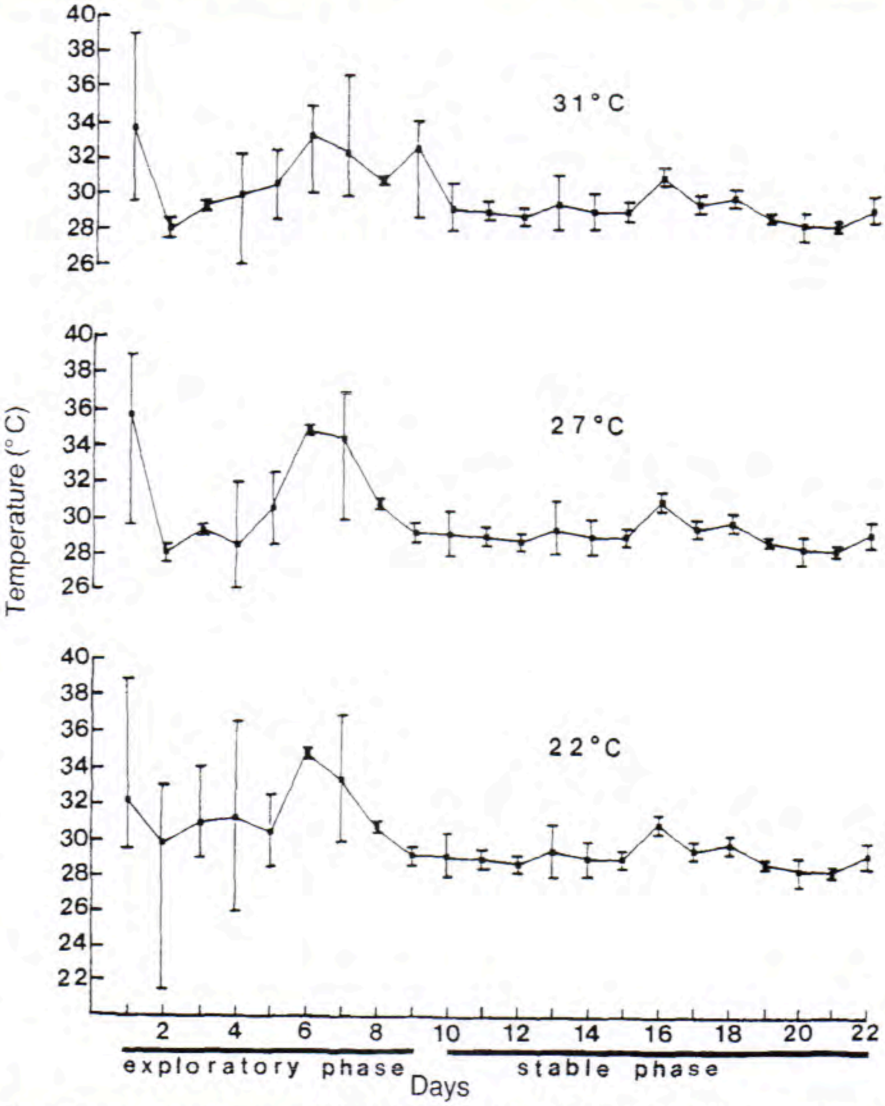

Fig. 1. Daily mean and range of preferred temperature for hybrid carp in a thermal gradient.

fish. Feeding did not appreciably reduce water clarity and fish could be clearly observed throughout the study. Uneaten plant remains were removed and water was added periodically to make up for evaporative loss.

After the completion of the thermal preferendum experiment, seven hybrid carp (average total length and weight, 171.5 cm, 37.4 g) were acclimated at 29° C for three days in a glass tank (89 cm long × 46 cm wide × 51 cm deep) with 166 l of water and aerated with air stones. The water temperature was raised by the addition of hot water and was maintained thermostatically. Initially, temperature was raised by 2° C per day up to 35° C, which corresponded to the mean maximum temperature encountered by the hybrids during the exploratory phase (Fig. 1). Thereafter, water temperature was raised by 1° C per day increments. At each of the test temperatures, the fish were observed for 24 h for occurrence of mortalities. Criteria for death were the cessation of body, fin, and opercular movements.

The upper ultimate incipient lethal temperature (Cocking 1959) was estimated by graphical interpolation at which 50% of the test stock died. During the temperature tolerance test a small amount of water cress was provided for approximately one hour after raising the test temperature.

Results

Temperature preference

In the 12 July observations, seven fish (one, four, and two fish of the 22° C, 27° C and 31° C acclimation groups, respectively) were noted in the compartment at 38.7° C, the highest temperature available in the gradient tank. Of these, three of the 27° C and two of the 31° C acclimated fish died soon after handling to check for tag numbers while the other two hybrids survived for the remainder of the experiment. Furthermore, four fish (one each from 27° C and 31° C, and two from the 22° C acclimation groups) were in the compartment at 34.8° C. When the intercompartmental doors were opened after checking the other compartments, a number of fish darted into the 38.7° C compartment and exhibited signs of stress. These fish were guided into cooler compartments but three fish died soon after. Of the eight hybrids that died due to a combination of handling and heat stress, three each were from the 31° C and 27° C, and two from the 22° C acclimation groups. Handling of the fish was subsequently reduced or avoided especially in the warmer water compartments. Fish were not handled after the 10th day of the experiment since the hybrids schooled and moved as a unit.

On the second day of the study, one fish acclimated at 22° C was observed in the 21° C compartment. From the third day onwards, all fish were recorded in the gradient above 26° C. Figure 1 shows the daily mean temperature preference for each of the three acclimation groups. During the first nine days, the mean daily preferred temperature varied widely from 28° C to 35° C, indicating an exploratory behavior of the hybrids while they sampled various temperatures prior to the selection of the final thermal preferendum. The fish generally moved as individuals at the beginning of the exploratory phase but schooling behavior became more evident as time progressed.

By the 10th day, all the hybrids of the three acclimation groups gravitated to the final thermal preferendum (Fig. 1). During the 13 day (10th through 22nd day) stable phase the daily preferred mean temperature was between 28° C and 30° C

Table 1. Frequency of occurrence of hybrid carp in the thermal gradient.

Temperature (° C)	Frequency of occurrence (%)	
	Exploratory phase	Stable phase
21	0.8	–
27	3.3	–
28	6.6	30.6
29	16.5	61.9
30	33.9	–
31	6.6	7.5
32	3.3	–
33	2.5	–
34	14.9	–
36	5.8	–
38	5.8	–

except on the 16th day when it was 31° C. On this day the 28° C to 30° C temperature range was not distinctly available in the gradient, (i.e. confined to a limited area near the intercompartmental opening) and the hybrids gravitated to the 31° C compartment rather than the available 27° C compartment. The mean preferred temperature during the stable phase was 29.2° C with no difference between the three acclimation groups.

The three acclimation groups showed similar frequency distributional patterns in the gradient during the exploratory period hence the data were pooled. The pooled frequency of occurrence had a bimodal distribution with a major mode at 30° C and a minor mode at 34° C (Table 1). During the stable phase the hybrids moved as a school with a single mode at 29° C representing the final thermal preferendum.

Temperature tolerance

Mortalities at various test temperatures in each 24-h period were recorded, the first mortality occurring at 37° C. Once the fish exhibited loss of equilibrium, death occurred within 1.5 h. The ultimate upper incipient lethal temperature (TL50) was estimated as 39.2° C by graphical interpolation. The single fish that survived to 41° C died 8 h and 50 min later.

The observed normal feeding activity of entering vegetation clumps, and tearing loose and consuming plant material, was reduced at 35° C. Above 35° C normal feeding behavior was not observed, however they would strike, rarely, at loose pieces of vegetation in the water column, most of which were rejected. It was observed that at 35° C the school was less cohesive and at 37° C schooling behavior was not evident.

Discussion

Due to the extended nature of the thermal preference test, each of the compartments was provided daily with equal amounts of water cress. Since all compartments in the gradient tank had the same amount of food, food availability probably had little effect on the test results.

It was reported that preferred temperatures increased with increase in acclimation temperatures (Ferguson 1958, Cherry et al. 1977, Richards & Ibara 1978), but the hybrids of this study showed no such relationship with the 22° C and 27° C acclimated fish selecting a higher mean acute temperature than the 31° C fish during the exploratory phase (Fig. 1). This could be characteristic of the hybrid carp or the range of acclimation temperatures is too narrow to differentially influence this hybrid of subtropical species. After the 10-day exploratory phase, all the hybrids, irrespective of thermal acclimation, gravitated to a modal preferred temperature of 29° C. This indicates that extended test periods may be necessary to establish the final thermal preferenda for some species of fish.

Initially, during the exploratory phase, the hybrids explored temperatures higher than their final thermal preferendum. Some of the fish that entered the warmest compartment (38.7° C) on the first day of the experiment died due to a combination of handling and heat stress as it was close to their upper ultimate incipient lethal temperature (39.2° C). Such responses have previously been attributed to low thermal responsiveness (Meldrim & Gift 1971, Beitinger & Magnuson 1976), novel, stressful laboratory environments (Kleerekoper et al. 1974, Reynolds 1977) and to an overshoot during gravitation to the final preferendum (Badenhuizen 1967).

Low thermal responsiveness is a phenomenon reported for temperate species acclimated to late fall and winter water temperatures, which fail to avoid stressful warm temperatures in a thermal gradient. It has been suggested that this response is due to a behavioral acclimation mechanism whereby the fish will select warmer temperatures nearer the final thermal preferendum faster than they can physiologically adapt to them (Beitinger & Magnuson 1976, Richards et al. 1977). On the first day of the experiment 52% of the hybrids were in the compartments with stressful water temperatures, equal to or above 35° C, as judged by the loss of school cohesiveness and reduced feeding during the temperature tolerance test. However, since the acclimation temperatures of the hybrids were near or above the spawning temperatures of the parental species (Kuronuma 1958, Martino 1974) and the temperatures initially explored were well above the final thermal preferendum, the low thermal responsiveness phenomenon is not applicable to these hybrids. The exploration of higher temperatures in the gradient by the hybrids was probably a response to the novel laboratory environment and an overshoot during gravitation to the final thermal preferendum. The hybrids avoided temperatures above 35° C after the first day of exploration in the gradient and subsequently gravitated to their final thermal preferendum of 29° C, indicating that the initial exploration of stressful high temperatures and subsequent habituation increased the precision of thermoregulatory responses of the hybrids. The ability to perceive fine thermal gradients after environmental stress was suggested by Brett (1956).

During the temperature tolerance test the hybrids were provided with feed for limited periods of time. This is not a standard procedure as it is possible for feeding to increase respiratory stress due to assimilation costs which can lower the lethal temperature (Fry 1971). The hybrids' normal feeding behavior was altered at 35° C and above this temperature the feed ingested was minimal and probably did not significantly increase respiratory stress. Both feeding and schooling behavior were first affected at 35° C, indicative of thermal stress.

Fish exposed to slowly increasing temperature can acclimate to the new temperature somewhat, while no acclimation is possible when temperature rises quickly (Cocking 1959). Since the hybrids of this study were exposed to slowly increasing test temperatures, the estimated ultimate upper incipient lethal temperature may be higher than if the fish were subjected to instantaneous exposure to higher test temperatures. Although some researchers use direct transfer of fish to various temperatures in calculating incipient lethal temperatures, exposure of fish to slowly increasing temperatures without handling them is appropriate because in a body of water temperature rises slowly due to the high heat capacity of water.

References cited

Badenhuizen, T.R. 1967. Temperatures selected by *Tilapia mossambica* (Peters) in a test tank with a horizontal temperature gradient. Hydrobiologia 30: 541–554.

Beitinger, T.L. & J.J. Magnuson. 1976. Low thermal responsiveness in the bluegill, *Lepomis macrochirus*. J. Fish. Res. Board Can. 33: 293–295.

Brett, J.R. 1956. Some principles in the thermal requirements of fishes. Quart. Rev. Biol. 31: 75–87.

Cassani, J.R. 1981. Feeding behavior of underyearling hybrids of the grass carp, *Ctenopharyngodon idella*, female, and the bighead, *Hypophthalmichthys nobilis*, male, on selected species of aquatic plants. J. Fish Biol. 18: 127–133.

Cherry, D.S., K.L. Dickson, J. Cairns Jr. & J.R. Stauffer. 1977. Preferred, avoided, and lethal temperatures of fish during rising temperature conditions. J. Fish. Res. Board Can. 34: 239–246.

Cocking, A.W. 1959. The effects of high temperatures on roach (*Rutilus rutilus*). II. The effects of temperature increasing at a constant rate. J. Exp. Biol. 36: 217–226.

Ferguson, R.G. 1958. The preferred temperature of fish and their midsummer distribution in temperate lakes and streams. J. Fish. Res. Board Can. 15: 607–624.

Fry, F.E.J. 1971. The effects of environmental factors on the physiology of fish. pp. 1–98. *In:* W.S. Hoar & D.J. Randall (ed.) Fish Physiology, Academic Press, New York.

Kilambi, R.V. & A. Zdinak. 1980. Food preference and growth of grass carp, *Ctenopharyngodon idella*, and hybrid carp, *C. idella* female x *Aristichthys nobilis* male. pp. 281–286. *In:* Proc. V Int. Symp. Biol. Contr. Weeds. Brisbane, Australia.

Kilambi, R.V. & A. Zdinak. 1981. Comparison of early developmental stages and adults of grass carp, *Ctenopharyngodon idella*, and hybrid carp (female grass carp × male bighead, *Aristichthys nobilis*). J. Fish Biol. 19: 457–465.

Kilambi, R.V. & A. Zdinak. 1982. Food intake and growth of hybrid carp (female grass carp, *Ctenopharyngodon idella* × male bighead, *Aristichthys* (*Hypophthalmichthys*) *nobilis*) fed on zooplankton and *Chara*. J. Fish Biol. 21: 63–67.

Kleerekoper, H., J. Matis, P. Gensler & P. Maynard. 1974. Exploratory behavior of goldfish *Crassius auratus*. Anim. Behav. 22: 124–132.

Kuronuma, K. 1958. Spawn taking of Chinese carp in Tone River, Japan. Indo Pacific Fish. Counc. Curr. Affairs Bull. 22: 1–3.

Marian, T. & Z. Krasznai. 1978. Karyological investigations on *Ctenopharyngodon idella* and *Hypophthalmichthys nobilis* and their crossbreeding. Aquacultura Hungarica (Szarvas) 1: 44–50.

Martino, K.V. 1974. Natural reproduction of *Ctenopharyngodon idella* (Valenciennes) in the lower Volga waters. Hydrobiol. J. 10: 91–93.

Meldrim, J.W. & J.J. Gift. 1971. Temperature preference, avoidance and shock experiments with estuarine fishes. Ichthyol. Assoc. Bull. 7. 75 pp.

Reynolds, W.W. 1977. Temperature as a proximate factor in orientation behavior. J. Fish. Res. Board Can. 34: 734–739.

Richards, F.P., W.W. Reynolds & R.W. McCauley (ed.) 1977. Temperature preference studies in environmental impact assessments: an overview with procedural recommendations. Panel discussion. J. Fish. Res. Board Can. 34: 752–754.

Richards, F.P. & R.M. Ibara. 1978. The preferred temperature of the brown bullhead, *Ictalurus nebulosus*, with reference to its orientation to the discharge canal of a nuclear power plant. Trans. Amer. Fish Soc. 107: 288–294.

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1614

Effects of Cold Shock on Vulnerability of Juvenile Channel Catfish (*Ictalurus punctatus*) and Largemouth Bass (*Micropterus salmoides*) to Predation

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Coutant, C. C., H. M. Ducharme Jr., and J. R. Fisher. 1974. Effects of cold shock on vulnerability of juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) to predation. J. Fish. Res. Board Can. 31: 351–354.

Acute cold stress caused increased predation on juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) by unstressed adult largemouth bass when temperature differentials were 9 and 7 C or more, respectively, (base temperatures 16 and 17 C). Predation rate tended to increase exponentially with increasing temperature differential. Catfish held 1 h in the cold water were only slightly less susceptible to predation than were others tested immediately after the temperature change.

Coutant, C. C., H. M. Ducharme Jr., and J. R. Fisher. 1974. Effects of cold shock on vulnerability of juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) to predation. J. Fish. Res. Board Can. 31: 351–354.

Un stress aigu par le froid entraîne une prédation accrue sur les jeunes barbues de rivière (*Ictalurus punctatus*) et achigans à grande bouche (*Micropterus salmoides*) par des achigans adultes non soumis à un tel stress, lorsque les différences de température sont de 9 et 7 C ou plus, respectivement (par rapport à des températures de base de 16 et 17 C). Le taux de prédation augmente exponentiellement avec l'augmentation de la différence de température. Les barbues maintenues pendant 1 h dans l'eau froide ne sont que légèrement moins vulnérables à la prédation que les autres qui sont soumises aux essais immédiatement après le changement de température.

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In this study, we sought to determine if sublethal abrupt decreases in temperature would measurably increase the susceptibility of juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) to predation by adult largemouth bass. Mortalities have been reported from cold shocks to fish living in, and metabolically acclimated to, warm discharge waters of thermal electric power stations (Michigan Water Resources Commission unpublished data; Pennsylvania Fish Commission unpublished data; Williams et al. 1971; U.S. Atomic Energy Commission 1972). Deaths have occurred when the heat source was suddenly terminated, when the thermal plume was rapidly dispersed by winds or currents, or when temperature at the plant intake dropped rapidly. Natural temperature drops, such as in the Great Lakes in summer when winds shift the epilimnion and cause upwelling of cold hypolimnetic water, have caused cold kills (Emery 1970).

To adequately regulate power plant shutdown to protect aquatic life, the tolerable thermal decreases must be known, not only for direct death, but for sublethal stresses that may markedly decrease long-term survival. The experiments reported here simulate field conditions where juvenile fishes that have resided in a warmed area long enough to become acclimated to the high temperatures disperse into the surrounding waters when the heated discharge terminates. The small fishes then encounter predators that have not themselves experienced the temperature drop. Both largemouth bass and channel catfish are warmwater fishes that are known to be attracted to warm discharges when ambient water is cool (e.g. Trembley 1965). We did not study the equally valid question of simultaneous cold shock of predators and prey.

Materials and methods — These experiments tested the relative survival of cold-shocked and unshocked prey when groups of the two were offered simultaneously to adult largemouth bass and about half of the combined number were allowed to be eaten. The protocol was modified from that reported by Bams (1967) and Coutant (1973). Juvenile fish from a com-

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mon stock were randomly separated into groups, differentially marked, and held for more than 1 wk in 90-liter aquaria: one for each of several warm temperatures (Table 1) and others for control (unshocked) fish held at the same temperature as the predators. The fish were marked with a liquid nitrogen cold-branding technique (Coutant 1972), test fish on one side and control fish on the other. To provide simultaneous addition of test and control fish to the predator tank (17 C for bass, 16 C for catfish), groups of 15 catfish and 20 bass from an acclimation temperature and the predation temperature were combined in a 9-liter plastic pail at the predation temperature. In some tests, the acclimated fish were held at the predation temperature for 1 h prior to mixing with control fish (to test for possible recovery from the initial cold shock or progressive debilitation by cold). In tests without a holding period, the contents of the pail (fish and water) were added within 15 s to the predator tank.

Predation took place in 1.2-m-diam cylindrical fiberglass tanks with water depths of 65 cm. There were no structures other than inlet pipe, center outflow standpipe, and tank walls and bottom to provide protection for the prey. There were three or four predators per tank.

TABLE 1. Mean survival proportions for juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) acclimated to various temperatures and preyed on by adult largemouth bass at 16 and 17 C, respectively.

Acclimation Temp (*C*)	Survival proportion	
	Test	Control[a]
Channel catfish, no holding		
16	0.60(4)[b]	0.60
20	0.70(2)	0.56
22	0.67(2)	0.73
25	0.40(3)	0.82[c]
30	0.33(3)	0.87[c]
34	0.09(3)	0.96[c]
Channel catfish, 1-h holding		
22	0.65(3)	0.47
25	0.30(2)	0.70[c]
30	0.40(3)	0.80[c]
34	0.20(3)	0.89[c]
Largemouth bass, no holding		
17	0.48(3)	0.55
20	0.65(3)	0.52
24	0.44(4)	0.61[c]
30	0.05(3)	0.75[c]

[a] A fish held at predation temperature.

[b] Numbers of replicates; 15 catfish and 20 bass per replicate.

[c] Difference from equal numbers of survivors significant at $P < 0.05$.

After introduction of the prey, predators were allowed a maximum of 0.5 h to eat approximately 50% of the prey fish, at which point survivors were removed and test and control fish were counted. Length and weight determinations were made on channel catfish to determine if size was an important factor in the results. Predation for more than 0.5 h was undesirable since recovery from the initial shock or progressive debilitation by cold would be unaccounted for. Surviving prey were not used in subsequent tests. Surviving catfish were held at the control temperature for 1 mo or longer to observe any direct mortality of the test fish.

The statistic used to express the difference in predation rates on the two groups of fish is the ratio $d_p = i_1/i_2$ (Bams 1967), where i_1 and i_2 are, respectively, the instantaneous mortality rates of the test and control groups. The instantaneous mortality rate when time is a unit interval is given by $i = -\log_e s$, where s = survival proportion (i.e. number at finish divided by number at start). Group d_p was calculated for replicates by summing the numbers s. The chi-square analysis was used to test for homogeneity among replicate trials and for significance of observed differences in predation.

Both juvenile largemouth bass and channel catfish were obtained from the U.S. Fish and Wildlife Service, Frankfort National Fish Laboratory, Frankfort, Kentucky. They were maintained for several weeks in our laboratory to recover from stresses of transportation. At time of testing, bass averaged 47.8 ± 5.07 (SD) mm and 1.13 ± 0.41 g, and catfish averaged 75.0 ± 7.90 mm and 3.05 ± 0.64 g. Predator bass, 500–1300 g, were captured by electrofishing from nearby Clinch River (Watts Bar Reservoir) and maintained in laboratory tanks for several months prior to the tests.

Temperatures in all tanks were maintained within ±0.2 C of desired temperatures (Table 1) with temperature controllers attached to 1000-W quartz rod heaters. A flow of about 0.5 liter/min passed through each tank continuously. Artificial lighting was maintained in a 12-h photoperiod.

Results — Channel catfish and largemouth bass fed to predators immediately after a temperature decrease were preyed upon in greater numbers ($P < 0.05$) than controls when the decrease was 9 and 7 C, or more, respectively, (Table 1). Channel catfish held for 1 h at the predation temperature before predation were less susceptible than those immediately exposed, although they were still preyed upon in significantly greater numbers after a 9 C temperature decrease.

The ratios of instantaneous predation rates tended to increase above 1 when the temperature change exceeded about 6 C (Fig. 1). Thereafter the increase tended to be exponential. There was also a consistent tendency ($P > 0.05$) for d_p ratios to be less than 1 after the test fish received temperature decreases less than about 6 C.

Surviving catfish from both test and control groups were similar in length to the stock fish (74.8 ± 0.64, 75.3 ± 0.64, and 75.0 ± 0.79, respectively). There was no statistical difference ($P > 0.05$).

Catfish that survived predation were held for several weeks at 16 C without direct mortality. Those which had been acclimated to 34 C, however, showed behavioral signs of stress (e.g. sluggishness, erratic swimming) that lasted for at least 24 h.

Discussion — These experimental results have shown statistically, or exhibited trends that strongly suggest, a progression of cold stress effects on young channel catfish and largemouth bass with increasing temperature differential. Most clearly, there is a debilitation of catfish and bass at differentials of 9 and 7 C or more, respectively, that decreases their ability to survive predation.

The trends indicate that tolerance may be surpassed when the differential is in the vicinity of 6 C (for base temperatures of 16 or 17 C). Although statistical significance of differences at $P = 0.05$ were not attained until larger differentials than this were reached, there is no assurance that ecological significance corresponds with the 0.05 probability level. Further experimentation, particularly with additional replicates, would be necessary to establish the exact differential that would first give statistical significance. Much more research, involving discrete field populations of catfish and bass, would be required for accurate estimation of ecologically significant levels of predation.

The pattern of response to increasing stress from temperature change in these experiments (i.e. a possible enhancement of survival relative to controls by small changes and a rapidly increasing relative susceptibility to predation with progressively larger differentials) is similar in form to responses shown to heat stress (Coutant 1973). The similarity may derive from similar behavioral and physiological manifestations of stress that affect the sequence of events leading to prey capture. The effects of temperature decrease seemed to range from stimulation by contact with the cold water to depression of the

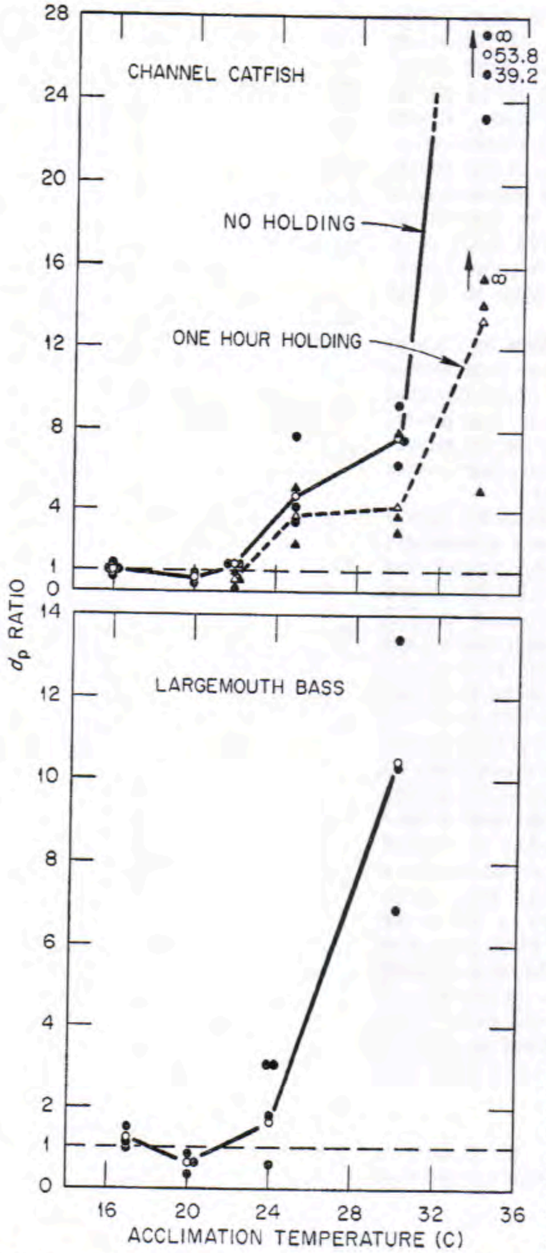

FIG. 1. Ratios of experimental instantaneous predation rates (d_p) for juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) acclimated to various temperatures and preyed on by adult largemouth bass at 16 and 17 C, respectively. Both species were preyed on immediately after instantaneous transfer from the acclimation temperature to the predation temperature, and catfish also after 1-h holding at 16 C. Solid characters represent individual tests; open characters, combined replicates. A d_p ratio of 1 indicates identical susceptibilities of cold-shocked and unshocked (control) fish to predation.

1614

fish into a cold coma as was seen by Brett (1956). After small temperature decreases, all fish swam vigorously in the predation tank. After larger temperature decreases, shocked fish rested on the bottom in an apparently "benumbed" state, whereas control fish avoided predators and sought refuge at the perimeter of the tank's surface. In heat shock, there was also a period of reduced responsiveness even before the fish obviously lost equilibrium (Coutant 1973). Recovery from cold coma must be gradual, because tests after 1 h showed only slightly reduced effects compared with those for immediate predation.

Similarity in responses to cold stress by channel catfish and largemouth bass in these experiments corresponds well with other similarities reported in the literature. The two species are warmwater fishes with similar optimum temperatures for growth (Strawn 1961, 1970) and similar lethal temperatures (Hart 1952; Allen and Strawn 1967).

The minimum decrease in temperature that clearly increased predation on catfish in these experiments (9 C) is considerably less than the temperature decrease necessary for direct death. This was shown when fish acclimated to 34 C were placed in 16 C water without mortalities (although behavioral signs of stress lasted several hours). Hart (1952) showed that channel catfish adults could be cooled from as high as 25 C to 0 C without 50% mortality.

The most critical time for abrupt thermal decreases at power plants that would kill fish would likely be in winter when the base temperature would be near 0 C rather than in the 16–17 C range studied here. The importance of selective predation on stressed juveniles could be less then, however, because many young would have attained larger size. Large predators could also be less active in the winter months. The base temperatures used here may reasonably approximate those conditions in summer and fall when increased predation on juveniles of certain species could be an important power plant impact. The losses would go unnoticed in pollution control inspections since no carcasses would remain to identify the incidents.

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Allen, K. O., and K. Strawn. 1967. Heat tolerance of channel catfish. Proc. 21st Annu. Conf. S.E. Assoc. Game Fish Comm. 399–411.

Bams, R. A. 1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. J. Fish. Res. Board Can. 24: 1117–1153.

Brett, J. R. 1956. Some principles in the thermal requirements of fish. Q. Rev. Biol. 31: 75–87.

Coutant, C. C. 1972. Successful cold branding of non-salmonids. Prog. Fish-Cult. 34: 131–132.

1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. J. Fish. Res. Board Can. 30: 965–973.

Emery, A. R. 1970. Fish and crayfish mortalities due to an internal seiche in Georgian Bay, Lake Huron. J. Fish. Res. Board Can. 27: 1165–1168.

Hart, J. S. 1952. Geographic variations of some physiological and morphological characters in certain freshwater fish. Publ. Ont. Fish. Res. Lab. LXXII: 79 p.

Strawn, K. 1961. Growth of the largemouth bab. fry at various temperatures. Trans. Am. Fish. Soc. 90: 334–335.

1970. Beneficial uses of warm water discharges in surface waters, p. 143–156. *In* M. Eisenbud and G. Gleason [ed.] Electric power and thermal discharges. Gordon and Breach, New York, N.Y.

Trembley, F. J. 1965. Effects of cooling water from steam-electric power plants on stream biota, p. 334–345. *In* C. A. Tarzewell [ed.] Biological problems in water pollution. U.S. Public Health Service, Cincinnati, Ohio. Publ. No. 999–WP-25.

U.S. Atomic Energy Commission. 1972. Fish kill from sudden drop in cooling water temperature. CO Inquiry Rep. No. 50–219/72–30, USAEC Division of Compliance, Region 1, Newark, N.J. 2 p.

Williams, G. C., et al. 1971. Studies on the effects of a steam-electric generating plant on the marine environment at Northport, New York. State Univ. N.Y. Mar. Sci. Res. Cent. Tech. Rep. No. 9: 119 p.