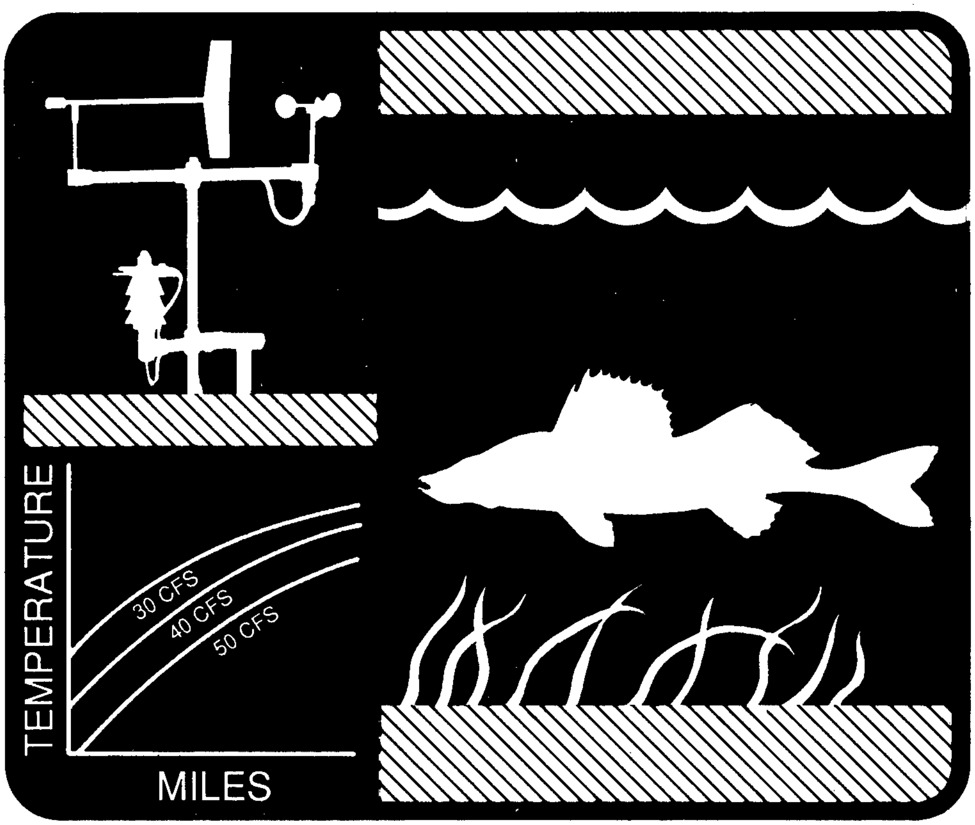
Evaluating Temperature Regimes for Protection of Walleye



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By Carl L. Armour

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Abstract. Geographic distribution and population success of walleye (*Stizostedion v. vitreum*) are affected by temperature regimes. Environmental alterations that can affect temperatures include altered flows, channel configurations, and discharges from reservoirs. The purpose of this report is to provide fishery biologists with information for use in evaluating alternative temperature regimes for their potential to protect and enhance walleye habitat. Temperature information for walleye life history and behavior is included in addition to procedures for applying the information in evaluating alternative temperature regimes for walleye habitat quality.

Key words: Alternative temperature regimes, *Stizostedion v. vitreum*, walleye, water temperature.

The walleye (*Stizostedion v. vitreum*), a coolwater fish, is the largest member of the perch family in America. Because it is an esteemed sport fish there is public demand for protecting and improving its habitat. Walleye populations are affected by many variables (Fig. 1), of which water temperature is extremely important.

Water temperature has been defined as an ecological resource (Magnuson et al. 1979). It affects all life stages and activities of walleye (e.g., spawning migrations, spawning, egg and larval incubation, and growth of fry and older fish). Indirectly, water temperature affects many variables that can affect walleye, including food availability, toxicity of waterborne pollutants, oxygen content of water, and biochemical oxygen demand.

Biologists do not understand all of the effects of water temperature on walleye from an environmental impact assessment perspective. However, enough is known about direct effects to make some evaluations. The objective of this report is to provide biologists with information for evaluating alterative temperature regimes (such as might result from impounding a river) for protection or enhancement of walleye populations.

Evaluation Methods

Use of Life History Information

Before performing evaluations of alternative temperature regimes, the life history stages that might be affected should be identified. Temperature information (Table 1) for those life stages can then be used as a starting point for analyses. When using information in Table 1, you must consider the geographic source of the information. For example, spawning occurs earlier in the year at more southerly latitudes. If spawning is delayed by a cooler temperature regime in your evaluation you

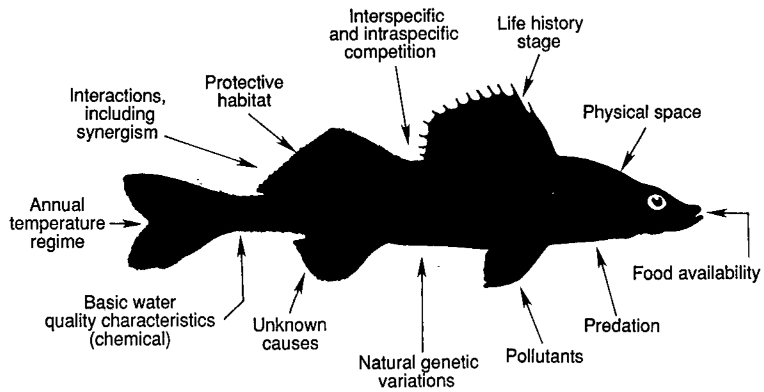

Fig. 1. Examples of environmental variables that collectively determine responses of a fish population to temperature regimes.

Table 1. *Temperature data compiled from the literature for walleye* (Stizostedion vitreum).

Temperature data for activity and life stages	Observation[a]	Reference and fish source	Comments
Spawning Runs			
When water temperature increased to about 2.8° C activity increased and most fish moved upstream	F	Paragamian (1989), Cedar River, Iowa	Movements of radio-tagged fish were studied
Water temperature seemed to control runs, and the main run occurred at 4.4–5.6° C	F	Rawson (1957), Montreal and Potato rivers, Saskatchewan	Little movement was observed at temperatures below 3.3° C
Begins when temperatures are 3.3–6.7° C	F	Niemuth et al. (1959), Wisconsin	Males are first to seek spawning grounds
Begins at 3.3–6.7° C	GS	Herman (1947), Wolf River, Wisconsin	In 1946, spawning began at 14.4° C
Spawning migration range is 3.3–6.7° C	GS	Becker (1983), general observation for Wisconsin walleyes	Begins soon after ice-out
Most of the migration occurred between 3.9 and 9.4° C	F	Arnold (1960), Provo River, Utah	The migration occurred mainly at night, and males preceded females to spawning sites
Heavy run commences at about 4.4° C	F	Bradshaw and Muir (1960), area below Bobcaygeon Dam, Ontario	Most of the spawning occurred between 6.1 and 8.3° C; spawning thought to have been completed at 10° C after which numbers of spawners declined
Spawning			
Occurred 3.3–15.6° C, 2.2–12.2° C, and 3.9–11.1° C	F	Priegel (1970), Wisconsin; Fox River marshes, Spoehr's Marsh in Wolf River, and LakeWinnebago, respectively, Wisconsin	In Fox River marshes peak period temperatures were 5.6–7.8° C; spawning was between March 30 and April 28 and was usually completed by mid-April; males were observed at Spoehr's Marsh in 1961 and 1962 when temperatures were 2.2° C; the earliest spawning in the marsh was April 2 and the latest was April 25; the earliest spawning in Lake Winnebago was April 7, 1966, and the latest was May 4, 1965

Table 1. *Continued.*

Temperature data for activity and life stages	Observation[a]	Reference and fish source	Comments
Temperature was approximately 5° C when spawning terminated	F	Paragamian (1989), Cedar River, Iowa	Radio-tagged fish were studied
Adults moved to spawning riffle when temperatures averaged 10° C, and the mean temperature ranged from 11.0 and 12.5° C the evening before eggs were collected	F	Paragamian (1989), Cedar River, Iowa	Eggs were collected in drift nets set below the spawning site; the author stated that spawning occurred at about 11° C
For six seasons, the range of average daily water temperatures during spawning was 3.3–11.1° C	F	Rawson (1957), Montreal and Potato rivers, Saskatchewan	The diurnal variation in temperature was approximately 2.2° C
Range of 5.3–12.2° C for 10 seasons Eggs were observed as early as March 31 and as late as April 21	F	Busch et al. (1975), western Lake Erie	Observations are based on mean daily temperatures; the mean of the daily means for mid-spawning was 6.8° C
Maximum activity was at 7.7–10° C	F	Rawson (1957), Montreal and Potato rivers, Saskatchewan	The range of spawning temperatures in two rivers was 3.3–11.1° C
Throughout the geographic range, the lowest recorded spawning temperature was 2.2° C compared with the highest of 15.6° C	GS	Hokanson (1977), observations from a literature review	Hokanson (1977) classified walleye as temperate mesotherms; a critical need is a gonadal development period at less than 12° C
Reaches peak at 8.9–10.0° C	F	Niemuth et al. (1959), Wisconsin	Spawning was observed at 6.1–17.2° C
Active spawning occurs at 5.6° C	F	Priegel (1966), Montello River, Wisconsin	Fish migrated from Lake Puckaway
Spawning was in the range 6.7–12.4° C	E	Ellis and Giles (1965), Whiteshell Provincial Park, Manitoba	Adult fish were captured and held in spawning facilities
Range is 8.9–12.8° C	GS	Piper et al. (1982), general hatchery observations	Optimum temperatures for fertilization, incubation, and fry survival are 6.1–12.2° C, 8.9–15.0° C, and 15–21.1° C
Best temperatures are probably between 7.2 and 10° C and preferably between 7.8 and 8.9° C	F	Cobb (1923), Rainy Lake, Minnesota	Reported that eggs are taken at temperatures as high as 17.2° C but as a rule are poor, and that good hatches occurred when eggs were subjected to temperatures so low that slush ice formed in the water
Occurred in the 9.0–15.5° C mean temperature range in 1987 and in the 3.0–13.0° C range in 1988	F	Rabern (1989), spawning sites associated with Lake Burton, Georgia	Spawning was most intense at 9.8° C in 1987 compared with 10° C in 1988
Occurred at 6.1° C	F	Derback (1947), Heming Creek, Manitoba, Canada	Spawning ceased when temperatures dropped to 5.0° C and spawners migrated back to Heming Lake; no fish returned to spawn when the temperatures rose; females caught in the lake were absorbing eggs, and there was a year class failure

Table 1. *Continued.*

Temperature data for activity and life stages	Observation[a]	Reference and fish source	Comments
Spawning ordinarily peaks at 5.6–10° C	GS	Becker (1983), general observation for Wisconsin walleyes	Spawning was observed at temperatures as high as 17.2° C
Begins at 6.7–8.9° C but has been documented to occur within the range of 5.6–11.1° C	GS	Scott and Crossman (1973), general observations for Canadian fish	Prespawning behavior may initiate at 1.1° C
Begins at ice-out when temperatures approximate 4.4° C	F	Linder et al. (n.d.), general statement	Males usually exhibit more aggressive behavior and are caught more readily than females; males congregate first when water is about 1.1° C; they are joined by females at temperatures 3.3–5.6° C
Spawning condition fish were sampled in water ranging from 8 to 12° C	F	Fitz and Holbrook (1978), Norris Reservoir, Tennessee	Captured by electrofishing in headwaters in the Clinch and Powell rivers
Occurs around 10° C	GS	Huet (1986), general statement with applications to hatcheries	Reported that spawning occurs from April to mid-May, depending on geographic region; incubation takes about 20 days at 10° C
Temperature range was 5.0–14.4° C	F	Grinstead (1971), Canton Reservoir, Oklahoma	The author concluded that spawning temperatures were in the range reported for other regions
Spawners were observed most years when temperatures ranged from 7.2 to 10.0° C, and spawning usually occurred at night	F	Eschmeyer (1952), Lake Gogebic, Michigan	The peak abundance of spawners was usually the first week of May. Spawning at 1330 h at 13.3° C was observed on 1 May 1942.
Occurred at temperatures less than 4.4° C	F	Eschmeyer (1952), Muskegon River, Michigan	The temperature range at 1500 h was 4.4–8.3° C during the spawning season; because spawning was at night the water temperature was less than that reported for the lower end of the afternoon range; peak spawning occurred when the 1500-h range was 4.4–6.7° C
Marginal temperatures in the 12–15° C range during the spawning period were thought to have limited spawning success	F	Prentice and Clark (1978), seven Texas reservoirs	Reported that the optimum temperature range for spawning is 6–12° C
During spawning, temperatures ranged from 3.3 to 8.9° C	F	Mraz (1962), Pike and LaBelle lakes, Wisconsin	Most of the spawning occurred during a temperature rise period when the temperatures rose to 8.9° C
Occurs at about 7.2° C	GS	Clay (1975), general observation for Kentucky walleye	Begins in March; young-of-the-year fish are 15–20 cm by the first winter of life
Eggs observed when water was 5.0° C	F	Newburg (1975), improved spawning shoal in Lake Osakis, Minnesota	Peak spawning occurred on April 25 when temperatures ranged from 6.7 to 9.4° C
Fertilization, incubation, and hatching			
The best temperature range for fertilization and incubation	E	Koenst and Smith (1976), adults were from Wisconsin	The results are based on constant temperature experiments with six

Table 1. *Continued.*

Temperature data for activity and life stages	Observation[a]	Reference and fish source	Comments
was 6–12° C		lakes	treatments ranging from 6.0 to 20.9° C during fertilization and incubation; egg survival to the hatch stage exceeded 60% at temperatures ≤12° C; the highest survival was 84% at 6° C
Independent of the fertilization temperature, the mean hatching rate exceeding 42% in the 8.9 to 15° C range	E	Koenst and Smith (1976), adults were Wisconsin fish	The highest fertilization temperature at which at least 41% hatching occurred was 17.9° C, and the incubation temperature was 15° C
Observed at 7.2–7.8° C	F	Arnold (1960), Provo River, Utah	Observed only at night between 1900 h and 2400 h
Reported ranges of incubation temperatures were 2.2–18.9, 4.4–12.8, and 5–17.8° C	F	Priegel (1970), Spoehr's Marsh, Lake Winnebago, and Fox River marshes, Wisconsin, respectively	Embryo development and short incubation periods were associated with daytime temperatures exceeding 10° C that did not decline below 7.2° C for an extended time; no correlation could be made between water temperatures and embryo survival
8.8–11.0° C was range of mean incubation temperatures from 1960 to 1970	F	Busch et al. (1975), western Lake Erie	For good to excellent year-class success, water warming occurred during spawning and incubation; the rate was usually above 0.28° C per day
For the daily mean temperature (continuous recording) 388 temperature units were required for hatching	E	Allbaugh and Manz (1964), western Lake Erie	When temperature units for all time intervals were averaged, 391 temperature units were required for hatching
Egg incubation occurred at 5.0–17.8° C	F	Johnson (1961), Lake Winnibogosh, Minnesota	The range represents the lowest minimum and the highest maximum recorded for the incubation period
Incubating eggs: Eyed stage at 234–274 thermal units Began to hatch 398–462 thermal units End of hatch 467–478 thermal units	E	Hurley (1972), Talbot and Napanee rivers, Ontario	The experiment was conducted in a laboratory with eggs from wild fish
Fluctuations of 4.4° C did not reduce survival of incubating eggs compared with controls	E	Allbaugh and Manz (1964), western Lake Erie	Throughout the 22-day incubation period, temperatures were elevated 0.6° C every 48 h to mimic natural conditions; on three occasions, temperatures were elevated 4.4° C above the base temperature for 4 h and then reduced to the base; the base temperature approximated 6.7° C at the start of the experiment compared with about 12.2° C at the end; the mean hatch rate for treatments was 32% compared with 28% for controls; the highest temperature during the experiment was approximately 16.7° C
The highest sac fry survival was at a temperature range of 8.9–20.9° C	E	Koenst and Smith (1976), adults were Wisconsin fish	Within the range, survival was 78–98%; no fry survived to the

Table 1. *Continued.*

Temperature data for activity and life stages	Observation[a]	Reference and fish source	Comments
and the stage was designated from hatching time to disappearance of the yolk sac			juvenile stage at temperatures less than 18.1° C, and at this temperature survival was 1% compared with 8% at 20.9° C; the sac fry stage was from hatching until disappearance of the yolk sac; fry at 9 and 12° C did not feed and they died; some fry fed at 15° C
Eggs hatch in 21 days at water temperatures of 10–12.8° C	GS	Priegel (1968), Lake Winnebago area, Wisconsin	Noted that for sauger (*Stizostedion canadense*) that are closely related, hatching occurs in 13–15 days at the temperature range
Eggs hatch in: 26 days at 4.4° C 21 days at 10–12.8° C 7 days at 13.9° C	GS	Niemuth et al. (1959), Wisconsin	Fry are approximately 13 mm at hatching
Temperatures from 18.3 to 21.1° C were fatal to "large" numbers of incubating eggs	H	Butler (1937), Lake Manitoba, Canada	Besides temperatures in the reported range, the water contained unspecified amounts of suspended sediment
Daily temperature units: Eggs to hatch = 300 Hatch to active swimming = 20	GS	Piper et al. (1982), general observations for hatcheries	Active swimming to start of feeding requires 20 units
Survival of eggs to hatching stage in waters where temperatures exceed 12° C can be improved by stripping and fertilizing eggs in water chilled to 7.2° C	E	Prentice and Dean (1977), eggs from Texas reservoir adults	Stated that in reservoirs the temperature for optimum survival is 6–12° C; recommended chilling eggs at incubation and incubating them within the optimum temperature zone following tempering; the hatch rate for chilled eggs ranged from 43.9 to 56.4% compared with the 12.2–21.7% range in waters exceeding 12° C
In the 15–15.6° C incubation range, a 90% hatching rate is not unusual	H	Kimsey (1958),[b] Kansas hatcheries	Two to 5 days are required from the eyed stage to hatching for the temperature range
During artificial spawning, newly taken eggs should be kept between 4.4 and 10° C	H	Kimsey (1958),[b] general observation	Reported that a temperature of 1.7° C was not harmful; with temperatures exceeding 12.8° C and turbid water conditions, fungus problems occurred in incubation jars
Eggs hatch in 7 days at a mean temperature of about 13.9° C compared with 28 days at about 4.4° C and 18–20 days at 8.9° C	H	Kimsey (1958),[b] general observation	Reported that vigorous and healthy fry were produced at 8.9° C
For a fry stocking program, water containing incubating eggs was heated to 12.2–13.3° C; when hatching began, water was lowered to about 7.2° C during an 8-h period to slow the incubation process and to enhance	E	Valentine and Peterson (1974), eggs were from New York hatchery fish	The day after the temperature reduction, eggs were transferred to 9.5-L capped containers with 0.9 L of eggs per container; oxygen was added before capping; nearly all of the eggs hatched en route to the hatching site; the approach was

Table 1. *Continued.*

Temperature data for activity and life stages	Observation[a]	Reference and fish source	Comments
survival			recommended to reduce prestocking fry mortality
Growth			
Optimum temperature was 22–28° C	E	Hokanson and Koenst (1986), Minnesota	Pond-reared juvenile fish were used in experiments; in the temperature range, at least 80% of maximum growth was attained
Virtually no growth at temperatures below 12° C	E	Kelso (1972), West Blue Lake, Manitoba	The fish were age II–VI
Maximum juvenile growth occurred at 22.1° C	E	Koenst and Smith (1976), adults were from Wisconsin lakes	Growth was expressed as percent change in weight per day; treatment temperatures ranged from 18.1 to 28° C; at temperatures ≤22.1° C, survival was 100% compared with 80% at higher temperatures
Optimum growth of juveniles at 26° C	E	Hokanson and Koenst (1986), Minnesota	The experiment was conducted with eight treatments ranging from 16 to 30° C
Best growth of age 0 fish at 22° C	E	Huh et al. (1976), Wisconsin	Growth for different photoperiods was studied; treatment temperatures ranged from 16 to 22° C; the fish were fed twice daily at a total rate of 3% of body wet weight
Temperatures in the low 20's (° C) are optimal for fingerling growth	H	Nagel (1976), London, Ohio hatchery	A disadvantage is that temperatures in the low 20's (° C) are optimal for pathogens; lowering temperatures to 15.6° C reduces disease problems but walleye growth is reduced about 33%
Under artificial propagation conditions the fish should be reared at temperatures near 22.2° C	E	Calbert et al. (1974), Wisconsin fingerlings	Growth rates peaked at a constant temperature of 22.2° C; the fish were fed prepared pellets
Growth of young-of-year fish stopped at temperatures below 10° C	F	Forney (1966), Oneida Lake, New York	Reported that very little growth occurred between October 1 and the first week of May due to low temperatures
Other			
Maintenance requirements (MR) in mg/g at 12° C: Age II, weight 170 g, MR = 38.2 Age III, weight 477 g, MR = 36.5 Age IV, weight 683 g, MR = 36.7 Age V, weight 889 g, MR = 37.3	E	Kelso (1972), West Blue Lake, Manitoba	Kelso (1972) concluded that maintenance requirements were independent of size; results based on experiments involving feeding of frozen emerald shiners (*Notropis atherinoides*); maintenance requirements between temperatures of 4 and 12° C were similar but increased greatly above 12° C; based on energy requirements alone, the following equations are the best fits for temperature and maintenance (M): mg/g/week $\log M = 1.366 + 0.029T$

Table 1. *Continued.*

Temperature data for activity and life stages	Observation[a]	Reference and fish source	Comments
			($r = 0.979$) cal/g/week $\log M = 1.286 + 0.029T$ ($r = 0.980$) where T = temperature (° C)
At 16° C the effect of walleye size and assimilation efficiency is represented by $Y = 96.85 - 0.0045X$, where X = size in grams (wet weight)	E	Kelso (1972), West Blue Lake, Manitoba	Fish in the experiment ranged from approximately 100 to 500 g
Optimum long-term mean annual air temperature for sustained yield is 2.0° C	E	Schlesinger and Regier (1983)	Data from intensively fished lakes in Canada and the northern United States were used for curvilinear analyses; the authors noted that native walleye populations occur in the southern United States when the long-term mean annual air temperature approaches 20° C; the curvilinear equation ($R^2 = 0.729$) for sustained yield (SY) was: $SY = 0.3866\,(TEMP) - 0.0558\,(TEMP^2) - 0.0105\,(TEMP^3) + 0.0011(TEMP^4) - 0.4478$ where SY = kg/ha and TEMP = long-term mean annual air temperature in ° C; equation recommended for the TEMP range of 5 to 9° C
At temperatures near the summer maximum, walleyes selected water approximately 25° C	F	Dendy (1945), Norris Reservoir, Tennessee	Applied to conditions where oxygen concentrations were approximately 3.5–7.0 parts per million (ppm); the selected depth, depending on oxygen conditions, approximated 6–9 m; fish were gill netted; because walleye demonstrate negative phototaxis, light effects should be considered when distribution is evaluated
To avoid temperatures above 24° C in the epilimnion, fish utilized hypoxic water	F	Fitz and Holbrook (1978), Norris Reservoir, Tennessee	During the summer, when stratification was most intense, fish were close to the thermocline even if oxygen was 1–2 ppm; fish were sampled by gill nets
When decreasing water temperature approached 5° C most fish overwintered in pools 1.5–3.0 m deep	F	Paragamian (1989), Cedar River, Iowa	Adult fish were radio-tagged and behavior was studied
Good to excellent year-class success occurred when the rate of water warming was steady and rapid (i.e., generally exceeding 0.28° C per day during spawning and incubation period)	F	Busch et al. (1975), western Lake Erie	Relative year-class strength was based on the mean number of young-of-year walleyes sampled per hour; the rationale for the criterion is that with warming water, spawning and embryological development periods are shortened to contribute to reduced

Table 1. *Continued.*

Temperature data for activity and life stages	Observation[a]	Reference and fish source	Comments
			mortality; young-of-year walleyes were sampled by trawling
Adult walleye tolerated and were most active in the range of 15–18° C	F	Rawson (1957), Lac La Ronge, Saskatchewan	Observation based on temperatures at which the most fish were caught in gill nets
Some walleyes entered deep pools when summer temperatures approximated 30° C	F	Paragamian (1989), Cedar River, Iowa	Movements of radio-tagged adults were studied
Walleyes would be expected to be found, at least in summer, at temperatures between 15.6 and 26.7° C	GS	Regier et al. (1969), western Lake Erie	The authors reported that walleye populations in the Rock River in Illinois tolerate elevated temperatures approximating 29.5° C; however, they concluded that the fish prefer 21.1–22.2° C in the western Lake Erie area
When surface temperatures in lakes exceed 22.2° C, fish retreat from shallow waters over reefs and bars and along the shoreline to deeper and cooler waters	GS	Eddy and Underhill (1974), reference to fish in northern latitudes	Stated that in July and August fish are at or near the thermocline
Sustaining populations existed in waters with extremes approaching 32.2° C	GS	Kimsey (1958), Vicente Reservoir, California	It was not clear if the fish had access to cooler water during upper extreme conditions
Fingerling walleye stocked at a surface temperature of 24° C experienced good survival	F	Luebke (1978), Alcoa Lake, Texas	Survival rates were not documented, and fish stocked at 30° C were stressed, which may have resulted in poor growth and survival
Preferred temperatures exceeded 21.1° C in a lake	F	May and Gloss (1979), Lake Powell, Arizona and Utah	Horizontal gill nets were used to sample fish; the fish did not demonstrate a well-defined depth preference
Fry feeding may begin at 10–15° C	H	Nickum (1978), geographically nonspecific	Reported for natural environments if a normal warming pattern follows spawning
During the spawning season walleye selected deep water away from spawning sites when temperatures were below 7.2° C	F	Arnold (1960), Provo River, Utah	Observations based on nightly counts on spawning grounds
Walleye were successful in an unstratified lake where summer temperatures sometimes exceeded 26.7° C and in another lake where upper temperatures ranged from 25.6 to 27.8° C	GS	Kimsey (1958), observations were for Clear Lake, Iowa, and Lake of the Woods, Minnesota, respectively	For Clear Lake, artificial stocking was required to maintain a walleye population
Walleye fry were stocked in rearing ponds at water temperatures ranging from 10 to 12.8° C	H	Kimsey (1958),[b] Iowa rearing ponds	Maximum temperatures in ponds were about 26.7° C during the hottest part of the day compared with about 22.2° C during the coolest time at night
A shallow part of a reservoir was vacated at temperatures approximating 21° C	F	Hall (1982), Jamestown Reservoir, North Dakota	Movements of walleye were studied by biotelemetry

Table 1. *Continued.*

Temperature data for activity and life stages	Observation[a]	Reference and fish source	Comments
Temperature preference was 12–18° C	F	Ager (1976), Center Hill Reservoir, Tennessee	Movements were monitored by biotelemetry
Walleye exhibit a strong aversion to temperatures of 24° C	F	Momot et al. (1977), general statement for Tennessee	Cited information was provided by R. B. Fitz and J. A. Holbrook, Tennessee Valley Authority
Greatest net catches were at depths with temperatures ranging from 13 to 18° C in Lac La Ronge, Canada	F	Scott and Crossman (1973), general information	Greatest catches in Wisconsin were in water at depths with temperatures of 20.6° C
Better-aerated walleye lakes seldom have surface temperatures exceeding 26.7° C	F	Kimsey (1958),[b] Minnesota lakes	Associated species include yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), rock bass (*Ambloplites rupestris*), and burbot (*Lota lota*)
Suitable walleye waters should have temperatures of 15.6–21.1° C available	F	Kimsey (1958),[b] Montana	Assumed to mean cool refuge waters for access during hot periods
At least two changes of water per hour ranging from 10 to 15° C recommended for fry culture	R	Nickum (1978), I assumed that the fry were from New York stocks	After feeding begins the water temperature may be raised to 20° C, which seems to be the optimal feeding temperature
Two water exchanges per hour with 20–22° C water is recommended for fingerling culture	H	Nickum (1978), I assumed that the fish were from New York stock	Recommended that dim lighting should be maintained no longer than 16 h/day; the author reported that temperatures higher than 20° C promote a greater incidence of disease, particularly for bacterial infections; for postfingerlings, 20° C water is acceptable
Feeding rates versus temperatures: °C — Rates (% of body wt.) 12.8–15.6 — 6 16.1–18.3 — 8 18.9–21.1 — 15 21.7–23.9 — 40 24.4–26.7 — 50	H	Cheshire and Steele (1972), White Lake Rearing Station, Ontario	No. 4 trout granules were fed as a percentage of fingerling body weight; temperatures were about 26.7° C by mid-July
Angling success is minimal or nonexistent at 6.1–11.1° C when spawning is occurring; often the resumption of aggressive feeding can occur after spawning when temperatures are in the 11.7–13.3° C range; summer peak period of fast action is when water temperatures are approximately 18–23° C	F	Linder et al. (n.d.), general field observations	During the summer peak period, the transition to a warmer water environment is complete with insect hatches and the maturity of rooted aquatic vegetation; when water is 0–0.6° C, walleyes are sluggish in flowing water and they select quiet water out of the main flow
Walleyes utilized water with a summer temperature of 26–27° C	F	Eley et al. (1967), Keystone Reservoir, Oklahoma	Sampling was with a vertical gill net that extended from the surface to the bottom; walleye utilized water to a depth of 4 m; most of the water at that depth had O_2 concentrations of approximately 6 ppm; concentra-

Table 1. *Continued.*

Temperature data for activity and life stages	Observation[a]	Reference and fish source	Comments
			tions of 4 ppm occurred at depths of approximately 7.5 m where temperatures approximated 24–26° C
Walleye seemed to avoid temperatures above 24° C in May–August during reservoir stratification	F	Fitz and Holbrook (1978), Norris Reservoir, Tennessee	To avoid high temperatures, the fish would enter water with 1–2 ppm O_2; sampling was with vertical gill nets and the fish were near the thermocline
Walleye ranged into deeper, cooler water when temperatures rose above 21.1° C	F	Johnson (1968), Lake Winniboshish area, Minnesota	Fish were not found on shoals in late fall when temperatures ranged from 6.7 to 8.9° C and they sought deeper, warmer water; tolerance for temperatures above 21.1° C seems to decrease as age and size increase; noted that walleye can tolerate temperatures in the 21.1–26.7° C range, but this is outside their comfort zone in Minnesota
Most active feeding occurred in October at 12.8–13.3° C	F	Arnold (1960), Utah Lake, Utah	Feeding was curtailed during hot and cold weather; during the summer period, feeding was curtailed when temperatures in deeper water exceeded 23.9° C
Nematode infestations of walleye occurred in a heated reservoir where temperatures did not drop to 7° C to curtail the development of nematode eggs	F	Maddux and Applegate (1984), Grant County, South Dakota	Parasitism in heated and nonheated reservoirs was compared; optimum temperatures for parasites prevailed in the heated reservoir where the lowest reading was always above 19° C; yearling fish were sampled
Juvenile walleyes could not be acclimated at temperatures >23.5° C	E	Beamish (1990), White Lake, Ontario	Experiments were conducted to evaluate O_2 consumption at different swimming speeds ranging from 0 to 45 cm/s; the fish were acclimated to five treatment temperatures ranging from 5 to 23.5° C; between 5 and 20° C the fish could swim at all speeds; at 23.5° C, they were unable to swim for the 60-min test period at current speeds >35 cm/s
There may be racial differences in maximum temperatures that can be tolerated during egg incubation (i.e., eggs from a Texas lake developed at 20° C but the temperature was unsuitable for eggs from Ontario)	E	Hubbs (1971), Lake Meredith, Texas, and Thames River, Ontario, respectively	The Ontario eggs were adversely affected at 16.5° C; details were not provided about the experimental design; I recommend that the results regarding racial differences should be considered as provisional until verification research is conducted

[a] F = natural field conditions; GS = general statement; E = experimental with treatments; H = hatchery.

[b] Kimsey (1958) included a compilation of literature abstracts and correspondence from fisheries biologists.

Table 2. *Reported avoidance temperatures of walleye in summer periods.*

Temperature (° C)	Location	Authors
24	Norris Reservoir, Tennessee	Fitz and Hollbrook (1978)[a]
26.7	Western Lake Erie	Regier et al. (1969)
21	North Dakota	Hall (1982)
27	Oklahoma	Eley et al. (1967)
21.1	Minnesota	Johnson (1968)

[a]Subsequent study demonstrated that behavior was affected by light as much or more than by temperature (William Wrenn, Tennessee Valley Authority, Athens, Ala., personal communication).

must determine if conditions will be suitable for adequate summer growth of that year class. Regarding direct effects of water temperature on year-class strength of percids, Koonce et al. (1977) reported that severe temperature regimes may be a limitation most frequently at the northern and southern boundaries of their geographic ranges.

All decisions involving water temperature should be confirmed with fishery biologists knowledgeable about walleye life history for a specific geographic area because reported walleye responses to temperature vary in the literature. For example, the reported range for spawning in Tennessee is 7.8–11.7° C, compared with 3.3-15.6° C for Wisconsin. Another example involves summer temperatures at which adults exhibit avoidance behavior. Avoidance behavior began at about 21° C in Minnesota, but in Oklahoma walleyes did not avoid temperatures less than 27° C (Table 2). Care must be taken in evaluating avoidance behavior, however, because variables other than temperature (e.g., light, dissolved oxygen, food) may be involved.

If accurate temperature information can be simulated using a computer model, a flow regime to protect walleyes can be recommended. For example, in Table 3 flow regime C would be acceptable for walleye egg fertilization and incubation because the range of thermal tolerance would not be exceeded.

The use of average water temperatures should be avoided. Average conditions might include minimum or maximum temperatures that cannot be tolerated by some life stage of walleye.

Another consideration when evaluating temperature regimes is short-term exposure to intolerable temperatures (Brungs and Jones 1977). If short-term temperature tolerance information is unavailable for walleyes (e.g., hours that can be tolerated by a life stage for a particular temperature), assume that any temperature outside the observed range in the field for a life stage or activity will be detrimental.

Extrapolation of results from laboratory experiments to the field should be done cautiously because physical, chemical, and biological variables that are excluded from the experiments can exist in the field, and this can affect how a fish population responds to a temperature regime. In lieu of other information, experimental results may be used as a basis for analyses, with provisional agreement among those concerned that they are appropriate for field application. Also, participants must agree in advance that the analytical procedure is acceptable for evaluating alternative temperature regimes and that the assumptions are reasonable, and the technical rationale for the assumptions should be documented. For example, assuming that the predicted mean and range of temperatures would be within the tolerance zone for successful hatching of wall-

Table 3. *Hypothetical temperatures for the walleye egg fertilization and incubation period.*

	Simulated flow regime		
	A	B	C
Temperature range[a] (° C)	3.3–7.2	4.4–24.4	6.1–11.1
Are temperatures tolerable?	No	No	Yes

[a]The acceptable range reported by Hokanson (1990a) is 4.7–18.2° C.

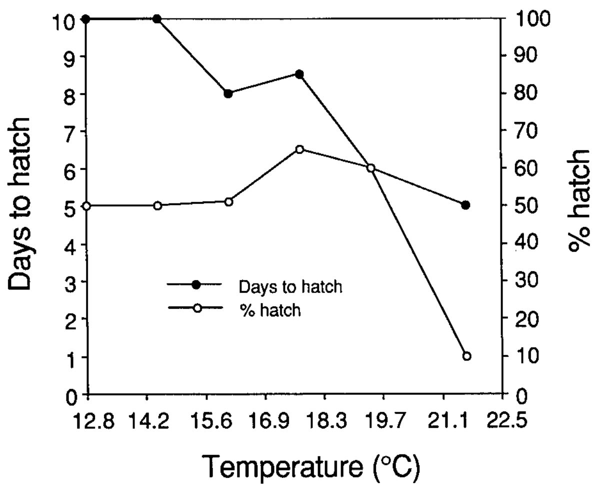

Fig. 2. Relation of walleye (*Stizostedion vitreum*) egg incubation temperature to days to hatch and percent hatching. The eggs were from Wisconsin walleyes (from Anonymous 1967), and the temperatures were constant.

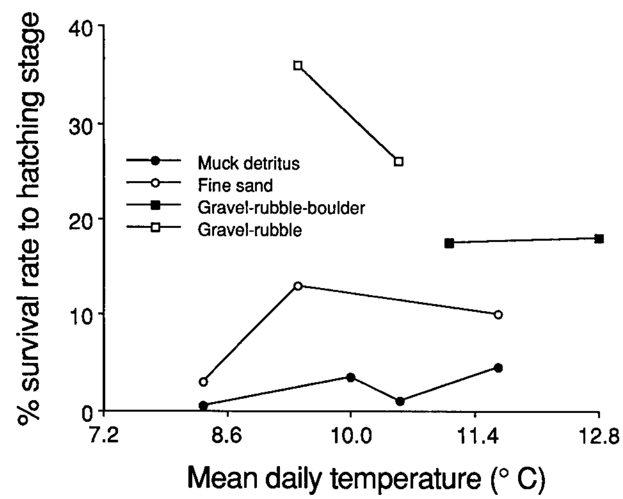

Fig. 3. Relation of mean daily temperatures to survival rate of walleye eggs to the hatching stage for four substrates. The eggs were from Minnesota stock (from Johnson 1961).

eye eggs, days to hatch and survival rate could be estimated from experimental information (Fig. 2). This information could be used to recommend a regime for the highest survival rate. If the desirable hatch rate is 50% or higher, temperatures greater than 20° C should be avoided. Because the data are from constant-temperature experiments, the recommended independent variable would be the mean temperature for the incubation period, provided that extremes would be within the range of 4.7 to 18.2° C (Hokanson 1990a).

When evaluating temperature regimes for walleye, you should try to determine if other environmental variables might affect their success. For example, when the influence of spawning substrates was studied for daily mean temperatures ranging from 8.3 to 11.7° C, the survival rate for eggs to the hatching stage for gravel–rubble was 27–36% compared with less than 5% for muck–detritus (Fig. 3; Johnson 1961). Thus, where muck and detritus substrates prevail, walleye reproduction would probably not be enhanced even with ideal temperatures.

If the concern is upper temperatures that should not be exceeded for juvenile survival in summer, information from Ohio experiments should be considered (Table 4; Wrenn and Forsythe 1978). The four treatments were ambient (18.5–30° C from late April through August) and 2, 4, and 6° C above ambient. Survival was 63% when temperatures did not exceed 30° C compared with no survival when the upper temperature rose to 34.5° C. With the exception of the ambient plus 6° C test temperature for which the maximum tolerance temperature was exceeded, there was no significant difference in yield for the treatments (Table 4).

Following development of computer-simulated summer temperatures, a decision on a temperature regime for a site could be based on temperatures that theoretically would be most favorable for juvenile survival. For example, assuming that maximum tolerance temperatures were not exceeded, for a regime with an average temperature of 31.2° C the predicted mortality from temperature effects alone would be about 50% (Fig. 4).

Use of Temperature Envelopes

Another option for evaluating alternative temperature regimes for walleyes is the walleye temperature envelope (Biesinger et al. 1979; Hokanson et al. 1990). The temperature envelope is

Table 4. *Statistics for temperature regimes for mortality, survival, and yield for juvenile walleyes in an experimental ecosystem. The fish, from Ohio experiments, were exposed to four temperature treatments (Wrenn and Forsythe 1978).*

Temperature regime	Temperature range from late April through August[a] (° C)	Extended period of elevated temperatures	Specific mortality per day (%)	118-day survival (%)	Yield $\bar{x} \pm$ SD (kg/ha)	Production (g/m^2)
Ambient	18.5–30	28° C for 78 days	0.41	63	36 ± 8.4	5.6
Ambient + 2° C	19.7–31.5	NR[b]	0.52	54	29 ± 11.3	5.4
Ambient + 4° C	21.0–33.3	32–33° C for 75 days	0.66	46	18 ± 6.6	4.0
Ambient + 6° C	22.4–34.5	NR	TM[c]	0	0	0

[a] In the text, temperatures were reported as means of daily temperatures at 0700 and 1530 h and as the average minimum daily temperatures. I assumed that the temperatures at 0700 and 1530 h were averaged.
[b] NR = not reported.
[c] TM = total mortality.

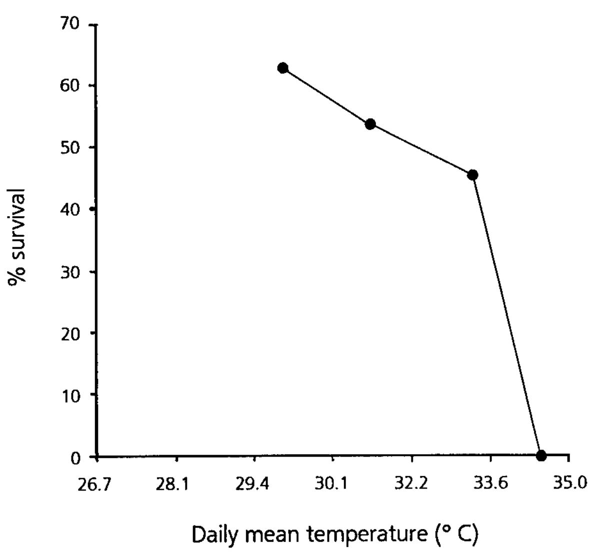

Fig. 4. Percent survival of juvenile walleyes as related to daily mean temperatures. The temperatures represent the mean of readings at 0700 and 1530 h (from Wrenn and Forsythe 1978). The experiment was for 118 days in May through September.

bounded by the 5 and 95% cumulative frequencies of weekly mean temperatures (Fig. 5). It was developed with information from sites throughout North America where temperature information and walleye data were available. Temperature information for walleyes and other fish may be found in the U.S. Environmental Protection Agency's Fish Temperature Data Base Management System (FTDBMS) located at the Duluth, Minn., Environmental Research Laboratory.

To use the temperature envelope, you would compare the range of simulated weekly mean temperatures with the temperatures for the same period in the temperature envelope. If they fall within the bounds of the envelope they would be acceptable. In Table 5, for example, flow regimes A and B would be acceptable for spawning and summer growth, but temperatures for both periods for flow regime C would be unacceptable.

For data in the FTDBMS (Stefan et al. 1992), the highest temperatures for the 95% curves for most species are 1–3° C lower than the upper ultimate incipient lethal temperature (UUILT) and approximate the zero net growth (ZNG) temperature. The definition of UUILT is the highest temperature at which tolerance does not increase with increasing acclimation temperature. For walleyes, the UUILT is about 4.3° C above the upper bound of the temperature envelope, and the ZNG value also exceeds the 95% curve (Fig. 5).

Another assessment approach would be to modify the temperature envelope technique by using historical, stream-specific temperature data to develop an envelope bounded by weekly maximum and minimum temperatures. The analysis would then be based on simulated weekly maximum and minimum temperatures (Fig. 6). If weekly extremes are used instead of means, chances for identifying limiting conditions are enhanced. Theoretically, simulated temperatures during

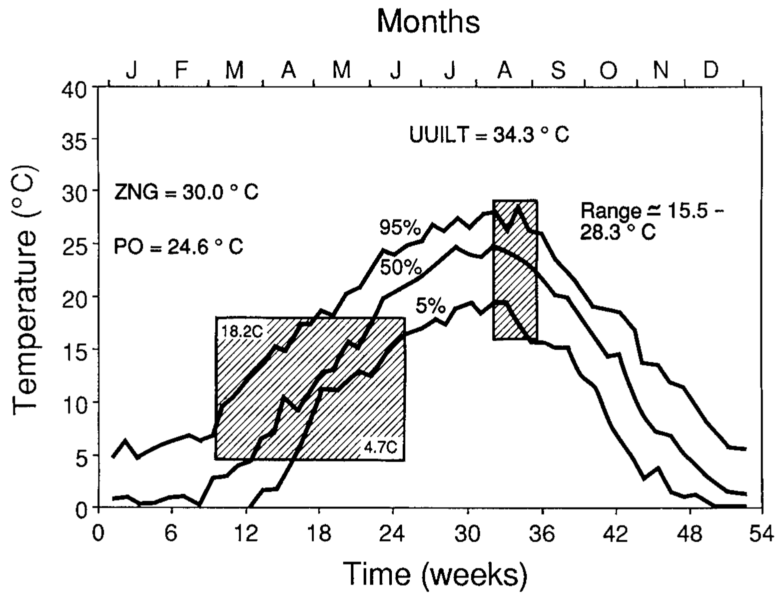

Fig. 5. Temperature envelope for walleyes bounded by the 5 and 95% weekly mean water temperatures (Hokanson 1990a). The *larger rectangle* represents the duration and range of spawning temperatures for multiple geographic sites; for a specific site, spawning occurs during 1–3 weeks. The *smaller rectangle* represents the range of temperatures during the hottest weeks of the year. UUILT = upper ultimate incipient lethal temperature (defined as the highest temperature at which tolerance does not increase with increasing acclimation temperatures); ZNG = zero net growth (defined as temperatures under experimental conditions at which instantaneous growth and mortality rates for populations are equal); and PO = physiological optimum (defined as temperature under experimental conditions approximating that for optimum growth, stamina, heart performance, and other functions). Hokanson (1990a) assumed that temperatures within the envelope are suitable for walleyes.

Table 5. *Hypothetical temperature regimes (° C) for comparison with the walleye temperature envelope.*[a]

	Simulated flow regime		
	A	B	C
Range of temperatures for hottest 3 weeks of summer[b]	17–24	18–25	22–32
Range of temperatures during the spawning period	5–17	6–18	10–22

[a] Comparison by the temperature envelope method of the U.S. Environmental Protection Agency.

[b] The theoretically acceptable range for the hottest period of summer (Fig. 5) is about 15.5–28.3° C compared with 4.7–18.2° C for the spawning period.

spawning migration, spawning, and growth are preferable over existing conditions because the temperature range conforms more closely with bounds in the rectangles (Fig. 6). For the incubation period, problems would be predicted for both regimes because, for part of the period, temperatures are outside the rectangle for incubation. If natural reproduction were the goal in this example, neither temperature regime would be acceptable. However, a fishery might be maintained by stocking walleye fry or fingerlings. The rectangles delineate the duration and recommended temperatures for a site for various periods for walleye life stages.

There could be sites where walleyes might be successful, but the temperature regime might be theoretically marginal in quality; for example, during the growth period, the weekly mean and weekly maximum temperatures might exceed existing temperatures that theoretically are near or exceed tolerance levels (Fig. 7). In this situation, compare historical temperatures to simulated tempera-

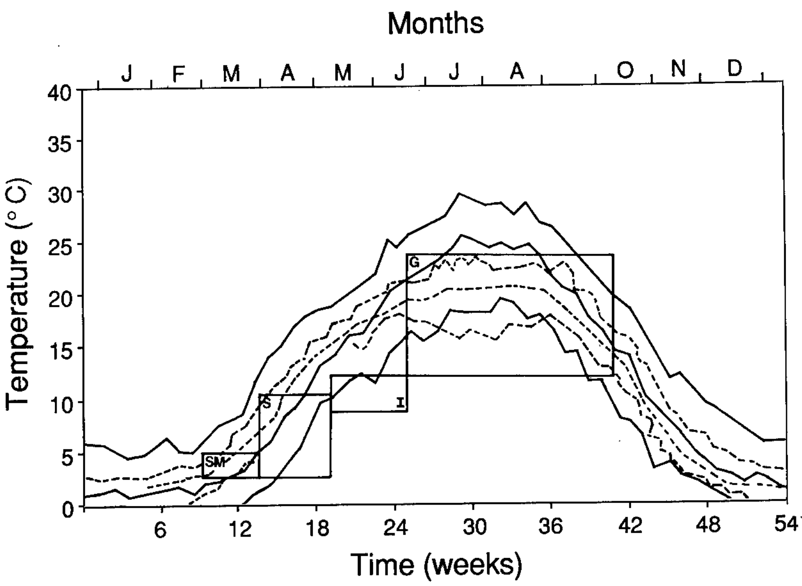

Fig. 6. Historical and simulated temperatures for a hypothetical stream. *Solid lines* represent weekly maximum, minimum, and mean temperatures for existing conditions; *dotted lines* represent simulated conditions; *rectangles* represent temperature ranges and durations for life history stages (i.e., SM = spawning migration, S = spawning, I = egg and larvae incubation, G = growth). The configuration of rectangles must be specified for a variable (e.g., recommended temperature range and duration of incubation).

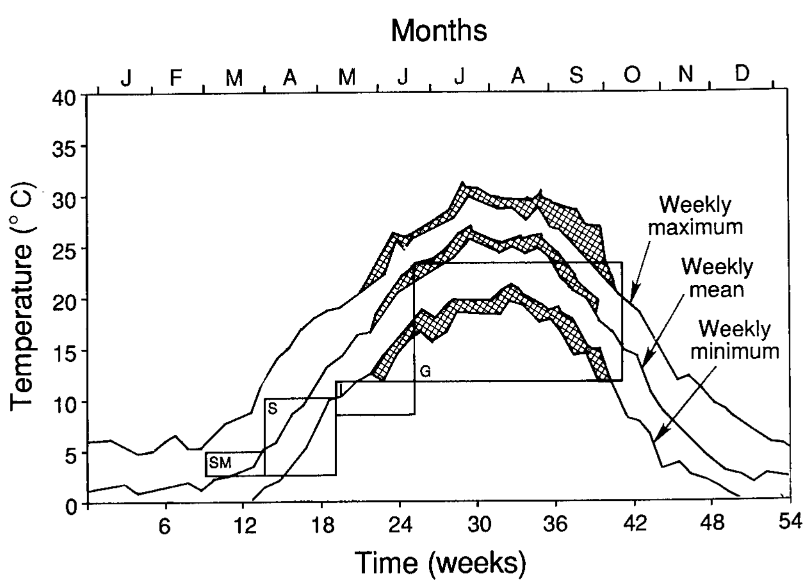

Fig. 7. Historical and simulated temperatures for a hypothetical stream in which temperatures are theoretically marginal, but walleyes are successful. The *stippled zone* represents temperature deviations from historical conditions; *rectangles* represent life history stages (i.e., SM = spawning migration, S = spawning, I = egg and larvae incubation, G = growth). The configuration of rectangles must be specified for a variable (e.g., recommended temperature range and duration for egg incubation).

tures to evaluate potential for adverse effects during periods of deviations from historical conditions. For the example, simulated weekly mean and weekly maximum temperatures for the growth period are worse in comparison to the range within the rectangle.

The recommended approach for deciding on a regime to recommend is to select one for which simulated temperature deviations would not exceed the existing conditions for a life stage. If it is impractical to implement a regime for which temperatures would not worsen from a theoretical perspective, one option would be a regime with the least amount of deviation from existing conditions; albeit there would be a possibility that the slightest alteration could be detrimental.

Another approach to consider would be to rank alternative regimes in a decreasing order of preference according to numbers of days that recommended temperatures would be exceeded. This could include days that the mean weekly temperature for the 95% walleye envelope (Fig. 5) would be exceeded during the hottest period of the summer. Also, rankings could be based on days that temperature would be within bounds for adequate growth (Stefan et al. 1992).

Use of Experimental Growth Results

Hokanson and Koenst (1986) revised growth estimates for juvenile walleye reported by Smith and Koenst (1975). The revision was based on experiments conducted over a period of weeks in late winter while the fish were fed excess rations. The line of best fit (Fig. 8; $R^2 = 0.85$) was described by the following equation:

$$G = 1.98 + 0.177X - 0.0218X^2 - 0.0017X^3$$

where

G = specific growth rate (percent change in weight per day) and

X = water temperature (° C−23).

This equation could be used to estimate growth for alternative temperature regimes (Table 6). For example, hypothetical flow regime A, with an average temperature of 21.7° C, would be most conducive to growth. The inherent assumptions are that excess rations would be available and that growth in the field would approximate that in the laboratory.

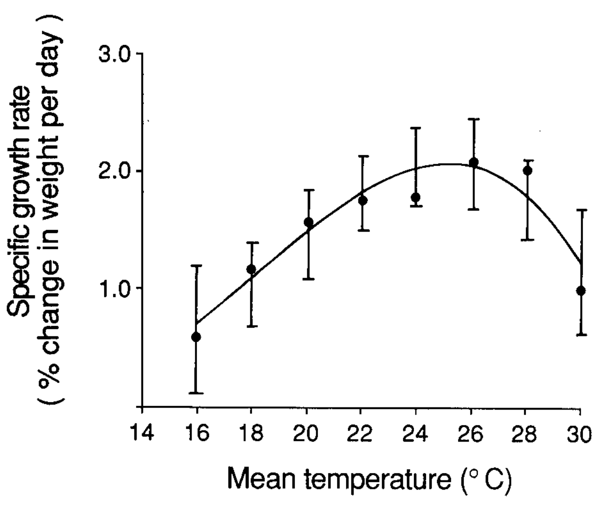

Fig. 8. Relation between water temperature and specific growth rate of juvenile walleyes. The observed data points and the 95% confidence limits for predicted values are indicated (Hokanson and Koenst 1986).

Table 6. *Estimated growth rates and potential total weights of juvenile walleyes for three hypothetical flow regimes.*[a]

	Flow regime		
	A	B	C
Average temperature (° C) during juvenile growth period	21.7	21.1	16.7
Growth rate (percent change per day)	1.70[b]	1.57	0.42
Weight (g) 120 days after growing season began	201[c]	172	44

[a] For this example, the initial weight at the beginning of the 120-day growing season was specified as 26.6 g.

[b] Growth rate = 1.98 + 0.177 (-1.3) - 0.0218 $(-1.3)^2$ - 0.0017 $(-1.3)^2$ = 1.70.

[c] g = 26.6 antilog 120 log 1.0170 = (26.6) (7.5599) = 201.093.

General Considerations

Several problems confront biologists responsible for performing temperature studies involving alternative flow regimes: deciding on acceptable temperature criteria, obtaining accurate simulated temperature data, predicting the influences of temperature in combination with other variables, and extrapolating results from controlled experiments to field conditions.

There is considerable variation in the temperatures reported for specific life stages of walleye. This emphasizes the necessity of collaborating with walleye biologists to agree on appropriate site-specific criteria and to document decisions. Otherwise, the validity of recommendations may be challenged by individuals with adversarial positions, based on their own analyses. To support your decisions, you should also refer to temperature information in the National Academy of Sciences and National Academy of Engineering (1974) "blue book" and the U.S.

Environmental Protection Agency (1976) "red book." Another useful literature source is that by Brungs and Jones (1977), who address temperature criteria for freshwater fish, including effects of short-term exposure to extreme temperatures. Reports by Hokanson (1990a, 1990b) and Hokanson et al. (1990, 1991) also contain information relevant to altered temperature regimes.

Geographic appropriateness is an important consideration when selecting temperature criteria. Based on research results for species with broad latitudinal distributions, Conover (1990) reported that for some species there is an inverse relation between capacity for growth and the length of the growing season. However, Colby and Nepszy (1981) reported that walleyes at first annulus are smaller at higher latitudes compared with southern stocks. There is also evidence that growth rates of older fish are greater for northern walleye that are stocked in the South (Colby et al. 1979).

Obtaining accurate simulated temperature data can be difficult because models may not be applicable to sites where the temperature studies were performed. When temperature data from simulation models must be used, you should ask the providers the following questions: What is the range of extreme temperatures that would occur? Are simulated temperatures representative of a 24-h period or a specified portion of the day? What is the degree of statistical confidence for estimates, including maximum, minimum, and mean temperatures? If technically defensible and verifiable answers are not provided, the information should be considered speculative. Also, ensure that the assumptions of the models are documented.

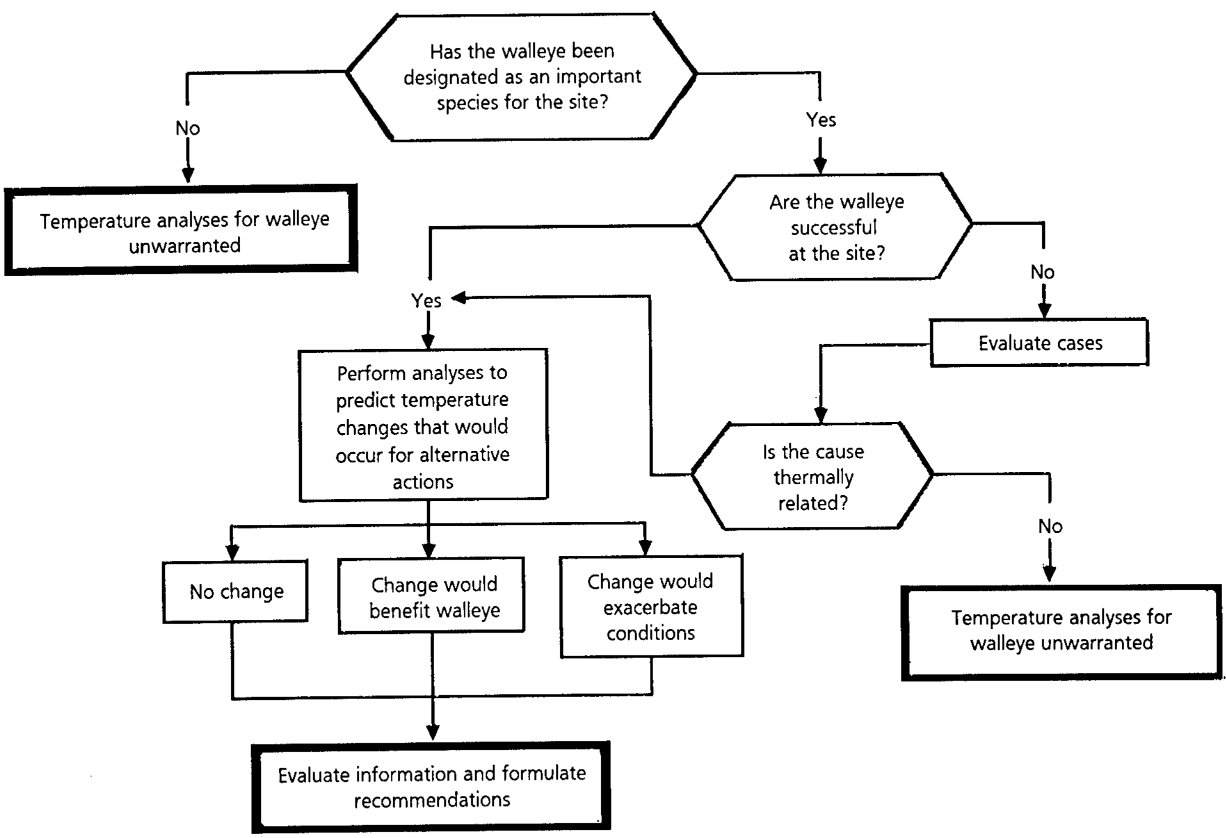

Fig. 9. Flow chart for the temperature analysis process for walleyes.

Accurate predictions about the influences on fish populations of temperature in combination with other variables, including pollutants, are not possible for field applications. In addition to different types of responses (e.g., synergism) that confound attempts to understand and explain the influences of other variables in combination with temperature regimes, fish populations have intrinsic traits that influence population densities on a yearly basis. There can also be yearly differences in population numbers attributed to natural environmental variation and stresses.

Given the difficulties of predicting population responses to temperature regimes in combination with other variables, you should evaluate whether other environmental variables might affect the fish population independent of temperature effects. The problem analysis method shown in Fig. 9 should be helpful. If walleyes are absent and establishment is being considered, all limiting factors must be designated, including physical, chemical, and biological conditions that might affect success. One reference that should be useful for such an evaluation is the walleye habitat suitability index model of McMahon et al. (1984).

Technical limitations affecting use of experimental data in temperature evaluation studies exist. Fish responses in controlled experiments can be affected by several variables, including thermal acclimation history, genetics, health and size of test fish, and unexplained experimental variation. Furthermore, under field conditions a different set of variables might exist, which would prohibit direct extrapolation of experimental results. For these reasons, when temperature analyses are based on experiments reported in the literature, the results should be presented in relative terms. This means the results simply represent a hypothetical ranking of a response (e.g., theoretically, growth would be better for flow regime A than regime B, assuming that there are no limitations due to food or other variables) from a temperature perspective, and the precise magnitude of difference cannot be inferred.

Finally, this guidance is not designed to be all-inclusive regarding ways that temperature evaluation studies could be conducted. For example, bioenergetics models (Kitchell et al. 1977) may be useful tools for these types of studies.

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