Fish in Winter –
Changes in Latitudes, Changes in Attitudes

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Fish Wintering Strategies Don't Remain Quite the Same

Fish are directly influenced by the temperature of their environment because temperature has a major controlling effect over all physiological processes. Through interactions between tolerance and lake characteristics, temperature shapes the geographic distribution of fish species. In North America, a latitudinal climatic gradient of long-and-cold winters in the north to short-and-warm winters in the south is accompanied by a gradient in life-history strategies of many freshwater fish. These include changes in somatic growth, size and age at maturity, reproductive investment, time of spawning, and longevity.

The latitudinal gradient in temperatures is illustrated by water temperature in lakes from Ontario to Puerto Rico (Figure 1). Annual temperature means span from 7 to 27°C at 1-m depth. Aside from the large differences in means, annual variability in temperature increases with latitude. In Cerrillos Reservoir at 15.6°N monthly mean water temperatures varied 5.2°C annually, but in Lake Simcoe at 44.4°N temperature varied 22.2°C. Another interesting dynamic of water temperature fluctuations across latitudes is the rate of temperature rise and decline. In Cerrillos Reservoir temperature changed 5.2°C from peak to trough over six months (0.9°C/month), whereas in Lake Simcoe temperature changed 22.2°C over four months (5.6° C/month). The length of time temperature remained above 20°C ranged from a few weeks in Lake Simcoe to the whole year at Cerrillos Reservoir. These differences in temperature regime can have major direct effects on fish through control over biochemical processes, and indirect effects through control over their environment.

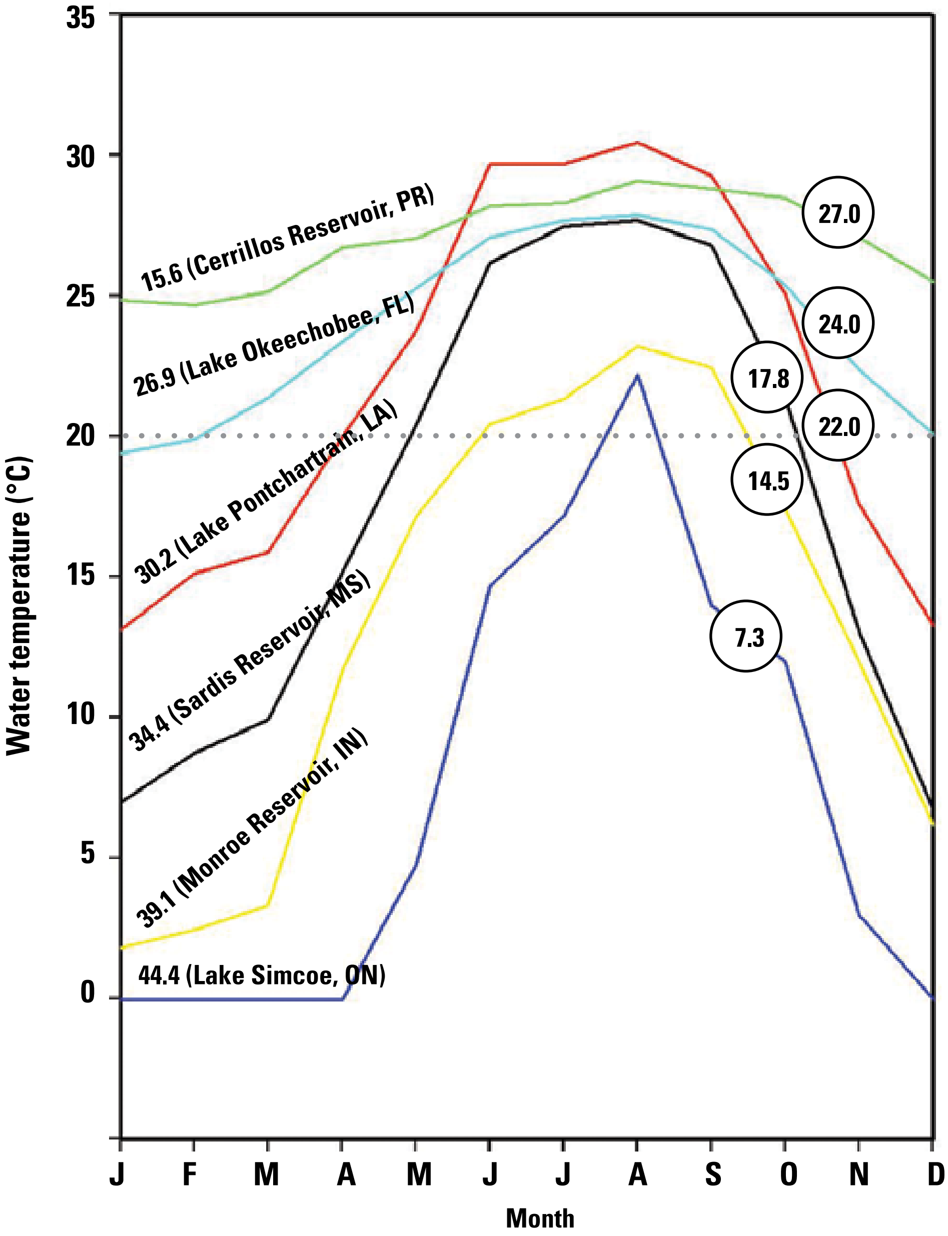

Figure 1. Mean monthly water temperatures 1-m below the surface at lakes and reservoirs across latitudes ranging from 15.6 to 44.4°N. Encircled numbers represent the annual mean.

Direct Effects of Winter

Most fish are ectotherms, meaning that their body temperature varies and approximately follows that of their environment. Ectothermy is advantageous because fish use gills for breathing, which requires that their body temperature trails water temperature to ensure efficient gas exchange between water, through a membrane, and the bloodstream (Fry 1971). Full oxygenation of blood through the gills is not a fast process, and a thermal gradient between the blood and the external water would further slow oxygenation.

This mismatch between the demand for oxygen and the capacity of the oxygen system to supply tissues is the primary mechanism that restricts fish tolerance to thermal extremes. Gas exchange is denied in frozen water, so fish are generally unable to tolerate freezing. The lowest possible temperature tolerated is near 0°C given that the freezing point of blood plasma is about -0.5 to -1.0°C. Some marine fishes have evolved antifreeze agents that can lower the freezing point of blood plasma and thereby lower lethal temperatures down to slightly below the freezing point of seawater, which is about -2°C. However, no such adaptations have been reported for freshwater fish.

Indirect Effects of Winter

The reductions in air temperature associated with winter in higher latitudes bring about a set of conditions that differ sharply from those that prevail in warmer months or in lower latitudes. The ice cover, existing continuously for several weeks, and often blanketed by snow, effectively separates the lake from the world above it. Several processes are affected or suspended by this ceiling of ice and snow. Aeration of the water by the agitation of wind and wave is prevented, and exchange of gases with the atmosphere by diffusion is greatly reduced or halted. Heat exchange between air and water is restricted, and light transmission into the water is reduced by the snow, sometimes almost to zero.

The biotic consequences of these changed conditions are many (Greenback 1945). Absence of wave action when lakes are frozen produces a stagnation that may drop dissolved oxygen and result in the elimination of some or all fish (i.e., winterkill). Shallow lakes with abundant vegetation or rich organic sediment are at especially high risk. Lakes that are subject to frequent winterkill events typically support a unique community of fish species that possess a range of specialized strategies for tolerating winter low oxygen conditions. Where winters are long and low oxygen levels are common and persistent, fish are unable to cope and fishless lakes may be common.

Fish Strategies to Cope with Winter's Direct and Indirect Effects

For a species to persist, it must not just survive harsh winter conditions but must also provide a survival advantage to its offspring. In this context, fish exhibit three general strategies to cope with winters, all centered on energy management strategies (Shuter et al. 2012). These include *energy storage* in preparation for winter, *energy conservation* to ensure reserves last the winter, and *energy allocation* to adequately apportion energy relative to the amount and timing required to successfully reproduce while allowing for individual survival and/or maximizing juvenile survival. Fish often use a mix of these strategies, with the mix varying across species, and across latitudes within the same species.

Energy storage. Temporal variability in somatic energy accumulation (mostly fat) is a widespread adaptation to seasonality. Most fish species accumulate energy over warm months and deplete it during the winter. Studies on various species of fish have demonstrated that high-latitude populations rapidly accumulate large energy reserves, which are depleted over the winter and then increased again before the subsequent breeding season. Lipids and glycogen are usually the first reserves to be used when fish are unable to forage because food becomes scarce or metabolism is reduced by cold temperature. If starvation periods are prolonged and energy reserves become depleted, fish may begin metabolizing muscle and liver tissue. Adult females are capable of using energy stored in ovaries that was formerly allocated to egg production. Conversely, populations in lower latitudes slowly accumulate relatively small reserves until spawning begins. Thus, fish in low latitudes show fewer propensities to accumulate fat and show a reduced annual variation in energy storage than fish in high-latitude populations.

For fish species with wide latitudinal distributions, the duration of their first growing season shrinks several folds with increasing latitude. Correspondingly, body size is smaller by the end of the growing season, but not by as much as the decline in the length of the growing season (Yamahira and Conover 2002). This occurrence suggests that the rate of growth within the growing season must be higher where the growing season is shorter. Because larger juveniles survive the winter better than smaller ones, selection for large body size may explain the faster growth at higher latitudes. This phenomenon has been reported for various species including Atlantic silverside *Menidia menidia*, Atlantic salmon *Salmo salar*, largemouth bass *Micropterus salmoides*, striped bass *Morone saxatilis*, and mummichog *Fundulus heteroclitus*.

Energy conservation. Strategies to conserve energy during winter include reduction of metabolism and selection of undemanding habitats. Reductions in metabolism have been linked to reductions in temperature and photoperiod that occur during winter at high latitudes. Such cues are increasingly lacking in lower latitudes, although probably not needed because winters are mild. Habitat selection strategies during winter often involve selection of suitable microhabitats such as stream or groundwater inflows, and deeper water where temperature may be more favorable. Some fish, like bullheads *Ameiurus* spp., take it a bit further and burrow in the mud or gravel for a little extra warmth.

Some species may benefit from ice cover and dark conditions. This is because in ice-free conditions both predator and prey may become more active. Decreased activity under reduced temperature and visibility will decrease metabolism and predation-risk. An exemplar winter specialist is the burbot *Lota lota*, which is most active in winter and exhibits little movement in summer. In summer burbot feeding and metabolic rates are reduced, and its energy stores are depleted. During winter, it is an efficient bottom feeder and predator and its energy stores are replenished. It may be advantageous for burbot to exhibit this reverse strategy because most of its competitors are relatively inactive in winter and thus burbot can reduce interspecific food competition and predation risk. As another example, gars *Lepisosteus* periodically surface to gulp air under low dissolved oxygen conditions because their gills are not sufficient to support the oxygen demand of elevated metabolism at higher temperature. When ice covers lakes, gars are unable to surface. During these periods when gars are unable to surface, the cold water temperature lowers their metabolism to a level that oxygen demands can be met with gills only, coupled with the higher dissolved oxygen concentration in cold water.

Energy allocation. Energy allocation strategies principally center on timing reproduction to ensure effective access by larvae to the summer production pulse, even at the expense of parental survival. To this end, timing of reproduction for many freshwater fish species in North America is directly linked to thermal strategy: fish with low preferred temperatures such as many salmonids and coregonids spawn mostly in the fall and fish that prefer warmer temperatures such as percids and centrarchids spawn in the spring. Timing seems to be signalled by temperature and photoperiod, which control a window of opportunity when reproduction can occur.

Many species adapted to the coldwater conditions of northern latitudes spawn in the fall. This strategy positions eggs to hatch and larvae to begin feeding at the onset of the spring production pulse when lingering cool temperatures maximize food consumption and assimilation efficiency. This strategy allows juveniles to maximize use of a short growing season. Conversely, species adapted to warm-water conditions perform best during periods of warmer temperature. Spawning in spring permits rapid embryo development in late spring and early summer and allow larval fish to begin feeding at a temperature when their feeding efficiency is high, and food availability is peaking.

Interestingly, the temporal window for reproduction varies latitudinally. A spring spawner that reproduces in the vicinity of 20^{o}C will have a wider spawning window in low latitudes than high latitudes, because temperature changes more slowly in low latitudes (Figure 1). Thus, low-latitude fish tend to have a longer spawning period, in which they may spawn multiple times, thereby allocating more energy to reproduction. This phenomenon is exaggerated by largemouth bass introduced into Puerto Rican reservoirs. The extended spawning season and associated multiple spawning events appear to limit growth once fish reach reproductive age. Extended spawning effort over a longer spawning period may increase energy demands, reduce opportunity for energy acquisition, limit growth capacity, reduce body maintenance and immune capacity, and may contribute to the observed accelerated mortality and short longevity.

A Latitudinal Gradient of Fish Communities

Latitudinal differences in winter characteristics and fish strategies to cope with the direct and indirect effects of winter have contributed to the development of a latitudinal gradient of fish communities with diverse winter tolerances (Magnuson et al. 1979; Figure 2). Coldwater fish inhabit higher latitudes and prefer temperatures below about 18^{o}C. They include families such as Salmonidae (trout and salmon), Osmeridae (smelts), and Cottidae (sculpins). Warmwater fish inhabit lower latitudes and prefer water temperatures greater than 25°C and thrive in temperatures that would quickly kill coldwater fish, but as water temperature drops their metabolism slows down earlier than coldwater taxa. They include families such as Centrarchidae (sunfishes, crappies, black basses), Ictaluridae (catfishes), and Moronidae (temperate basses). Warmwater fish become sluggish in winter and either stop feeding at 5-10^{o}C or only feed to meet base maintenance needs. Coolwater fish have intermediate temperature preferences ranging from 18 to 25^{o}C, have intermediate latitudinal distribution, and include families such as Esocidae (pikes) and Percidae (perches).

This diversity of winter tolerances produces gradients of fish communities that change not only latitudinally, but also seasonally and vertically. Seasonally, coldwater species are most active in winter; in fact, the winter water temperature allows coldwater fish to expand their range, venturing into habitats dominated by warmwater fish in summer. Vertically, coldwater species seek deep water in summer and can tolerate cooler and shallower water in winter, whereas warmwater species seek warmer deep water in winter and avoid cooler deep water in summer.

This gradient in fish communities is expected to shift as anticipated climate change is likely to cause warmer and shorter winters, reduced winter hypoxia in high latitudes, decreased dissolved oxygen levels in low latitudes, and disruption of the wintering energy management adaptations developed by fish over thousands of years. In northern latitudes of North America these changes may create havoc over specialized fish assemblages as coolwater and warmwater species will be able to expand northward and coldwater species are squeezed into narrower latitudes. Less attention has been given to consequences in southern latitudes, where a large pool of tropical species is available for mobilization from southern Florida and Central America. Nevertheless, factors affecting species latitudinal distribution interact in complex ways, and simple correlations with temperature changes are not always good predictors.

References

Greenback, J. 1945. Limnological conditions in ice-covered lakes, especially as related to winter-kill fish. *Ecology,* 15(4):343-392.

Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. Pages 1-98 *in* W.S. Hoar and D.J. Randall, eds., Fish Physiology, Volume VI. Academic Press, New York.

Magnuson, J.J., L.B. Crowder and P. A. Medvick. 1979. Temperature as an ecological resource. *Am Zool*, 19(1):331-343.

Shuter, B.J., A.G. Finstad, I.P. Helland, I. Zweimüller and F. Hölker. 2012. The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquat Sci,* 74:637-657.

Yamahira, K. and D.O. Conover. 2002. Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality? *Ecology,* 83(5):1252-1262.

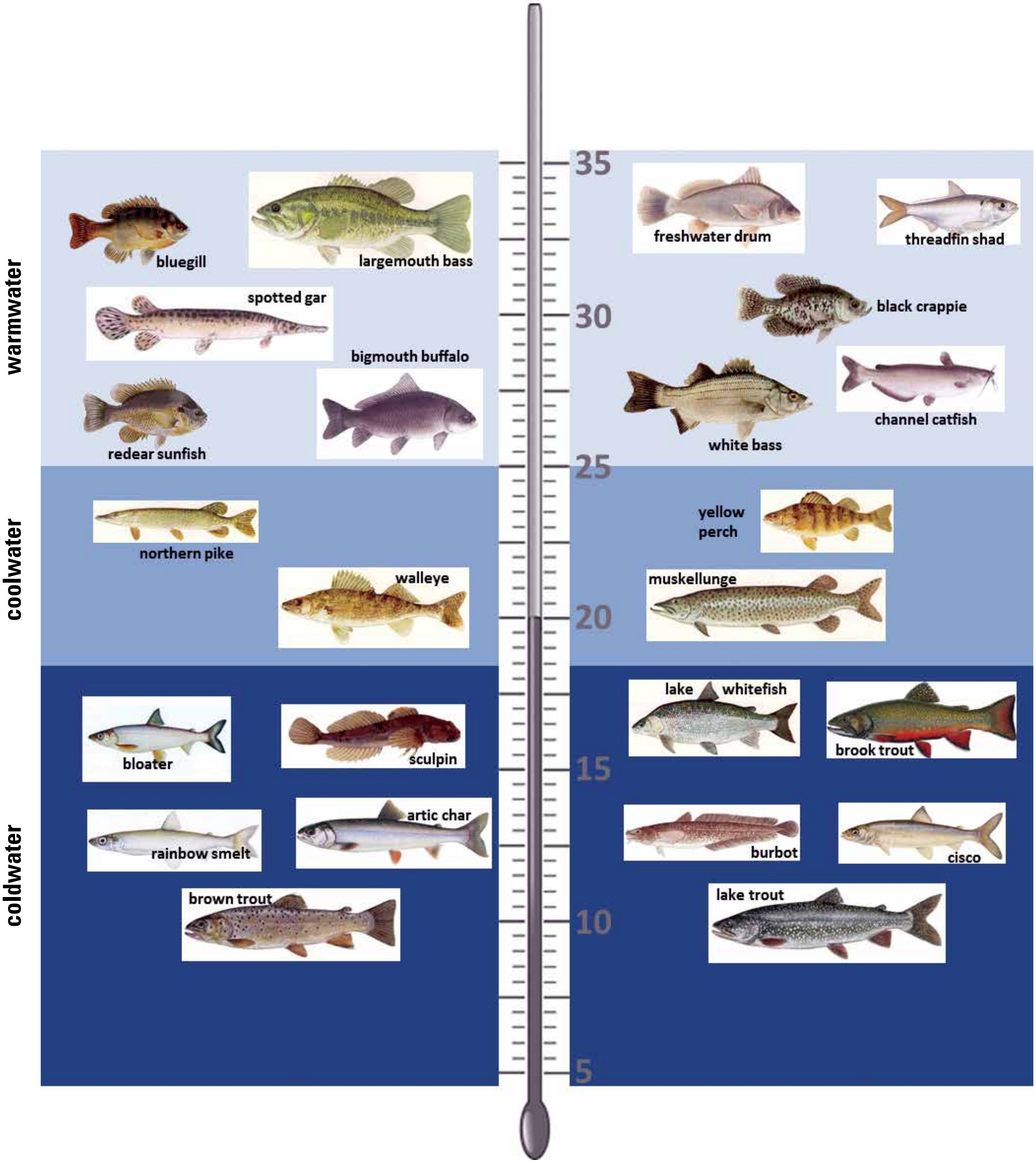

Figure 2. Examples of coldwater, coolwater, and warmwater species in North America. Coolwater and warmwater fish are spring spawners; coldwater fish spawn in fall or winter, although a few spawn at ice off.

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