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Thermal niche of fishes and global warming

Introduction

In 1979, we proposed the idea of a thermal niche for fishes as analogous to niches for other resources such as food type and size (Magnuson, Crowder & Medvick, 1979). In our view, competition occurs for space with the appropriate thermal properties in a manner similar to competition for places suitable for refuge or spawning. We concluded that 'fish do compete for thermal resources and that considerations of temperature as a resource are generally consistent with the characteristics of food as a resource.'

We defined the thermal niche of fishes as the preferred temperature ±2 °C or ±5 °C. This definition was derived from laboratory gradient studies which showed that fish spend two-thirds of their time within 2 °C and all of their time within 5 °C of their preferred temperature (Magnuson et al., 1979). A large number of, but not all, performance optima for individual species occur within these ranges (Magnuson et al., 1979; Jobling, 1981). In North America, freshwater fish have been grouped into three thermal guilds – coldwater, coolwater and warmwater – based on their temperature preference (Hokanson, 1977; Magnuson et al., 1979). Other criteria for the thermal niche, based on temperature acting as a controlling or a lethal factor, enrich the concept (see Fry paradigm below).

Global warming would be expected to alter the temperatures of lakes and streams and thus favour some species over others in relation to present conditions. This premise has led us to examine the potential effects of climate change on the thermal niche space of fishes for the Laurentian Great Lakes (Magnuson, Meisner & Hill, 1990) and small inland lakes of Wisconsin (DeStasio et al., 1996). Climate, lake thermal structure; and resulting size of habitat within the thermal niche were simulated for a doubling of greenhouse gases and compared with
simulations for the present climate. Our general conclusion was somewhat counter-intuitive: global warming would increase the size of habitat within the thermal niche not only for warmwater fish but also for coolwater and coldwater fish for deeper lakes at temperate latitudes.

The purposes of this chapter are to: (i) briefly review the concept of thermal niche with respect to Fry's paradigm of fish physiological ecology and Hutchinson's $N$-dimensional niche; (ii) evaluate the influence of environmental constraints that limit the fundamental niche to an actual or realized thermal niche; and (iii) consider the role of thermal niche in the potential effects of climate change on fish in small and large lakes.

Elements of the thermal niche

Fry paradigm

The late F.E.J. Fry at the University of Toronto, Canada, classified physical and chemical features of fish habitat as lethal, controlling, and directive factors on the basis of how they influenced fish (Fry, 1947, 1971; see also Kerr, 1990; Neill et al., 1994). Temperature could, for example, kill the fish, control physiological rates, and influence habitat preference (direct its location in a gradient). Some factors he also considered as limiting in supply, like oxygen, or capable of masking the influence of other factors. The range of conditions specified by these definitions is narrowest when defined as a directive factor, and progressively broader when defined as a controlling factor or a lethal factor (Fig. 1). These ranges can be used quantitatively to delimit the niche of a species or species life stage along a physical/chemical gradient or niche dimension.

Hutchinson's $N$-dimensional niche

The late G.E. Hutchinson of Yale University, USA, thought of the niche as a multidimensional world in biotic and abiotic gradients that described the environmental conditions in which the organism would do better than other species (Hutchinson, 1978). His earliest example was for temperature and food particle size as niche axes for zooplankton (Hutchinson, 1957, 1967). He also described areas of niche overlap and potential interaction between species in these $N$-dimensional worlds. In his view, competition was more likely for biotic axes than for abiotic axes. The non-interactive (fundamental) niche was without interaction with other species or based on that factor acting alone; the interactive (realized) niche was what the fish actually occupied in the field interacting with other species and factors.
Niches can be visualized graphically for 2 dimensions (Fig. 2) and 3 dimensions (Fig. 3). The 2-dimensional example (Fig. 2) quantifies the thermal axis as a directive factor and the prey size axis from optimum foraging data for three fishes. The 3-dimensional example is based on lethal effects of temperature, dissolved oxygen, and salinity on egg viability of Pacific cod (*Gadus macrocephalus*). Many major distribution patterns and differences in distribution patterns of fishes in time and space can be visualized well with only two or three niche axes.

Dealing with more than three environmental factors simultaneously soon becomes impossible graphically but successful attempts have been made with multivariate analyses of distributions of fishes across aquatic
Fig. 2. Two-dimensional niche of temperature and prey size for three species of fish at a size of 4 g (Fig. 4 in Magnuson et al., 1979). + indicates the centre of each 2-dimensional niche.

systems that differ in abiotic and biotic characteristics (e.g. Tonn & Magnuson, 1982; Rahel, 1984).

**The realized thermal niche**

The fundamental thermal niche can be used to describe optimum habitat with respect to temperature for particular fish during the growing season. It also can be used to indicate potential interactions with other species by explicitly evaluating overlap in thermal space. To the extent that organisms are able to occupy their fundamental thermal niche, they will be better able to escape predation or search for and capture prey, to grow faster, and to produce offspring sooner and in higher numbers than those that are less able to occupy their fundamental thermal niche.

However, fish live in a multivariate and changing world in which optimum conditions with respect to any single factor may not be achieved. The primary reasons that a fish may not occupy its funda-
Fig. 3. Three-dimensional niche in temperature, salinity, and oxygen for Pacific cod (*Gadus macrocephalus*) based on the environmental space in which 90% of the eggs hatch. (Adapted from Alderdice & Forrester, 1971.)

mental thermal niche are to be found in (i) the actual physical availability or existence of those temperatures in the ecosystem it inhabits, (ii) interactions among temperature and other abiotic and biotic niche axes, and (iii) intra- and interspecific competition with other organisms for thermal resources. The realized thermal niche represents the more constrained temperature distributions of fishes after these realities are taken into account.

**Seasonal constraints**

Seasonal variation in the realized thermal niche results from an opposition between the fish’s thermal behaviour and the constraints of the physical world. Recognizing the seasonal change in temperature occupation by temperate freshwater fish, Hokanson (1977) referred to
the warmwater fish as temperate eurytherms, the coolwater fish as temperate mesotherms, and the coldwater fish as temperate stenotherms, based on the seasonal variation in temperatures to which each group was exposed. Expected seasonal realizations of the thermal niche for these thermal guilds were diagrammed by MacLean and Magnuson (1977) with respect to depth for thermally stratified lakes and latitude for unstratified waters such as streams.

The constraint that seasonal temperature structure of lakes imposes on the thermal niche was apparent in the vertical distribution of fish in Pallette Lake, Wisconsin (Engel & Magnuson, 1976). In winter all species occupied water near 4 °C, while in warmer seasons they occupied the warmest waters available unless temperatures of surface waters exceeded their thermal niche temperatures; then they remained at their niche temperatures. Owing to these seasonal constraints on available temperatures, two coldwater species in the lake were able to occupy their thermal niches for only 5 months of the year and the coolwater species for only 2 months.

The idea that fish maintain their thermal preferences year round despite seasonal variability in temperatures, and will choose the warmest temperatures available providing the upper boundary of the thermal niche is not exceeded, is borne out by laboratory studies employing thermal gradients. The bluegill (Lepomis macrochirus) preferred warm temperatures, near 30 °C, regardless of photoperiod or acclimation temperatures (Magnuson & Beiting, 1978). Other species also prefer higher temperatures than occur in winter: bitterling (Rhodeus sericeus) (Zahn, 1963), yellow perch (Perca flavescens) (McCauley & Huggins, 1979) and larval sea lamprey (Petromyzon marinus) (Holmes & Lin, 1994). In winter, such fish would occupy the warmest waters available. A more precise behavioural mechanism seems unnecessary for closed water bodies where winter temperatures cannot be avoided by emigration. However, seasonal changes in temperature preference that can influence thermal distribution in winter do occur in some fish, for example juvenile Atlantic cod (Gadus morhua) (Clark & Green, 1991).

Interaction constraints among niche axes

The ability of fish to occupy their fundamental thermal niche depends very much on the suitability of other niche axes. Simply put, if a fish is to occupy its thermal niche, those temperatures must also co-occur within the dissolved oxygen niche (Kramer, 1987), the pH niche, etc. Such interactions can be viewed as environmental constraints in N-dimensional space that can be in opposition to the fishes' responses
Thermal niche and global warming

to temperature alone. For example, anoxic or low oxygen conditions in the deep, colder waters of eutrophic lakes and estuaries can prevent some fish from occupying their thermal niche (Rudstam & Magnuson, 1985; Coutant, 1987, 1990). It is the coincidence of suitable conditions along multiple niche axes that makes it possible for a species to occupy a particular habitat.

In the case of temperature and oxygen, and other pairs of axes such as conductivity and pH, or turbidity and prey density, direct physical/chemical relationships between the environmental factors will further influence the suitability of N-dimensional niches. In addition, fish response to one factor may be influenced by its response to the other. Warmer waters contain less oxygen than cooler waters and fish have higher metabolic demands at warmer temperatures. Thus, oxygen is more critical at warmer than at cooler temperatures. Not surprisingly, fish capable of aerial respiration are more likely to switch to air breathing in warmer than cooler waters (Johansen, Hanson & Lenfant, 1970). In an analogous case, pH is less buffered from change, and effects of low pH on fish eggs and larvae are more severe, in waters of lower ionic strength (Chulakasen, Nelson & Magnuson, 1989).

Interaction between axes is also evident when zooplanktivores that locate their prey visually have a smaller search field in more turbid waters (O'Brien, 1987). Ability to locate prey in the warmer surface waters could be reduced by phytoplankton blooms. Thus, the realized availability of prey in the warmest surface waters could be less than in deeper, clearer waters for fish with good scotopic vision. These examples help explain why a fish in an N-dimensional world may not occupy its thermal niche or may shift to a suboptimal temperature.

The distribution of prey also influences how a fish distributes itself with respect to its thermal niche (Crowder & Magnuson, 1983). Both prey abundance and occupied temperatures are linked closely to net energy gain and growth in fish. Behavioural thermoregulation maximizes growth through regulation of net energy gain given some level of ingestion. Optimal foraging predicts levels of energy intake given certain abundances and distributions of prey. Bioenergetics provides a mechanism for joint evaluating of food intake and food utilization. In simulations, the value of a food patch was determined not only by prey density, but also by the temperature of the patch. Warmer patches were, in a sense, more expensive and higher prey densities were required for a fish to achieve a positive energy budget.

An interesting question is whether the thermal niche changes systematically with prey abundance. At lower levels of prey abundance, net energy gain would be greater if the fish shifted to cooler temperatures;
at higher levels of prey abundance the fish could shift to more expensive, warmer habitats, and still achieve a greater net gain or growth (Spigarelli et al., 1974). Brandt (1993) evaluated food and temperature simultaneously through spatially explicit modelling of fish growth across thermal fronts (or thermoclines). The modelling results were consistent with these ideas: when food was distributed uniformly across the front, growth was highest at the optimum temperatures; lower temperatures produced better growth when food was low in abundance, and high food availability increased growth rate potential at the front.

Observational and experimental evidence for a level of functional interaction between prey abundance and behavioural thermal regulation is equivocal, but several field and laboratory studies suggest that it may occur. Vertical migration of several species appears to exemplify a set of behaviours that can optimize net energy intake for some species by feeding at suboptimal temperatures (too warm or too cold) where prey are abundant, and then either minimizing energy loss from metabolism by spending the non-feeding hours at cooler temperatures (Brett, 1971; Clark & Green, 1991), or maximizing digestion, food processing and growth by spending the non-feeding hours at warmer temperatures (Wurtzbaugh & Neverman, 1988). Rudstam and Magnuson (1985) observed that in eutrophic Lake Mendota with anoxic deep water in summer, a coldwater fish, the cisco (Coregonus artedii), occupied the warm epilimnetic waters and achieved large body sizes. These waters were more than 10 °C warmer than the middle temperature of their thermal niche. In oligotrophic Wisconsin lakes with adequate oxygen in deep water, the same species occupied the deeper, colder waters. In these unproductive lakes cisco did not reach large body size.

Results of experimental studies are somewhat contradictory. Several studies (Javaid & Anderson, 1967; Stuntz & Magnuson, 1976; Reynolds & Casterlin, 1979; Mac, 1985; Boltz, Siemien & Stauffer, 1987; Wildhaber & Crowder, 1990; Morgan, 1993) suggest that when ration is reduced, fish choose only slightly cooler temperatures. Also, Wildhaber and Crowder (1990) found that temperature was more important in choice of food patches than was the bioenergetic optimum based on both prey density and temperature. They suggested that temperature was a macrohabitat choice for fish and food density was chosen at a smaller scale of patchiness within thermal macrohabitats. Other interesting discussions of temperature as a micro- or macrohabitat feature in resource partitioning are in the literature on lizards (Hertz, 1992; Wikramanayake & Dryden, 1993).
Thermal niche and global warming

Fish do make brief feeding forays into waters that are suboptimal and would be lethal if prolonged (Hasler, 1945; Neil & Magnuson, 1974; Engel & Magnuson, 1976; Janssen & Giesy, 1984; Rahel & Nutzman, 1994). In these cases the conditions outside the thermal and oxygen niches are not ones in which the fish must or can dwell permanently. They are, or at least can be, lethal. Fish must simply resist the lethal or suboptimal conditions long enough to forage successfully and then return to waters within their thermal and oxygen niche. Such behaviours may grade into vertical migrations for energetic optimization as discussed above.

Finally, predators of fish are distributed along the thermal niche axis and could alter the value of inhabiting the thermal niche for prey fishes. Magnuson and Beutinger (1978) were not able to find much direct evidence for this. The reason may well have been related more to the difficulty of collecting such information than to the absence of the phenomenon. The parallel issue of fish weighing predation risk against access to prey has been evaluated in some detail (see discussion in Wildhaber & Crowder, 1991).

Competition for thermal resources

Magnuson et al. (1979) presented evidence that competition for thermal resources does occur. Interactions among fish along the thermal niche axis do result in familiar distributional properties characteristic of competition between species, such as thermal resource partitioning (Brandt, Magnuson & Crowder, 1980; Olson et al., 1988), thermal niche shifts (Crowder & Magnuson, 1982), niche complimentarity (Crowder, Magnuson & Brandt, 1981), and thermal niche compression (see Gehlbach, Bryan & Reno, 1978). Interspecific competition along the thermal niche axis alters their realized thermal niche. These interpretations are reviewed further by Crowder and Magnuson (1983) and Magnuson and Crowder (1984). Investigations of interspecific competition for suitable thermal space are made more complex by the physical/chemical constraints and interactions between niche axes discussed above.

Examples of realized thermal niches

Recent long-term and comparative regional studies have begun to provide a more complete view of the realized thermal niche of freshwater fish in temperate waters. Below we present interyear variations
in thermal niches for two lakes and compare the fundamental thermal niche and the realized thermal niche in lakes and streams.

**Interyear variation in thermal niche of lakes**

Interyear variation in climatic factors produced marked differences in observed thermal structure and thus habitat for coldwater (10 and 15 °C), coolwater (23 °C), and warmwater (27.5 °C) fish in Trout Lake and Lake Mendota, Wisconsin (Fig. 4). These graphs depict the fundamental thermal niche as constrained only by the existing temperatures in the lakes.

Several features are apparent and deserve comment. (i) The size of the habitat within the thermal niche was inversely related to the middle temperature of the niche; the warmwater habitat was the smallest and the 10 °C-coldwater fish had the largest habitat. Life at suboptimum temperatures was the rule, not the exception, for all guilds but especially for warm- and coolwater fish at these latitudes. (ii) The more southerly Lake Mendota had larger optimal thermal habitats for all guilds than the more northerly Trout Lake, with the possible exception of the 10 °C-coldwater niche. Small differences in latitude, about 3° here, significantly influenced the thermal values of a lake for all thermal guilds. Other differences between the lakes such as differences in water clarity and depth also may have influenced the differences. (iii) The warmwater 27.5 °C-niche was realized only in about one half of the years in Trout Lake. Trout Lake is near the northern boundary of many warmwater fish (see Becker, 1983). (iv) None of the thermal niches were realized in winter. Winter can be both a stressful season for fish (see Johnson & Evans, 1990; McCormick & Jensen, 1992) and important to reproductive biology (see Hokanson, 1977, Jones, Hokanson & McCormick, 1977). (v) Occasionally the 10 °C-coldwater niche occurred in the deepest waters which were certainly anoxic, for example 1985 in Lake Mendota. Extinction of coldwater fish without a flexible thermal niche would be likely to occur in such years. The only coldwater fish remaining in Lake Mendota is the cisco. (vi) Niche partitioning between the guilds was not complete. In these two lakes, the overlap in the thermal niche was quite apparent in the lakes' thermal structures between the 27.5- and 23 °C-niches, the 23- and 15 °C-niches, and the 15- and 10 °C-niches. (vii) Interyear differences did not appear to affect all thermal niches in any obvious directly or inversely proportional manner, either for within- or between-lake comparisons. A year with a small habitat for one thermal niche did not consistently have either a small or a large habitat for the other
Fig. 4. Time series of fundamental thermal niche sizes plotted against water depth for a warmwater (27.5 °C), a coolwater (23 °C), and two coldwater (15 and 10 °C) fish, based on the observed seasonal isotherms for (a) mesotrophic Trout Lake in northern Wisconsin, 1982–90 and (b) eutrophic Lake Mendota in southern Wisconsin, 1982–9. The broad thermal niches (10 °C wide) are filled in black. Water temperature data are from the Long-Term Ecological Research (LTER) North Temperate Lakes and Lake Mendota databases at the Center for Limnology, University of Wisconsin–Madison, USA.
niches. (viii) Differences among years resulted perhaps more from the seasonal duration of the thermal habitats than from the vertical extent of the thermal habitats. This was especially apparent in the 23 °C-niche for Trout Lake where the season was longest in 1987 and shortest in 1983 while the vertical extent was near 9 m in all years.

A number of other patterns were apparent, but the obvious point to note is that sizes of habitat within the thermal niches differed greatly among lakes, years and thermal guilds, given the observed climate of the 1980s in north temperate lakes. These differences have the potential to be used to evaluate interyear variations and long-term changes in the quality of fish habitat in lakes and other aquatic systems.

Comparisons with the realized thermal niche

Lakes

We compared the vertical temperature distributions of fish to their fundamental thermal niches and to the amounts of water available at various temperatures in several temperate lakes. Fish thermal distribution in nature, that is the realized thermal niche, results from the thermal behaviour of the fish (the fundamental thermal niche) and constraints set by the thermal habitat available (habitat availability). The resulting temperature distributions of fish in the deepest part of the lakes (Figs. 5–7) were derived from data on vertical distributions of temperature and fish on dates in late summer when temperature differences between surface and deep waters were greatest. The amount of habitat (water) at each temperature was summed for metres of the water column at each temperature; also, using the known area of the lake at each depth and thus the area at each temperature, the volume of the lake at each temperature was calculated. Depth distributions of fish were transformed to temperature distributions by summing the catches at each temperature and plotting their vertical distribution against temperature rather than depth. These observed thermal distributions of fish can be directly compared with the amount of habitat existing at each temperature, either the number of metres in the water column at each temperature or the volume of water in the lake at each temperature.

Three general distribution patterns are apparent (Figs. 5–7). First, fish occupied their thermal niche when those temperatures were abundant in the lake; second, fish occupied the most available temperatures even if those temperatures were not within their thermal niche; and third, fish often exhibited bimodal distributions which we interpreted as age-related differences or forays outside their thermal niche to feed.
Thermal niche and global warming

Compromises between inhabiting optimum thermal habitat and available thermal habitat resulted in the fish occupying different temperatures in different lakes, years, and seasons.

Cisco, a coldwater species

In Trout Lake, cisco distributions were centred at 9 °C in 1988, 7 °C in 1987, and 5–7 °C in 1989 (Fig. 5a), in direct response to differences in available temperatures in deep water. All of these temperatures were below the lower bound of their thermal niche by 2–6 °C. However, there is some uncertainty about the thermal niche for cisco. Here 15 °C was used for a midpoint as a general value for coregonid fish (Hewett & Johnson, 1987), but if 13 °C was used (Rudstam & Magnuson, 1985), the temperatures would be at or below the thermal niche by only 0–4 °C. Regardless, cisco were at or below the bounds of their thermal niche by either criterion. In Lake Mendota (Fig. 5b; Rudstam & Magnuson, 1985), cisco occupied temperatures 0–5 °C above the upper bounds of their thermal niche; they were unable to occupy permanently the deep and cold waters of this eutrophic lake because the hypolimnion was anoxic.

The fundamental thermal niche for cisco was located primarily at the thermocline which, owing to the sharp gradients of temperature, was a rather rare thermal habitat compared with the more thermally homogeneous epilimnion and hypolimnion. With their thermal flexibility, cisco in different lakes seemed able to use suboptimal habitats such as either the too-cold hypolimnion or the too-warm epilimnion in spite of a thermal preference for the rare temperatures between these two abundant habitats.

Yellow perch, a coolwater species

In Crystal Lake and Lake Mendota, yellow perch did occur within the bounds of their thermal niche in the warmer upper waters (Fig. 6a, b). However, the temperature that they occupied within the niche depended on habitat availability. The centre of this realized niche ranged from 21 to 27 °C in the various years in Lake Mendota and was constant at 21 °C in Crystal Lake, entirely in response to differences in the most abundant waters within the thermal niche. Most realized thermal niches of yellow perch were bimodal, with a second cooler mode 1–9 °C below the bounds of the thermal niche (Lake Mendota in 1986 and 1989; Crystal Lake in 1987 and 1989). The deeper, cooler mode probably resulted from feeding forays to eat zooplankton in the thermocline or macroinvertebrates on the bottom. Crystal Lake is
Fig. 5. Observed thermal distributions (the realized niche) of the coldwater fish (cisco) and distributions of the available thermal habitat measured as m (depth) of water and m³ (volume) of water at given temperatures in (a) Trout Lake in late July 1986, 1987 and 1989 and (b) Lake Mendota for late summer dates in August 1986 and late July 1987. The broad (10 °C-wide) and narrow (4 °C-wide) thermal niches are indicated by the horizontal bars above each distribution. Data are from the LTER project on North Temperate Lakes at the Center for Limnology, University of Wisconsin-Madison. Fish data were collected with vertical gill nets of various mesh sizes. Vertical gill nets were averaged from two successive nights; vertical temperatures were averaged from two profiles within c. 1 week before and after the gill net samples. See Rudstam and Magnuson (1985) for complete description of collection methods.
Fig. 6. Observed thermal distributions, i.e. the realized niche, of the coolwater fish (yellow perch) along with the thermal distributions of the available habitat measured as m (depth) or m³ (volume) of water at given temperatures in (a) Crystal Lake for August 1986, 1987 and 1989 and (b) Lake Mendota for August 1986, late July 1987 and August 1989. Definitions and methods as in Fig. 5.

Oligotrophic and food limitations are apparent in the slow growth of perch.

Changes in seasonal constraints on the thermal niche were apparent for cisco in Trout Lake (Fig. 7a) and yellow perch in Lake Mendota (Fig. 7b). In spring both species occupied waters colder than their thermal niche simply because no waters within the niche were available.
Fig. 7. Observed thermal distribution across seasons, i.e. the realized niche, from May to October 1992, of (a) the coldwater fish (cisco) in Trout Lake and (b) the coolwater fish (yellow perch) in Lake Mendota, along with the thermal distributions of the available habitat measured as m (depth) or m$^3$ (volume) at given temperatures. Stippled areas indicate temperatures with 5 mg l$^{-1}$ of dissolved oxygen or less. Other definitions and methods are as in Fig. 5.
Thermal niche and global warming

The same was true for yellow perch in June and October. In July and September for cisco, and in August for perch, temperatures within the thermal niche were available, and bimodal realized niches developed with one maximum within the thermal niche and the other in colder water. For cisco in Trout Lake the shallower, warmer mode was made up of young of the year and the deeper, colder mode of older fish. Resource partitioning between young and adults of the same species is reported for other species (Brandt, 1989). This appears to be general. Larger individuals occur at greater depths (Macpherson & Duarte, 1991) and in laboratory studies young fish of some species prefer warmer waters than do adults (McCauley & Read, 1973). Information on the thermal behaviour of cisco under laboratory conditions is too limited to provide estimates of preference for the various ages. For yellow perch in Lake Mendota the bimodality was not the result of age structure in the population; the small cooler mode in June and August probably represents fish in feeding forays to deeper, colder water.

Seasonal patterns in realized niche size did not appear to be constrained by low oxygen for cisco in Trout Lake but did for yellow perch in Lake Mendota (Fig. 7). Trout Lake had only a small zone of water below 5 mg l⁻¹ which developed by September. A few cisco continued to occupy the low oxygen waters either permanently or in forays to feed near the lake bottom. Lake Mendota had a large zone of water below 5 mg l⁻¹ which by August encompassed the entire cold mode of the yellow perch’s realized niche. A few yellow perch continued to make forays down to feed despite the low oxygen, which was typically 0 mg l⁻¹. The deeper, colder mode of yellow perch distribution did not include the most abundant coldwater habitat even though the June mode did when oxygen was not as constraining. Thus, low oxygen appeared to constrain perch feeding forays more in August than in June.

Streams

The temperature distribution of fish in streams of the USA has been summarized from a massive database by John G. Eaton and colleagues of the US Environmental Protection Agency, Duluth, Minnesota (Biesinger et al., 1979; Eaton et al., 1995; Eaton & Scheller, 1996). From this database they produce seasonal distributions of the temperature in stream locations at which certain fish species have been found. Their methods and criteria for data selection are provided in their papers. These distributions are being used by Eaton and colleagues to establish thermal criteria for fish, but they also provide the most extensive presentation of the realized thermal niche of fishes across the USA.
The realized thermal niche of the coolwater yellow perch and the warmwater largemouth bass (*Micropterus salmoides*) are presented for Wisconsin and the entire USA in Fig. 8. The joint influences of constraints from available temperatures and preference of fish for certain temperatures are both apparent.

Seasonal constraints from available temperatures were apparent in that the temperatures inhabited by cool- and warmwater fish were colder than their thermal niche, except in summer when the thermal distributions of yellow perch were remarkably close to temperature preferences of fish exhibited in the laboratory. This similarity was in both the central tendency and variability. Most occurrences were within the 10 °C range of the broad fundamental thermal niche. The exception was the largemouth bass (Fig. 8a, b) where the warmest temperatures of occurrence were at the lower boundary of their fundamental niche for Wisconsin and below the fundamental thermal niche for many places in the national data set even in summer. Apparently largemouth bass live in suboptimal thermal habitats in many areas; many of these occurrences may have coincided with the warmest temperatures available across the northern part of the US database.

Temperatures occupied by yellow perch in summer were not constrained by available temperatures in either the Wisconsin or the national database. When compared with temperatures occupied by largemouth bass for the national database, it was clear that warmer waters were available than those at which yellow perch occurred (Fig. 8a vs 8c). Similarly, the comparison of yellow perch occurrences in the more restricted Wisconsin database with their occurrences in the larger database for the USA (Fig. 8d vs 8c) indicated that Wisconsin contained river habitats with the full range of water temperatures used by this coolwater species. The implication of these results is that during summer, some fish move in the rivers to locations within their thermal niche, that is, they thermoregulate behaviourally if possible.

Differences in temperatures among adjacent streams that differ in size, position in the flow system, riparian vegetation, groundwater input, and heated waste effluents, may provide the heterogeneity in thermal habitat for stream fish to occupy their thermal niche. In mountainous regions with substantial altitudinal relief (Wyoming), the zonation of river fish according to temperatures has been documented (Rahel & Hubert, 1991; Rahel, Keleher & Anderson, 1996). Similarly, Meisner (1990) documented the seasonal movement of a coldwater fish, brook trout (*Salvelinus fontinalis*), based on seasonal changes in temperature distributions in Ontario trout streams. This same pattern was apparent in Eaton's database, but at an even larger spatial scale.
Fig. 8. Observed thermal distribution across seasons, i.e. realized thermal niche, of a warmwater and a coolwater fish in streams of the USA and Wisconsin from January to December with construction lines marking the 4 °C and 10 °C-wide thermal niches for each species. Niche widths are indicated at the margins of each panel. Warmwater: (a) largemouth bass for the USA; (b) largemouth bass for Wisconsin. Coolwater: (c) yellow perch for the USA; (d) yellow perch for Wisconsin. Data from the ‘Fish and Temperature Database Matching System’ (Eaton et al., 1995), provided for presentation by J.G. Eaton, Environmental Research Laboratory of the US Environmental Protection Agency, Duluth, MN 55811, USA.
The thermal niche and climate change

Climate change is expected to alter the size of realized thermal niche of fishes because it would change the annual pattern of thermal structure and would occur simultaneously with other changes in precipitation, cloudiness, windiness, and ice cover that would influence other niche axes of fishes. These direct and indirect influences of climate change on the realized thermal niche of fishes are considered below.

Thermal niche in lakes

We used climate models, General Circulation Models (GCMs), to create scenarios of possible future climates resulting from greater concentrations of greenhouse gases in the atmosphere (Magnuson et al., 1990; DeStasio et al., 1996). Common simulations are for present climates (1xCO₂ climates) and for a doubling of carbon dioxide (2xCO₂ climates). We took the output from four climate models to simulate changes in lake thermal structure using a physical model of lake mixing and heat transfer; the model was the Dynamic Reservoir Simulation Model (DYRESM) of Imberger and Patterson (1981). To estimate the change in thermal habitat for fish we compared the amount of habitat within the fundamental thermal niche simulated for present climates (1xCO₂ climates, i.e. BASE scenarios) and possible future climates (2xCO₂ scenarios).

Our simulations were for six North American temperate lakes ranging in area from 37 to 8,000,000 ha and in depth from 20 to 280 m (Magnuson et al., 1990; DeStasio et al., 1996). The broad (10 °C-wide) definition of the fundamental thermal niche was used for species with midpoints of their niche at 10 °C (lake trout, *Salvelinus namaycush*), 15 °C (cisco), 23 °C (yellow perch) and 27.5 °C (largemouth bass). The number of metres of depth within each thermal niche was summed across the year in units of metre months.

The habitat within the fundamental thermal niche increases with global warming for north temperate lakes (Magnuson et al., 1990; DeStasio et al., 1996). This is the expectation for large lakes like Lake Michigan as well as for small inland lakes, but notable differences occurred among species, lakes, and climate scenarios (Fig. 9).

With rare exceptions the 10 °C-coldwater fish had the largest thermal habitat, followed sequentially by the 15 °C-coldwater fish, the 23 °C-coolwater fish and the 27.5 °C-warmwater fish for all climate scenarios as well as for the BASE case (Fig. 9). For deeper lakes like Lake Michigan and Trout Lake, the increases in thermal habitat with 2xCO₂ climates were greater for the 10 °C-coldwater fish than for all warmer
Fig. 9. Changes in habitat within fundamental thermal niches simulated with a doubling of atmospheric CO₂ for warm-, cool- and cold-water fish for six north temperate lakes (Magnuson et al., 1990; DeStasio et al., 1996). Simulations are based on base climates for Lake Michigan from 1981 to 1984, Lake Erie for 1970 and 1975, and the other lakes for 1986, 1987 and 1989. Calculations for Lake Michigan included the upper 100 m which are the depths found in a transect across the lake at Milwaukee. The four climate scenarios from General Circulation Models were GFDL (General Fluid Dynamics Laboratory), GISS (Goddard Institute of Space Science), OSU (Oregon State University), and CCC (the Canadian Climate Centre). Methods and information on the climate models are detailed in Magnuson et al. (1990) and DeStasio et al. (1996).
water fish, while for the shallower lakes, 20–25 m deep, increases were
greater for one or more of the groups. Increases in thermal habitat
were similar for the 23 °C-coolwater fish and the 27.5 °C-warmwater
fish in each lake; they approximately doubled in size on average. Both
the 10 °C- and the 15 °C-coldwater fish demonstrated combinations of
decreases and increases in thermal habitat with climate warming among
lakes and scenarios; four out of 16 cases decreased for the 10 °C-fish,
and five out of 16 cases decreased for the 15 °C-fish. Decreases were
more likely for coldwater than for cool- and warmwater fish because
in the shallower lakes, the bottom waters were too warm in some
scenarios during summer.

Size of habitat within the fundamental thermal niche differed (Fig.
9). Lake Michigan, the largest and deepest lake, tended to have the
smallest thermal habitat for all fishes both in the BASE case and in
the most altered climate scenarios when measured as the percentage
of water depths within each niche. That is, Lake Michigan has the
largest fraction of total habitat that is suboptimal for each of the
thermal guilds. In only two scenarios with the 10 °C-coldwater fish
were the niche sizes larger than or comparable to the other lakes. The
thermal niches in Lake Michigan would have appeared even smaller
as a percentage of total water depths if a deeper part of the lake had
been used for the calculations of size; calculations were for the upper
100 m while some places are as deep as 280 m. Water temperatures
in Lake Michigan were below the thermal niche temperatures for all
fish most of the year.

Trout Lake was similar to Lake Michigan for the coldwater fish but
had more thermal habitat for cool- and warmwater fish than Lake
Michigan, when measured as the percentage of water depth within
each niche, because surface waters were warmer in this smaller lake.
This was generally true for the shallower lakes. Thermal habitat size
was also larger especially for the 15 °C-coldwater fish in the shallower
lakes than in Michigan in the BASE case and most scenarios. This
occurred because the deeper waters warmed more than they did in
Lake Michigan and even in Trout Lake; the smaller lakes have smaller
volumes per unit area and thus warm more with the same heat input
than larger lakes.

Before leaving the differences in thermal habitat sizes among lakes,
note should be taken of the measure used. We used % meter months,
the percentage of depths within the thermal niche summed across the
year. If an absolute measure of depths within the niche were used,
deeper lakes would be expected to have larger thermal habitat than
shallower lakes simply because they have more depths to be allocated
Thermal niche and global warming

to the niches than do shallower lakes. If bottom areas or volumes of water in each niche were used, large lakes like Lake Michigan would have immense thermal habitats compared with relatively tiny Crystal Lake. Volume and area measures also have been used to assess changes in thermal habitat (Christie and Regier, 1988; Stefan et al., 1995). There are advantages to each measure depending on the objectives of the analysis.

If we had used relative volumes or relative bottom areas rather than the relative depths, the size of the warmer niches would have increased relative to the colder niches because lakes have larger areas at the shallower/warmer strata than at the deeper/colder strata. However, for the lakes we analysed, thermal habitats still would be greater for colder water fish than for warmer water fish. Much of this cold habitat is accumulated during spring and autumn periods of mixing.

The different climate models provide a range of scenarios for changes in water temperatures with climate warming. The general similarity in the thermal habitat simulated with the various models, suggests that the results are robust at least in terms of direction of change. A doubling of CO₂ would generally increase thermal habitat for all thermal guilds in north temperate regions, at least for lakes like those considered here. This conclusion, however, is limited by its thermal centric view where only water temperatures and changes in water temperatures are considered in the life of fish. Many other environmental features of the fish world are likely to be altered by climate change.

Influence on other niche axes

Climate warming sounds deceptively simple to evaluate for one trying to judge effects of warmer climates on ectothermic heterotherms like fish. However, it would be a mistake to stop with a single, non-interactive niche axis approach to a complex issue as climate change. Factors likely to be altered by climate warming that should influence the realized thermal niche include changes in (i) the availability of dissolved oxygen resulting from altered productivities (Blumberg & Di Toro, 1990; Stefan, Hondzo & Fang, 1993; Stefan et al., 1995), water levels (Croley, 1990), and durations of summer stratification (DeStasio et al., 1996) and winter ice cover (Assel, 1991); (ii) littoral zone substrates, vegetation, and benthos resulting from altered water levels and flood regimes; (iii) the surface water connectivity between lakes and between rivers and their floodplains resulting from altered precipitation and evapotranspiration; (iv) lake chemistry from altered precipitation (Schindler et al., 1996; Webster et al., 1996),
groundwater discharge (Meisner, Rosenfeld & Regier, 1988), and associated inputs of nutrients, suspended solids, dissolved organic matter and acidity (Fec et al., 1996; Schindler et al., 1996); (v) lake productivity owing to altered lake chemistry and solar radiation; and (vi) the rates of invasion of warmth-loving exotics (Mandrak, 1989; Johnson & Evans, 1990; Shutler & Post, 1990; Edsall et al., 1993; Minns & Moore, 1995). Articles that touch on these and other factors that will interact with the thermal niche of fishes in a warming climate in north temperate waters are: Coutant (1981); Meisner et al. (1987), Magnuson et al. (1989), Regier et al. (1989), Smith (1991), Hill & Magnuson (1990), Schindler et al. (1990), Carpenter et al. (1992), McLain, Magnuson & Hill (1994), Stefan et al. (1995); Arnell et al. (1996); and Magnuson et al. (1996).

Temperature distributions and temperature dynamics are important features in the climate change ecology of fish. The dominant result from simulations is that thermal habitat for fish in north temperate lakes would increase. The signal of temperature in the success of fish populations is sufficiently strong that Christie and Regier (1988) were able to explain differences in yields of fish in large North American lakes from differences in the amount of optimum thermal habitat in the lakes. The temperature signal should be strong enough to project long-term changes in fish thermal habitat, but the fruits of such attempts await the future for confirmation or rejection. In the meantime, year-to-year variability and latitudinal differences in climate can provide a fertile testing ground for the ideas and simulations. The formalism of using temperature as a niche axis should help sort out the complex changes that may occur in a warming climate. Other properties in the environment of fish need to be incorporated into such a scheme. A useful beginning is provided by Stefan et al. (1995) who simulated realized niches for 2xCO₂ climates using both temperature and oxygen. Particularly important are those that are both responsive to climate change and important to fish.

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Thermal niche and global warming

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Thermal niche and global warming

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Thermal niche and global warming

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Thermal niche and global warming


