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# Likely responses to climate change of fish associations in the Laurentian Great Lakes Basin: concepts, methods and findings

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How a water body's temperature characteristics constrain organisms ecologically has been a continuing focus of interest in limnology and aquatic ecology for over a century now. A number of complementary scientific approaches are reviewed briefly. Progress in assessment of climate change is hampered by the still fragmentary and scattered scientific literature. A number of tentative generalizations are sketched. We expect that climate change of a type consistent with currently available scenarios will have severe consequences for Great Lakes fish and fisheries: in rivers that flow south, east or west and which contain isolated endemic species at the northerly edge of their ranges and which have no opportunity to migrate northwards; and where effects on the aquatic ecosystem of climate change interact synergistically and harmfully, as seems likely, with bad effects of other cultural stresses such as damming and nutrient loading.

## Introduction

Every aquatic ecologist and limnologist knows that environmental temperature, whether in the laboratory or in the field, is an important variable in any explanatory study of biological structures and processes. In the context of many studies, temperature has been treated as a noise variable — something that in itself is not meaningful but can be taken into account explicitly in order to sharpen the analysis, say by reducing the magnitude of the unexplained or error variance, or to externalize it from the focus of attention. Under such circumstances if some temperature dependency of a particular feature is modelled explicitly, the model selected is usually an ad hoc mathematical expression with some descriptive but little explanatory capability.

In contrast, habitat temperature has long been a meaningful variable for some researchers on the natural history of fish. These include some predecessors in our Toronto school, e.g. A. G. Huntsman, J. R. Dymond and F. E. J. Fry. Our Toronto group, which includes the numerous researchers trained at Toronto but then working elsewhere, has long interacted with expert colleagues at the University of Wisconsin–Madison and the U.S. National Laboratories at Oak Ridge, Tennessee, and with German limnologists and physiologists (for example, F. Ruttner, H. Precht and O. Kinne) in earlier decades. From these complex scientific interactions numerous meaningful insights have emerged. In the Great Lakes, the accrued knowledge provided insight into:

- the geographic and hydrographic seasonal distribution of fish by latitude and altitude;
- the year-to-year variability in recruitment of fish species especially in the northerly part of their ranges;
- the ecological effects of warm-water effluents from thermal electric generating plants; and
- the seasonal phenology of a species' life history features such as reproduction and growth as described in trophodynamic simulations.

To assess some likely effects of climatic change on fish we began in the mid 1980s by applying and adapting the accrued understanding to that issue. The first symposium on likely effects of climate change on fish was convened by researchers from Madison, Oak Ridge, and Toronto (Regier *et al.* 1990).

Through emergent evolutionary processes fish have internalized aspects of what were originally physical and thermodynamic constraints and have developed ways of using this systemic temperature feature. With respect to habitat temperature as a constraint and resource, the relatively ectothermic and active fish and many invertebrates are in an intermediate position between ectothermic and inactive plants and endothermic and active birds and mammals. Seasonally many fish and invertebrates oscillate between relatively inactive, "low-intelligence" states in which the temperature is too high or too low, and relatively active, "high intelligence" states, in which temperature is near optimal for the particular species.

## Iterations: field, laboratory, statistical and dynamic simulation studies

The scientific approach of the Madison–Oak Ridge–Toronto network, that focuses on the interrelationships between the ecology of fish and the habitat temperatures, has been to iterate between field studies, laboratory experiments, multivariate statistical analyses and dynamic simulation models. Tentative inferences were drawn from statistical analyses using data from ecological/limnological field studies which were generally comparative with respect to different populations of a species within a short period of one or more years and/or of a single population over a long period of many years. Hypothetical causal mechanisms relevant to the tentative inferences were then examined in formal laboratory experiments in which processes of the whole organism were at the focus of the "proximate reductionistic analysis". Dynamic simulation models were then created in an attempt to link explicitly the field observations, statistical generalizations and the laboratory findings. The realism and generality of a dynamic simulation were then tested with information from other field and laboratory studies somewhat beyond the conceptual, geographic and hydrographic limits of the information set on which the simulation was originally based.

The iterative approach sketched above was employed concurrently with a number of different species with somewhat different "temperature ecologies". Favourite species at the Toronto node of the network, in retrospect, were the salmonids brook trout (*Salvelinus fontinalis*) and sockeye salmon (*Oncorhynchus nerka*), and the centrarchid smallmouth bass (*Micropterus dolomieu*), with some attention to the percid yellow perch (*Perca flavescens*) and the cyprinid goldfish (*Carassius auratus*).

Before we present some likely effects of climate change on fish in the Laurentian Great Lakes Basin we provide a brief review of three selected conceptual and methodological studies completed recently at Toronto by the authors of this paper (Ing 1994, Lin 1995, Wichert 1995).

## Some compatible notions

A favourite way to summarize information on the temperature sensitivities of a particular fish species is here termed a "temperature tolerance polygon" or an "acclimation-response pattern". Fig. 1 depicts a version of such a pattern, and Fig. 2 shows simplified versions for three species (both from Lin 1995). From a review of relevant information on numerous fish species (Lin 1995) there appears to be a common qualitative pattern of temperature tolerance or acclimation-response. Quan-

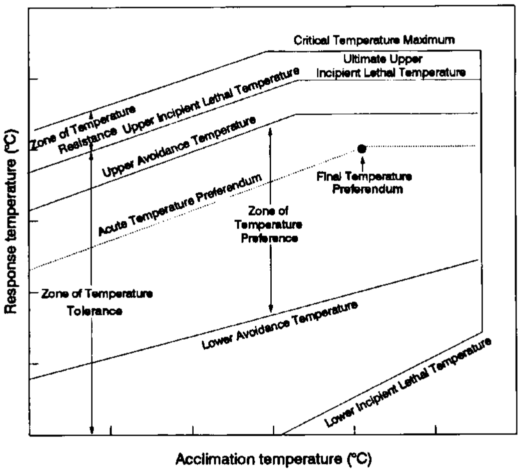

**Fig. 1**. A temperature tolerance polygon in which various survival thresholds and behavioral acts are related to response temperature with respect to acclimation temperature (modified from Wismer and Christie 1987).

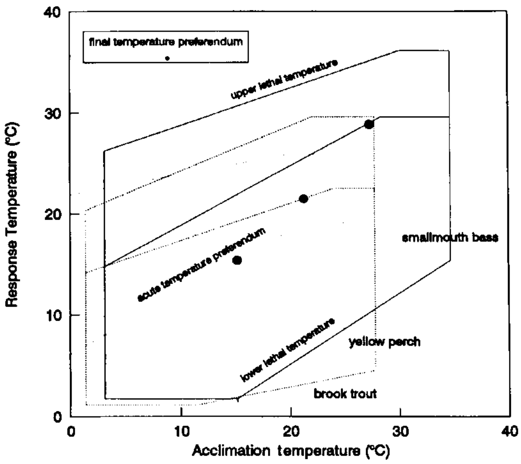

**Fig. 2**. Acute temperature preferenda and upper and lower lethal temperatures for brook trout (*Salvelinus fontinalis*), yellow perch (*Perca flavescens*) and smallmouth bass (*Micropterus dolomieui*).The polygons of three species are redrawn from diagrams in Brett (1956), Cherry *et al.* (1977) and Wismer and Christie (1987). The three slanted lines for the smallmouth bass polygon are labelled and the corresponding lines for the other species should be labelled similarly.

titatively the patterns differ. Fig. 2 shows an example of a salmonid species that prefers relatively cold water in summer and can survive relatively cold water in winter. It also shows an example of a percid which prefers waters somewhat warmer than the salmonid year round, and then a centrarchid species that prefers still warmer waters year round. Percichthyid species would be located further towards higher temperature and cichlid species even further. Some families, such as percids and cyprinids, appear to be more heterogeneous with respect to this aspect of a temperature pattern than are salmonids, centrarchids, percichthyids and cichlids.

The acclimation phenomenon is complex. Diagrams such as Figs. 1 and 2 and other notional generalizations that follow in this section usually relate to observations following a period of acclimation of specified length and in a particular season of the year since temperature phenomena usually have a phenological component. Behaviorally individuals or schools of fish may well move temporarily into waters with temperatures that appear to be grossly suboptimal or superoptimal, according to the generalizations in this section. Fish may temporarily risk temperatures in which they are adaptively far from equilibrium because a certain physiological or behavioral function may be enhanced temporarily as a result. But following temporary forays into such risky parts of their habitat they appear to revert, if they can, to temperatures close to their seasonal adaptive quasi-equilibrium. This opinion is based here on our shared judgement and not on careful and extensive study.

Patterns such as those in Figs. 1 and 2 implicitly have another dimension, i.e. relative organismal capability physiologically, behaviorally, and presumably subjectively with respect to well-being, "comfort" or lack of irritation. The literature contains many qualitative and quantitative inferences that relate some kind of capability or functional rate to temperature, some of which we have included below. Such inferences may be perceived to be vertical slices through the implicitly three dimensional Fig. 1. With many of these the relevant seasonal and acclimation regimes are not explicitly included in the generalizations.

The literature also contains comparisons across different species that show how two or more particular features of each pattern interrelate quantitatively, e.g. the optimal temperature for growth and the final temperature preferendum.

For fish numerous kinds of functional rates have been summarized, for quasi-equilibrium conditions with respect to acclimation and seasonal processes. Often the rates are in terms of the rapidity of some physical process per unit time and on other occasions in terms of the length of time required to complete some specified developmental or adaptive stage. With appropriate consideration to the measurement units used in such studies they can often be brought into a common mathematical form to make them directly comparable.

Numerous mathematical expressions have been used to describe one or more of the kinds of rate functions referred to above. Table 1 lists some 16 and provides comments on each (from Lin 1995). The mass or weight of an individual fish strongly influences most rate phenomena (Lin 1995); this issue is not addressed here.

Some of the relationships in Table 1 were based on some theoretical considerations, but none of the theoretical considerations for a particular relationship or model is strongly compelling, according to Lin (1995). Lin proposed the following rationale or set of criteria for selecting a particular model or coherent set of models:

— empirical insight into the underlying causal processes with respect to assumptions related to particular models;
— comparative information on how various kinds of processes have been fitted by a number of models;
— availability of a well-documented standard statistical method for fitting a particular model to data;
— degree of prior acceptance of a model in the refereed scientific literature;
— the usual Occam's razor criterion of choosing a simple over a complex form where other considerations are balanced;
— quasi-theoretical arguments which may help to understand the mechanisms involved and provide a basis for a firm generalization from at least two levels of biological organization (e.g. enzyme, organism, individual);
— operational considerations on how a fitted model will subsequently be used in further scientific or applied studies; and
— any personal biases or prior judgements of one's co-workers.

Based on an extensive literature search and on the statistical results of comparisons, the Arrhenius-type models, which include the Arrhenius (1889) in Fry (1971) (simple Arrhenius) and the Johnson and Thornley (1984)(compound Arrhenius) models as in Table 1, were found to approximate the general criteria above better than did the other models.

Commonly the Arrhenius model, whether simple or compound, takes 0 K as the "temperature

**Table 1**. A summary of formulae which describe the effects of temperature on rate processes. R is rate in inverse of time, T and T' are temperature in K and °C respectively; other symbols are constants. The comments are based on literature references as interpreted in the present study.

| Reference | Model | Comments |
|---|---|---|
| Réaumur (1735) | $R = A(T' - C)$ | Empirical, monotonic, common, poor fit |
| Berthelot (1862) | $R = AB^{T'}$ | Empirical, monotonic, $Q_{10}$, common, fair fit |
| Van't Hoff (1884) | $R = Ae^{BT'}$ | Theoretical, monotonic, common, limited range |
| Arrhenius (1889)[a] | $R = Ae^{-B/T}$ | Theoretical, monotonic, common, limited range |
| Harvey (1911) | $R = (A+T')/B$ | Empirical, monotonic, uncommon, poor fit |
| Janisch (1925) | $R = A/(B^{T'-C}+B^{-T'+C})$ | Empirical, unimodal, uncommon, fair fit |
| Bělehrádek (I, 1926) | $R = AT'^{-B}$ | Empirical, monotonic, common, poor fit |
| Bělehrádek (II, 1935) | $R = A(T' - C)^{-B}$ | Empirical, monotonic, common, good fit |
| Davidson (1942) | $R = C/(1 + e^{A-BT'})$ | Empirical, monotonic, common, good fit |
| Kavanau (1950) | $R = Ae^{-B/(T-C)}$ | Empirical, monotonic, uncommon, good fit |
| Krueger (1964) | $R = AB^{-1/(T'+C)}$ | Empirical, monotonic, uncommon, good fit |
| Colby and Brooke (1973) | $\ln(R) = A + BT'+CT'^2$ | Empirical, monotonic or unimodal, common, good fit |
| Bottrell (1975) | $\ln(R) = A + B \times \ln(T') + C \times (\ln(T'))^2$ | Empirical, monotonic or unimodal, uncommon, good fit |
| Ratkowsky (1983) | $R^{0.5} = B(T - T_{min})(1 - e^{C(T - Tmax)})$ | Empirical, unimodal, common, good fit |
| Johnson and Thornley (1984)[b] | $R = e^{A-B/T}/(1 + e^{C-D/T})$ | Theoretical, monotonic or unimodal, common, good fit |
| Pöckl and Timischl (1990) | $\ln(R) = A + B \times \ln(T') + C \times T'$ | Empirical, monotonic or unimodal, uncommon, good fit |

[a] This model is referred to as the "simple Arrhenius" in the present work.
[b] This model is also referred to as the "compound Arrhenius" in this work.
Note: Réaumur (1735) cited from Fry (1947), Berthelot (1862), Harvey (1911), Janisch (1925), Krueger (1964) cited from Fry (1971), Van't Hoff (1884) and Arrhenius (1889) cited from Cossins and Bowler (1987).

zero point" for a particular rate. That "standard measure", i.e. 0 K, is not a realistic zero point for chemical, biochemical and biological rate phenomena generally. Thus the "standard measure" leads to overestimates of the rate relationship at lower temperatures and provides estimates of positive finite rates below temperatures at which the fish can survive.

Also Arrhenius relationships, whether simple or compound, provide positive estimates of rate functions at temperatures beyond the maximum for survival. This is particularly marked with the simple Arrhenius relationship.

From the considerations of the preceding two paragraphs (see also Lin and Regier 1995) it is clear that one should not rely on the Arrhenius relationship as a model if one is particularly interested in rate phenomena near the lower or the upper temperature within a species' tolerance range. A fish species has behavioral thresholds at both limits of the adaptive range and finds ways to evade extreme temperatures, or dies. Conversely the Arrhenius models appear to provide useful and reliable descriptions for rate processes toward the central parts of the tolerance range that we consider to be particularly relevant for assessing likely effects of climate changes on organismal rates, except for overwintering and summer high temperature periods which cannot be evaded.

To facilitate a search for generalizations, Lin (1995) used the simple and compound Arrhenius with data sets on a variety of monotonic and unimodal response rates — with data points at the extreme upper and lower edges of the functional range given special consideration and sometimes deleted, in the light of the discussion above. Apparently the literature as yet contains no array of data sets for any species to yield a reliable set of behavioral thresholds and functional relationships for the numerous rate processes of potential interest here. Lin and Regier (1995) presented some of the more comprehensive and reliable data, and demonstrated how the appropriate Arrhenius model fitted each data set for a particular rate phenomenon for the two species brook trout and largemouth bass (*Micropterus salmoides*). In spite of the obvious shortcomings of available data, in this and other studies, some interesting and useful generalizations have been proposed and documented.

One proposed type of generalization by Lin (1995) is depicted in Figs. 3 to 5 for the three species brook trout, yellow perch and largemouth bass. The vertical axis in each figure is based on Lin's judgement of the relative complexity of each rate process, from the least complex at the bottom to the most complex at the top.

For each type of rate the horizontal range is taken from the literature, but seldom from studies that were designed explicitly to estimate the limits of that range. Instead the data on limits were usually stated as some author's informed judgement and based on some relevant laboratory and/or field study. The limits were not based on the fitted Arrhenius models, of course, because those models do not incorporate limits (see above).

The empty circles and solid points in Figs. 3 to 5 are derived from maxima in Arrhenius relationships fitted by Lin to data sets that he took to be reasonably reliable and relatively complete.

Based on the six cases examined by Lin (1995), three of which are shown here as Figs. 3 to 5, the relevant tolerance range appears to be broadest for relatively simple kinds of rate phenomena and narrowest for the more complex. Also the maximum of the rate appears to be close to the upper maximum of the tolerance range for comparatively simple phenomena but less close to that upper maximum for complex phenomena. The final temperature preferendum appears to be some 5 to 10°C below the upper limit of survival, and much further above the lower limit of survival. Altogether these ectotherms seem to have evolved to live dangerously but not too dangerously, and the behavioral capabilities appear to play a major role in selecting an approximate optimum.

Lin (1995) offered the following explanatory comments with respect to the six cases reviewed:

— limits of various physiological processes within a fish species are determined directly by the "denaturing" of the enzymatic system at the relevant temperatures, here an enzymatic system may consist of only one enzyme in a simple case or it may consist of an organized complex of enzymes in a less simple case;
— the particular temperature range in which numerous enzymes can function properly sets the temperature limits of survival;
— basal metabolism and digestion may be passive responses of the enzymatic system to the external environment, and not subject to di-

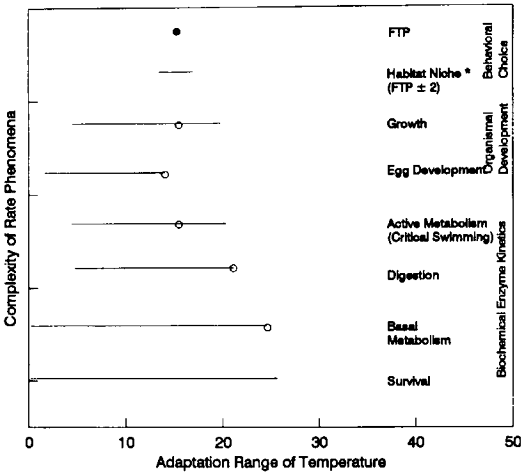

**Fig. 3.** Optimal temperatures and temperature ranges for temperature-dependent phenomena of physiological, developmental and behavioral types with brook trout, *Salvelinus fontinalis*. (FTP – final temperature preferendum.)

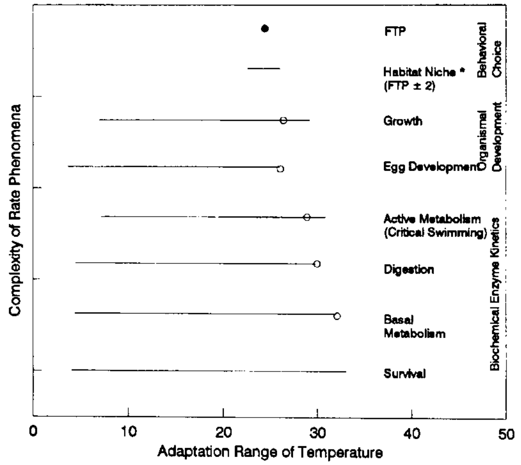

**Fig. 4.** Optimal temperatures and temperature ranges for temperature-dependent phenomena of physiological, developmental and behavioral types with yellow perch, *Perca flavescens*.

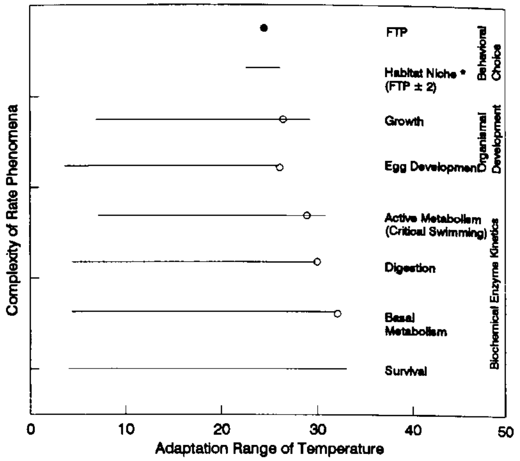

**Fig. 5.** Optimal temperatures and temperature ranges for temperature-dependent phenomena of physiological, developmental and behavioral types with large-mouth bass, *Micropterus salmoides*.

rect complex behavioral control;

— activities such as foraging and defense involve active responses that are strongly influenced by temperature-dependent biochemical enzyme kinetics but are also guided by complex behavioral capabilities;

— organismal ontogenetic development, including egg development and somatic growth, may involve development of an enzyme system as well as its functioning, and thus be more complex than catabolism and digestion; and

— behaviorally guided activities reflect evolution of intelligence, so that fish species adjust their position in the environment to influence their growth rate and enhance their activity potential.

The three categories of rate phenomena in Figs. 3–5 do not provide a clear-cut separation of various processes. Approximate as this ordering may be, a general temperature adaptation pattern is apparent for these fish species. In general, species adapted to cold, cool and warm-temperature water bodies show a similar "summary pattern" except for the left-right shifts along the temperature axis:

— the more "complex" the process, the "narrower" is the range of temperature tolerance;

— the somewhat anomalous lower temperature range for egg development may correspond to different spring or autumn temperature spawning periods, and the other physiological and behavioral processes summarized here are acclimated to summer temperatures;

— with respect to egg development it may be that maximizing the rate of development may be constrained by other life history considerations, e.g. relative safety from predators that may be comparatively less active at low temperatures or a biotic state of the spawning environment in which egg predators may be scarce at that time of year;

— the maximal point of a process is nearer the up-

per lethal limit than the lower lethal limits; and
- the maximal points of complex processes approximate the final temperature preferendum rather than the ultimate upper incipient lethal temperature as with the less complex processes.

## Habitat temperature and year class abundances

The technique of aging fish using data on annuli on scales was applied in the 1930s by our Toronto predecessors in comparative studies of a number of populations for a particular species. They inferred a synchrony of strong year classes in different populations of smallmouth bass, say, in southern Ontario. When the pattern of annuli on scales came to be used for backcalculating the amount of growth of a year class in different years, it was observed that strong year classes and above average growth tended to occur in the same years and that the summers of these years tended to be warmer meteorologically than other summers. Much research has been undertaken, and some is still underway, on the causal connections between these observations. A general inference: toward the northerly edge of the geographic range of a number of our fish species the young-of-year tend to grow better in warm summers and reach a relatively large size which then predisposes to their survival over the first winter. The relative abundance of the survivors is a key determinant of year class abundance. Dynamic simulation models have been developed for this combination of phenomena for a number of species (e.g. Shuter *et al.* 1980). A number of tests have been conducted concerning the realism of these simulation models (e.g. Shuter *et al.* 1985); the results were sufficiently encouraging so that the models have been used for assessing likely effects of climate warming (Regier *et al.* 1990).

In developing the dynamic simulation in the late 1970s (Shuter *et al.* 1980) we did not incorporate model components based explicitly on a general temperature-related function derived from laboratory studies like those sketched in the section above, e.g. the relevant Arrhenius model. Preliminary examination had shown that the growth function for smallmouth bass derived from some laboratory feeding studies, when combined with habitat temperature data of the kind available from the field observations, did not yield satisfactory results. So the temperature-related components in our simulation model were based on informed judgement and were not transparent with respect to the causality involved. A study was then undertaken to explore this problem further (Ing 1994).

Ing's exploratory study used a compendium of information on the smallmouth bass population of Lake Opeongo in Ontario. Estimates of the relative abundance of year classes of this population were available from B. J. Shuter (Ontario Ministry of Natural Resources) for the period 1937 to the present. Data on the summer temperature regime of surface water at one site on the lake were estimated using meteorological data from a weather recording station some 30 km away plus a transformation function of air temperatures and water temperatures based on a data series of concurrent air and water temperatures collected over the years 1964 to 1987. Spawning initiation temperature and date were inferred from field observations of over 600 spawning events between 1956 to 1965. The quantitative relationships of length of time required for a particular developmental stage and temperature was obtained from the literature (Ing 1994). The quantitative relationship between juvenile growth rate and temperature was inferred from laboratory studies (Ing 1994, Lin 1995). The overwinter survival as a function of size attained at the end of the first growing season was as estimated by Oliver *et al.* (1979) and Shuter *et al.* (1980).

When these components were assembled into a dynamic simulation and run with the relevant data it became apparent that the size attained at the end of the first growing season was too small, according to direct observations for some years and according to data from back-calculation of older members of the relevant year classes. Because the growth function was derived from laboratory studies in which ad libitum feeding to satiation was assured, it seemed unlikely that the growth function was seriously underestimated. We then speculated that the available habitat temperature data for the lake may underestimate the habitat temperatures actually experienced by the young bass. The data on habitat temperatures were then increased in an exploratory way, by standard 1°C increments, and the simulation run with the augmented temperatures. Only when the total increment reached 5°C, over the entire data series, did the estimated lengths at the end of the first growing season approximate those actually observed by direct sampling and/or estimated from back-calculation. But the results from these simulations, with habitat temperature data all increased by 5°C, did not yield meaningful results with respect to the observed direct relationship between average summer air temperatures and relative year class abundances over the span of years.

An hypothesis that emerged from this exploratory study was that the temperature estimates available for the one reference site in the lake did not approximate closely the temperature actually selected and experienced by the young-of-year bass in a bay some distance removed from the temperature reference site. These bass may have found much warmer sites than the one for which the data were estimated. Also the temperatures experienced by bass in different summers may not have been correlated closely with the water temperature estimates derived in part from air temperatures, because of differences in the spatial scales of these phenomena. Thus the available temperature data series may be both biassed and imprecise with respect to the issue of recruitment of smallmouth bass. Alternatively, or in addition, the growth model estimated from laboratory studies may be inappropriate for these field purposes; a "scope for growth" model might have been more appropriate, noting that a "scope for growth" as a function of temperature may be different in laboratory and field conditions.

## Habitat temperatures of species associations

For centuries stream anglers have been aware of the habitat temperature preferences of different species of fish. These preferences have been described quantitatively for the more valued of the stream fish by fisheries biologists. This knowledge has been used to protect some streams from the kind of human interventions that would have led to warming of stream waters beyond the tolerance limit of a valued species. The valued fish species may then have been used as an indicator species for the ecological quality of the whole stream ecosystem. If the species is also sensitive to other consequences of a suite of human interventions from which the stream ecosystem is to be protected, then the species may be used as an integrative indicator for the effects of the whole interactive set of interventions. In our part of the world the brook trout, or some other salmonid (Regier 1992), has often been used for such purposes, in streams and lakes. Because much is already known about the sensitivities of some integrative indicator species, and data series for populations in particular waters may already be many decades long, it would be timely and efficient to adapt the use of such species to assess and monitor the effects of climate change. A World Salmonid Watch has been proposed to mobilize this opportunity (Lin and Regier 1995).

Magnuson *et al.* (1979) developed the notion of habitat temperature as a "resource". A fish species was likely to be found in a relatively narrow temperature range of about 4°C which encompassed the final temperature preferendum, if such waters were available and not degraded by other influences. Christie and Regier (1988) found corroborating evidence with an indication that a species was likely to thrive in a particular body of water in proportion to the time-weighted measure of "optimal habitat", i.e. with temperature within the 4°C habitat niche, to be found in that water body. This inference was then applied to assess likely effects of climate warming on some species populations in some lakes, with estimates of changes in temperature regimes due to climate warming provided by hydrographers (Regier *et al.* 1990).

Wichert (1995) developed a kind of extension of the concepts of indicator species as related to temperature phenomena. He developed an index termed the Weighted Species Association Tolerance Index with respect to Water Temperature, *WSATI-WT*, of the fish association to be found in a particular locale of a stream.

$$WSAT-WT = \sum_{i=1}^{N} A_i FTP_i$$

where $A_i = n_i/Sn_i$, the relative abundance of each species as a proportion of total catch as estimated from data obtained by using a set of sampling gear that yields a relatively unbiased sample;

$n_i$ = the number of individuals of species $i$;

$N$ = the number of species found; and

$FTP_i$ = the final temperature preferendum of each species $i$.

This index is an overall weighted mean of the

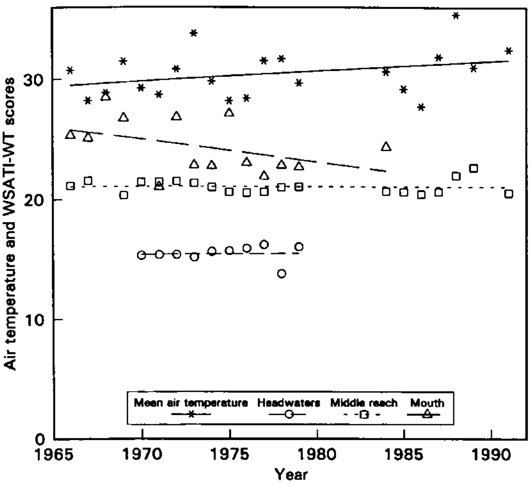

**Fig. 6**. Water temperature index scores at three sampling sites in the Duffins Creek Watershed over time as possibly related to 6 day mean maximum air temperatures (also see Fig. 7).

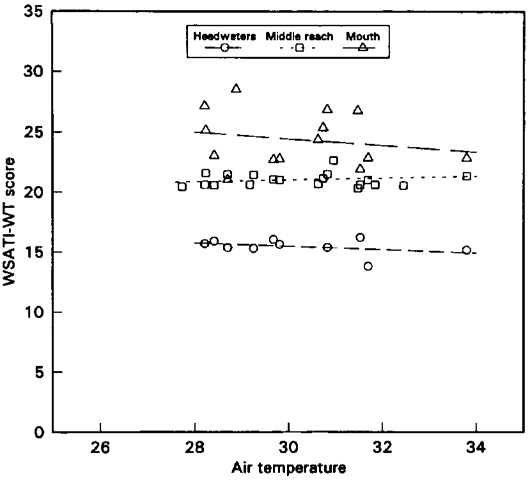

**Fig. 7**. Relationship of *WSATI-WT* scores for three locales in Duffins Creek — one near the headwaters, one in the middle reaches and one near the mouth — and the mean of the maximum air temperatures of the warmest six consecutive days of each summer from 1966–1993. The air temperatures were taken at a location 50 km west of the Duffins Creek watershed. Each data point on the figure represents an air temperature and a *WSATI-WT* score for one year in the 1966 to 1993 period.

*FTP* of the species present at a sampling site on a given occasion, normalized or standardized to a single fish basis by means of the $A_i$ term. Note that larval fish less than about 2 cm length pass through the gear and were not sampled in the present study. Data were collected in the months from early summer to early autumn.

The statistical behavior and any ecological meaning of this index were then investigated with data collected periodically since the 1940s from many sites on numerous streams in the Toronto Area (Wichert 1995, Wichert and Regier 1997, Wichert and Lin 1996). Figs. 6 and 7 are based on data collected in an appropriately standard way over the years in field trips in an undergraduate ecology course.

The measure obtained for *WSATI-WT*, for a site in a stream in which the site and an extensive upstream reach have not been altered for many years, appears to relate fairly closely to the average of the maximum annual stream temperature at that site. The measure appears to vary less from year to year than the actual maximum stream temperature, so that there appears to be some ecological inertia that interferes with rapid adaptation of a fish species to year to year differences by shifting its location upstream or downstream in response to hotter or colder air temperatures respectively. At some sites there have been gradual changes in the measure with the direction of the changes broadly consistent with general observations on human interventions that could be expected to change the water temperature regime. Thus this index may prove useful for monitoring effects of climate change in fish and may complement the use of geographic limits of the ranges of sensitive species for this purpose (see examples in Regier *et al.* 1990).

If the sampling protocol used to collect data on fish species present at sites in streams only focused on the presence or absence of species, rather than on the relative abundance of different species, then a simplified version, i.e. *SATI-WT*, is available (Wichert 1995). This index may also be used in situations where the sampling protocol in different time periods had different biases for different species, so long as the probability of actually catching a fish of a particular species when present at a site was not markedly different over time.

The *WSATI-WT* index, and its simplified version, have interesting and promising statistical and ecological characteristics (Wichert 1995). Whether they can be adapted for standing water ecosystems has not been explored.

## Ecological aspects of effects of climate change

In 1993–1995 the Intergovernmental Panel on Climate Change (IPCC) produced its second comprehensive report on the likely atmospheric features and timing of climatic change on biophysical assessments of effects and possible biophysical adaptations to such climate and on related institutional and political aspects. Because the first listed author of the present paper was one of the lead authors of IPCC/Fisheries (Everett *et al.* 1996), its contents may be taken to be consistent with the understanding of the authors of the present paper. The text related to freshwater fisheries in that chapter is summarized below.

The first fish populations responding to climate changes will probably be those in streams, which have a high rate of heat transfer from the air, on the warm or cold margins of their species' native ranges (Holmes 1990). Climate change will likely lead to earlier spring melting and greater amounts of winter runoff. Pristine and unregulated rivers and streams will be the most susceptible to warming and runoff damages. Managed rivers and streams have more impoundments with opportunities for coldwater species to find suitable temperatures. Managers can also control critical temperatures through water releases and the amount and timing of runoff.

Freshwater fish populations may be constrained to their watersheds. Except for lake and stream systems that run poleward (Regier and Holmes 1991) they cannot migrate beyond them but must endure or succumb (Shuter and Post 1990). In large drainage systems, some shifts to high (cooler) elevations may also occur (Meisner 1990). The flexibility for shifts will be much greater in north–south than in east–west flowing systems. Some additional movement may occur by intervention with stocking programs. Other species that cannot move or adapt may become extinct or suffer population decline (Coutant 1990). Some stocks in some streams and lakes are already at their maximum temperature limits (Matthews and Zimmerman 1990, New Zealand 1990).

Warming should produce a longer growing season for species that have not attained their maximum temperature limits (Shuter and Meisner 1992), but warming may also lead to increased thermal disassociation and thus to less productive conditions. For example, in rivers, low oxygen at low flows can severely limit fish production. Greater fish production should occur in high latitude lakes and reservoirs (Schlesinger and McCombie 1983). Tropical lakes have longer growing seasons and faster generational succession and usually produce higher fish yields than temperate lakes because fish mature at earlier ages. Mean annual air temperature is the most important factor in predicting lake fish production across latitudes (Schlesinger and Regier 1982), but changing rainfall patterns and flood regimes may have profound effects on river fish (Meisner and Shuter 1992).

In a study using fish bioenergetics models, certain Great Lakes fisheries were found to have potentially greater yields while others might collapse (Hill and Magnuson 1990). White perch, a species of low value, might be among those with increased range and improved recruitment because of a longer growing season and shorter, milder winters (Johnson and Evans 1990).

Yields in southern Lake Michigan and eastern Lake Erie are projected to remain about the same for lake trout and lake whitefish but increase for walleye. Thermal habitats are expected to increase except for cold water species in Lake Erie where some deep water would become anoxic in summer (Magnuson *et al.* 1990). Large lake fish production could increase about 6% with a 1°C rise in average annual air temperature (Meisner *et al.* 1987).

In large lakes there may well occur an invasion by warmwater exotic species (Mandrak 1989) where invasion routes are available. An example is the striped bass (*Morone saxatilis*). Warming could threaten the striped bass existence in the Gulf of Mexico and Florida coastal waters and southern USA lakes and reservoirs. However, east coast populations could move further north and perhaps enter the Great Lakes, where it might thrive in the lower lakes, and compete with salmonids (Coutant 1990).

Changes in species dominance may occur. Each population has adapted to an ecology with specific temporal and spatial features. For example, in New Zealand, native species occur throughout the nation while introduced species seem to be temperature-limited in their distribution, suggesting that indigenous species may be more resilient than exotics in a warming climate (New Zealand 1990). Species invasions and removals occur frequently, even without human causes, but climate and habitat change should accelerate them. Indigenous species will be subject to greater pressures from shifts in ecosystem structures than opportunistic exotics (Lodge 1993).

It is intuitive to expect poleward range movement for species with climate warming (Shuter and Post 1990). However, habitat, food supply, predators, pathogens and competitors must be within the species ability to cope. Further, there must be a suitable dispersion route, not blocked by land, or some property of the water, such as temperature, salinity, structure, and currents, or oxygen availability. Movement of animals without a natural dispersal path may require human intervention or hundreds or thousands of years (Kennedy 1990).

Positive factors associated with greater warming and precipitation at higher latitudes include faster growth and maturation rates, less winter mortalities due to cold or anoxia, and expanded habitats with ice retreat. These should offset negative factors such as increased summer anoxia, increased demands for food to support higher metabolism, possible negative changes in lake thermal structures, and reduced thermal habitat for cold water species. Individual effects are difficult to integrate. However, since warm water lakes generally have higher productivity than cold water lakes, and since existing warm water lakes will be in areas with the least change in temperature, it is reasonable to expect higher overall productivity from freshwater systems. Most warming should occur during fall and winter and summer nighttime temperatures. This will greatly help all species that have problems with cold. Streams may be no more likely to reach high lethal temperatures. Lastly, fishery managers heavily manipulate freshwater fisheries in much of the world. They constantly change species mixes to support angler and market preferences and changing habitats. This will dampen damages and heighten benefits from climate change.

In the remainder of the present paper we turn to some ecological considerations relevant to northerly freshwater fish and fisheries with respect to likely climatic change as described in Everett *et al.* (1996).

## History of glaciation and taxon plasticity

Much of the land area of the northerly part of our biosphere has been under continental ice sheets repeatedly in recent geological history. The geographic limits of distribution of countless species have been gradually transposed with the advance of an ice sheet and populations of the species then became adapted to habitats that differed in many ways from those of an inter-glaciation period. Many generations later fish populations again returned to the former geographic regions, now much changed due to scouring, deepening and other effects of glaciation.

Taxa of a number of families of freshwater and anadromous fish in northerly parts of North America appear to have been quite adaptive with respect to phenomena of the scale of continental glaciation. These include salmonids and especially salmonines and coregonines, esocids, osmerids, some percids such as *Perca* and *Stizostedion* species, some cyprinids, etc. Has their geological and evolutionary history as related to glaciation pre-adapted such taxa to the likely consequences of an unprecedented degree of climate warming? This question has not attracted much attention by experts on fish, apparently.

The genetics of salmonids, as related to habitat adaptability, appear to be unusually plastic. Polyploidy is apparently the rule, and the possible redundancies of genetic information may contribute to the plasticity with respect to natural phenomena. But such plasticity did not pre-adapt individual salmonid taxa generally to the habitat consequences of modern human industrial development (Loftus and Regier 1972).

The concept of a "species" is always an abstraction and especially so with salmonids. What the evolutionary entity should be taken to be, in a particular scientific/practical context, remains a perplexing issue. Should it be a distinctive locally adapted population, an eco-taxon, a sub-species, a species, a genus or a sub-family — with each of these as defined by consensus within a suitably expert network of peers among the systematists? One can perhaps make a case for each of these, in a particular setting relevant to it.

In North America, the evolutionary systematic diversity, ecological functional complexity and biogeographic mosaic diversity of the salmonid association has been greatly simplified during the past two centuries. The story has been sketched generally (Loftus and Regier 1972) and with respect to some particular contexts (Goodier 1981). This general phenomenon may well be relevant to an assessment of the consequences of climate change. Presumably regions with genetically simplified fauna in grossly modified habitats may be vulnerable to more extinctions, in the already depauperate faunal association, than regions that are more nearly pristine in this respect.

As a general rule, the adverse effects of different kinds of human interventions in the Laurentian Great Lakes, say, appear to interact synergistically in an undesirable pathological way (Rapport and Regier 1995). This was taken to be a threat generally by Everett *et al.* (1996).

## Translocation corridors

Biogeographic research on the fish species present in different waters of Canada shows that there were barriers to the re-colonization of some water by some species following deglaciation. Some of these barriers appear to have been effective for the approximately 8000 years since the last case of deglaciation (Mandrak 1995). Minns and Moore (1992) have begun to examine such inferences with respect to their application to forecasting effects of climate change.

Mandrak (1989) also focused attention on the southerly border of the Great Lakes region, which appears to be quite porous with respect to northward invasion of the Great Lakes Basin by more southerly species following climate warming. He developed a set of criteria with which to assess the likelihood of such invasion by a wide variety of fish species. None of the likely invaders from contiguous southerly watersheds appeared to be a threat with respect to becoming a major pest in the Great Lake Basin.

The general direction in which the water in a river system flows has particular relevance to effects of climate change. In North America the temperature-related geographic boundaries of biomes tend to trend in a northwest–southeast direction. The warming effects of climate change will likely transpose such boundaries towards the northeast, as a broad and imprecise generalization. River basins that empty towards the northeast thus contain corridors along which a warm-sensitive species can translocate with climate warming. For river basins that empty in a general southwesterly direction of the shifting temperature isoline, warm-sensitive species may be stranded unless the boundaries between watersheds are appropriately porous or unless humans undertake appropriate rescue operations.

In North America as in Eurasia, much of the northerly or boreal area of the continent drains northward (Regier and Holmes 1991). The Great Lakes drainage dips quite far south before it turns northeastward again, but the deep lakes will presumably provide deepwater refugia for many warm-sensitive species.

Even with respect to river basins that trend northeastward, some sub-basins trend in the opposite direction before joining the main river. Such sub-basins may become traps for species populations, especially if climate change were to occur quite rapidly.

## The Great Lakes Basin, in particular

Comparatively much attention has been directed to assessing the effects of climate warming on Great Lakes fish and fisheries (e.g. Meisner *et al.* 1987, Regier *et al.* 1988, Magnuson *et al.* 1989, Regier *et al.* 1989, 1990, Regier 1993, Everett *et al.* 1996).

As already stated, the Great Lakes Basin fish association is now severely depauperate in many locales with respect to native taxa, especially at the level of organization below the conventional genus level. For the native taxa, climate warming will likely bring some new distresses and will likely exacerbate synergistically the adverse effects, separately and interactively, of prior distresses. There may be specific aspects of the degradation syndrome for which climate warming may act as a mitigative factor, but such instances have not yet been documented, apparently.

A wide variety of exotic species of fish and other taxa have now become "naturalized" in the Great Lakes Basin. Some of these, notably clupeids, osmerids and salmonids, came together in a self-organizing way to create a new pelagic association of a general type that did not exist previously in the Great Lakes (Regier and Kay 1996). This pelagic association bears some resemblance to the association of anadromous species of the shelf seas off North America. These shelf seas are enriched from land and from subsurface upwelling of deeper waters onto the continental shelf. The pelagic association, largely of exotic taxa, in the Great Lakes may have better pre-adapted capability to effects of climate warming than the pristine benthic association of indigenous taxa had.

Massive programs to rehabilitate the Great Lakes ecosystem are fostering a recovery of some of the general features of the pristine benthic association and suppressing some features of the exotic pelagic association. At this level of generality, a partial recovery of the benthic association may make the entire Great Lakes fish association somewhat more sensitive to the effects of climate warming.

Climate warming may well make the Great Lakes ecosystem more hospitable to exotic species, some of which have few redeeming qualities, as is the case with some exotics already in the lake. Ships generally use water as ballast and such water inevitably contains organisms of the type present in the locales where the ballast was pumped into the ships. Many of the current generation of ships are designed architecturally so that effective "sterilization" of such ballast water is not possible. Also not all the water can be exchanged for less risky water, as in the open ocean, because of vessel design features. Many ship owners and masters have been irresponsible heretofore with respect to the ballast water problem. Though many of this breed of exploitive environmental abusers will likely mend their ways, however grudgingly, some criminal elements will likely persist for another generation or more. Thus continuing infestation with exotic species by ballast water can be expected for some decades to come. Permanent closure of the St. Lawrence Seaway into the Great Lakes should perhaps be expedited, for this and other reasons.

Within the Great Lakes the very indistinct vertical and horizontal boundaries between different sub-associations of fish species will likely translocate with climate warming. The "boundaries" of the salmonid domain will likely shrink to deeper waters and in a northerly direction, because the southerly part of the Great Lakes is the southerly limit of most of the salmonid taxa. The esocids, percids and cyprinids will likely adapt by substitution of species within families at a particular locale, because the Great Lakes Basin is not at a northerly or southerly limit for taxa of these families generally. The Great Lakes was the northerly limit for numerous centrarchid species and for percichthyids (white bass) and taxa of these families will likely extend their domains further offshore into the lakes and in a northerly direction. All of these families have species that are accepted as valued by angler, artisanal and commercial fishers.

Warming of the Great Lakes, ceteris paribus, will likely lead to some increases in productivity of the fish association (Regier *et al.* 1990). But efforts to reverse cultural eutrophication through cultural oligotrophication may now be causing an opposing trend. With rehabilitation, the economic or cultural value per unit mass of the available fish species will increase, and such values may not be much affected overall by the substitution by warm-adapted species of the previous cold-adapted species in a particular locale.

As is apparent from the above sketch, the ecosystemic dynamics of the Great Lakes Basin waters are now turbulent (see also Regier and Kay 1996). It would be unrealistic to expect that a definitive assessment of effects of climate change could be achieved for this ecosystem, even if a reliable scenario of atmospheric warming were available. Major events that no one will have predicted will occur. But the emergence of surprises has been a repeated occurrence for a century now. So one reliable forecast or assessment may be: new unpredictable events will emerge in this ecosystem which will remain turbulent for some decades into the future. After the fact it may be possible to sort out what the role of climate change was with some of these events. Meanwhile a "strategy of no regret" may imply that further rehabilitation of this degraded ecosystem makes good sense, on balance.

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