Climate Change and an Ecosystem-Resource Adaptation Approach for Vulnerable Lakes in the Boreal Plain Ecozone

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Executive Summary

All major climate-change agenda efforts in recent years echo the need for more empirical scientific information about climate change and adaptation to freshwater ecosystem impacts. The adaptation research undertaken in this study begins the process of providing answers to the general question posed by resource managers and other stakeholders, “What options can we choose from to ensure the sustainability of the aquatic resources under our stewardship?” More specifically, the research results in a systematic methodological framework which resource managers could build on to determine adaptation options for specific lake types, as well as examples with respect to such options.

Research concentrates on the numerous larger lakes in the Boreal Plain which, although they are not necessarily “cold” lakes, tend towards the “cold” end of the temperature spectrum. The biophysical components of these lakes are highly vulnerable and, unlike some of the smallest lakes, which could simply disappear if climate change impacts were extreme, many of the biophysical elements of these lakes would probably continue to exist. The research in this study addresses resources in relation to climate change and adaptation at three levels of ecological organization. The three are lake habitat, intermediate levels in food webs, primarily small-bodied fish species, and large-bodied fish species.

This study focuses primarily on two large-bodied cold-water species, lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*), both salmonids. All analyses begin under the umbrella of climate-related total allowable catch, or TAC, probably the most direct, integrative, management tool. Yield calculations per se have been based on relatively simple empirical models, in which fishery yields are related to summer thermal habitats.

Two lakes were selected for inclusion, Lake Winnipeg and Kingsmere Lake, Prince Albert National Park, as examples of a large but relatively shallow water body and a relatively deep system respectively. Lake Winnipeg deserves special attention simply because it is one of the world’s great lakes. Kingsmere Lake provides one of the few examples of a cold, dilute system for which one can investigate process and pattern, in an integrated manner, across a range of trophic or food web levels.

This study offers resource managers the only set of empirical harvesting models for cold freshwater fish which will conserve population structure in the target populations. These models are based on climate-related habitat features. These models substantially improve the precision of previous efforts; more importantly however, they add accuracy through the incorporation of conservation considerations. Continued use of any previous empirical models will ultimately have disastrous effects on all freshwater fisheries, if they haven’t already. The new climate-based TAC models are highly predictive for most lakes, but analyses indicate the model for lake trout may be inadequate for lakes <1000 km^2 in surface area. More work is needed in the development of the lake whitefish TAC for all lakes, regardless of size, since sustained yields may yet be overestimated by the model developed in this study. As a great lake, we need to

know far more about all aspects of Lake Winnipeg to manage it properly, regardless of the issue or context.

It is probable that we can best adapt to climate change through proper management of our remaining fish stocks. Additional management adaptation requirements include the development of adequate fishery monitoring programs, few of which exist in the Boreal Plains Ecozone. In the short term, management agencies across the Boreal Plain Ecozone should implement a moratorium on lake trout fishing; this is the only real hope for the lake trout of the ecozone. The management agencies should also implement a comprehensive in-depth assessment of the state of surviving lake trout populations. Lake trout in the Boreal Plain are in a similar situation to that of large carnivores in the Rocky Mountains, where the fate of the “last of the last, not the last of the best” (c.f. P. Paquet) is at stake.

1. General introduction

There has been little, if any, research on adaptations to climate change impacts on the ecosystem resources of Canadian lakes. All major climate-change agenda efforts in recent years (e.g. Canada Country Study-Prairie Internet Conference 1998) echo the need for more empirical scientific information about climate change and adaptation to freshwater ecosystem impacts. The prairie provinces' portion of the Canada Country Study (CCS) emphasizes that the "information gap is especially significant in light of the fact that freshwater systems are critical to...sustainability and are tightly coupled to both climate and land use activities" (Herrington et al. 1997). The synthesis of the CCS follow-up symposium (CCAF 1998) lists water and ecosystem-related concerns as two of the priority areas for research, based on the recommendations of at least seven of the nine working groups. In particular, the CCAF has identified adaptation research based on the retrospective analysis of the variation in ecosystem impacts as an immediate priority, especially with respect to fisheries' ecosystem concerns (CCAF 1998).

The adaptation research undertaken in this study begins the process of providing answers to the general question posed by resource managers and other stakeholders, "What options can we choose from to ensure the sustainability of the aquatic resources under our stewardship?" More specifically, the research results in a systematic methodological framework (elements of a basic "expert system", e.g. Booty et al. 1992, Koning et al. 1998) which resource managers could build on to determine adaptation options for specific lake types, as well as examples with respect to such options. The conceptual basis for the approach is that the generally accepted principle that ecosystem health and integrity are paramount, and that caution with respect to human actions is a guiding philosophy. These aspects are particularly poignant, since the adaptation of management practises to climate change may have as much or more of an effect on resources as climate change per se.

The study builds on the analytical approach taken in the MacKenzie Basin Impact Study (MBIS; Melville 1997) portion of the Canada Country Study. Adaptation interpretations are based on climate relationships established by way of multivariate empirical equations, incorporating both seasonal and interannual variation in biophysical variables. Research concentrates on the numerous larger lakes in the Boreal Plain Ecozone which, although they are not necessarily "cold" lakes, tend towards the "cold" end of the temperature spectrum. The biophysical components of these lakes are highly vulnerable and, unlike some of the smallest lakes, which could simply disappear if climate change impacts were extreme, many of the biophysical elements of these lakes would probably continue to exist.

1.1 Adaptation approach

The research in this study addresses resources in relation to climate change and adaptation at three levels of ecological organization. The three are lake habitat, intermediate levels in food webs, primarily small-bodied fish species, and large-bodied fish species.

At the habitat level, examples of concerns with respect to climate change are reductions in vertical mixing and oxygen concentrations. There is a spectrum of adaptation options available to resource managers. One possibility with respect to decreased oxygen, for example, would be to oxygenate directly, currently the practise in a few prairie lakes. A more feasible, cost-effective yet sophisticated approach to adaptation might begin with changing the way fish communities are manipulated through harvesting. Adaptation in this way could result in altered nutrient pathways, changing patterns of organic decomposition thus oxygen depletion.

The second set of resources examined is based on projected impacts in the relationship between fish at intermediate levels in food webs, and climate, other physical variables and food web consumers. These fish feed a variety of larger fish, birds and mammals, for example, and are highly sensitive to climate influences. A major concern is that, via a number of factors, climate change will affect these fish, resulting in increased competition with the young of large-bodied fish species, and excessive numbers of water birds. Increasingly, these considerations cause confrontations across the prairies with some of the more active resources users. Adaptation could require numerous changes in the ways we treat habitat and harvest large-bodied fish.

The third resource area requiring investigation is the way in which we manage large-bodied fish species, particularly with respect to the species composition of assemblages, and the extent and timing of harvests. An important adaptation issue, for example, is the suggestion that warm water fish species could be introduced to replace cold water species, which might disappear. We don’t know where many of the cold water species will disappear, and any new species would currently constitute the introduction of exotics. The introduction of exotic species could displace important species which could thrive, even improve, under changed climate regimes, and disrupt lake community structure and function.

This study focuses primarily on two large-bodied cold-water species, lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*), both salmonids. All analyses begin under the umbrella of climate-related total allowable catch, or TAC, probably the most direct, integrative, management tool. The process of yield determination in a climate context is currently based on an intermediate step, which includes thermal habitat quantification and prediction:

$$\text{climate} \rightarrow \text{thermal habitat} \rightarrow \text{yield}$$

I investigate whitefish from the perspective of thermal habitat area, since whitefish are bottom feeders. Lake trout are investigated via thermal habitat volume, since they are more dependent on planktonic trophic pathways. The study also includes lake herring or cisco (*Coregonus artedi*), which is fished in some lakes, however no TAC models appear to exist for this species.

Yield calculations per se have been based on the relatively simple empirical models of Christie and Regier (1988), in which fishery yields are related to summer thermal habitats -

lake whitefish	$\log_{10} SY = 0.60 \log_{10} THA + 2.14$	$R^2 = 0.66$
lake trout	$\log_{10} SY = 0.81 \log_{10} THV + 0.94$	$R^2 = 0.86$

where SY is sustained yield in $kg^{-1}y^{-1}$, THV is summer thermal habitat volume in hectometres^3• $10d^{-1}$ from June 5 to September 2, and THA is summer thermal habitat area in hectares•$10d^{-1}$ for the same period as THV. R^2 is the variation explained by the regressions. Schlesinger and Regier (1983) proposed the term “sustained yield” (SY) for species-specific estimates of stable maximum catch, values of which were used to compute the regressions. These values are considered to be estimates of the maximum sustainable yield (MSY), however there is no way of determining the extent to which they differ (e.g. Schesinger and Regier 1983).

Thermal habitats can be defined in two ways. The “narrow” habitat is the median preferred temperature ±2˚C, the range within which a fish in a preference tank in the laboratory will spend two-thirds of its time. The “broad” habitat is the median preferred temperature ±5˚C, the range within which a fish chooses to spend all of its time if such temperatures are available. Pelagic volumes within the thermal habitats for each species would be calculated from isotherm representations of thermal structure and the hypsographic, cumulative area versus depth, curves for the lakes (Christie and Regier 1988).

All applications of the yield models in this study incorporate a new parameter, a biodiversity conservation coefficient or correction factor, which would allow for the preservation of age and size structure in harvested populations (e.g. Melville 2001). Most of the fisheries used as examples to generate the models of Christie and Regier (1988) crashed subsequent to the period represented by the ‘sustained’ yield data. The biodiversity Conservation Coefficient or CC equals the yield of Christie and Regier (1988) divided by a yield limit, 0.05 kg ha^{-1} and 0.10 kg ha^{-1} for lake trout and lake whitefish respectively. The CC varies between 0 and x, some unknown value which precedes the extirpation of a population. For $0 \leq CC < 1$, the traditional sustained catch of Christie and Regier will increase, for $CC = 1$, it will remain the same, and for $CC > 1$, the sustained catch will decrease. The value for lake trout is relatively robust (Melville 2001), while the value for lake whitefish is still more subjective.

Arguably, lake whitefish constitute the most important commercial species in the ecozone historically, serving such diverse areas as the smoked and gefilte fish markets. They have somewhat of a dual role ecologically, with young fish serving as food for top predators such as lake trout. Lake herring fill a similar role. Adult whitefish occupy a summit position in benthic trophic pathways, while lake herring occupy more of an intermediate position in planktonic pathways.

Lake trout have special ecological attributes and requirements which elevate the importance of lake trout to society. Lake trout grow slowly, take about a decade to mature and then spawn infrequently, processes through which it can take at least three decades for an individual to contribute fully to the biological potential of a population. They product relatively small numbers of eggs, which must endure harsh conditions as the eggs overwinter on the spawning grounds. On the whole, lake trout require cold temperatures and high concentrations of oxygen. In view of these facts, lake trout constitute a classic indicator of ecosystem health for cold oligotrophic lakes, both within Canada and internationally.

Lake trout are on the decline in Canada, and nowhere moreso than in the Boreal Plain Ecozone (Melville 2001). The advent of industrial fishing in the boreal plain the late 1800's initiated the demise of many of the lake trout populations. In the early years, commercial fishers took most of the catch using gill nets. As the commercial catch decreased, the recreational side of the industry grew, particularly through the middle of the last century. Currently, recreational anglers catch most of the lake trout fished in the boreal plain.

The study period with respect to Kingsmere Lake is particularly exciting. The environmental data include various years of El Niño-ENSO extremes, including one of the two strongest El Niño’s this century (1997-1998) (Wolter and Timlin 1998), part of the longest (1993-94) (Nicholls et al. 1996), and two La Nina’s (1995-96, 1998-99) (e.g. NCEP 1999)

2. Study ecoregion and lake examples

The forested Boreal Plain Ecozone (Fig. 1) of western Canada stretches from southeastern Manitoba northwest to Great Slave Lake, in the North West Territories, and east-central British Columbia. The ecozone is in the middle of the Interior Plain of western Canada, which extends from the Prairie Ecozone in the south, through the Boreal Plain Ecozone, and up the Mackenzie River valley (Boreal Taiga) to the Arctic Ocean. These ecozones consist largely of loose surficial material rather than bedrock. The Boreal Plain contains many lakes distributed in an irregular manner throughout the ecozone. The Interior Plain ecozones have experienced the largest increases in temperature in Canada over the last century (Hengeveld 1991; Gullett and Skinner 1992).

Two lakes were selected for inclusion, Lake Winnipeg (e.g Davidoff et al. 1973) and Kingsmere Lake, Prince Albert National Park (Fig. 1), as examples of a large but relatively shallow water body and a relatively deep system respectively. Lake Winnipeg deserves special attention simply because it is one of the world’s great lakes. Kingsmere Lake, with a surface area of about 50 km^2 and a maximum depth of 49 m, provides one of the few examples of a cold, dilute system for which one can investigate process and pattern, in an integrated manner, across a range of trophic or food web levels. The relative difference in maximum depths of these example lakes helps contrast the factors one must consider in management adaptation across the spectrum of lake depths.

The first records of commercial whitefish production from Lake Winnipeg occur in 1883. By 1875 the city of Winnipeg had grown to 5000 people and the first Icelandic settlers had reached the shores of Lake Winnipeg. Fishing was their heritage and shipments of whitefish, *Coregonus clupeaformis*, and other species, reached Winnipeg aboard the new steam schooners engaged in the lumber trade. Prior to 1883, old records indicate a production of about 136,000 kg of whitefish annually in the vicinity of Fort Alexander, most of which was probably consumed locally. It was the custom of the Red River farmers about 1850 to visit Grand Marais late in the fall to fish for a supply of whitefish for the winter, and much of the annual production was probably taken during the spawning run. For over 50 years, the lake produced an average of about 1,360,000 kg of whitefish annually in the commercial catch. The annual catch ranged from a high of 3.4 million kg in 1904 to a low of 0.318 million kg in 1936. More recently, the largest catches barely exceeded the smallest catches in former years, except for 1936.

For much of the initial period, the trend of declining whitefish catches caused considerable concern in industry and government circles. Records of the Manitoba fisheries for over 30 years indicated the continual recurrence of the complaint that Lake Winnipeg waters were being over-fished, and that the total depletion of the fisheries was threatened. Subsequent investigations concluded that, in spite of the excessive fishing, or over-fishing, the supply of whitefish in Lake Winnipeg was still enormous, and concluded that there were no sufficient grounds for serious fear as to the future. Subsequently, over-fishing depleted the whitefish fishery.

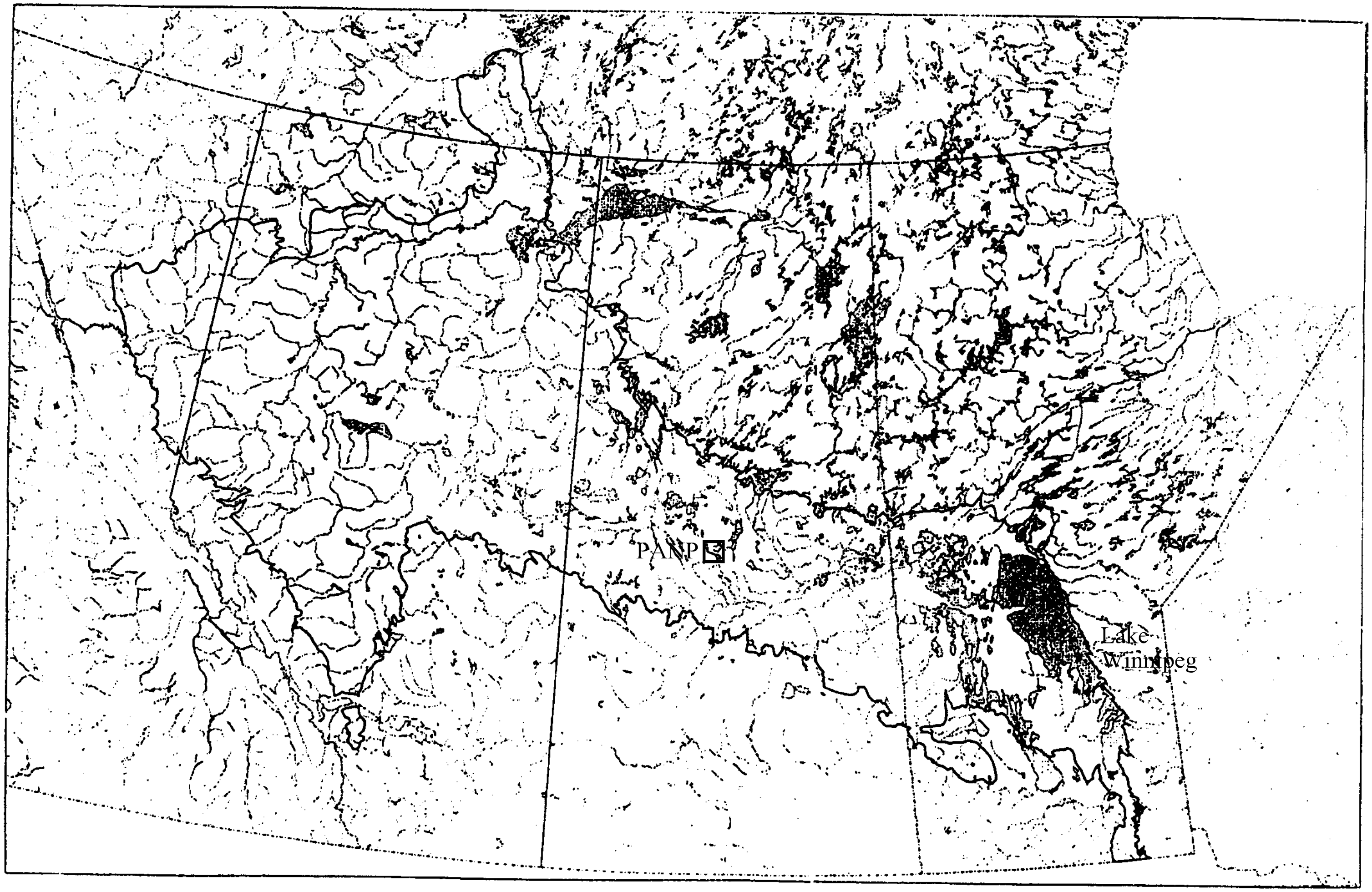

Fig. 1 Outline of the Boreal Plain Ecozone of western Canada in relation to regional political boundaries. Labels indicate example lake locations.

In contrast, intensive fishing began about 1920 on Kingsmere Lake, at which time most of the catch went to a winter net fishery. Lake trout made up a substantial proportion of the catch, second only to whitefish. Recreational angling also became more common but at lower levels of effort. Commercial fishing on Kingsmere ended in 1926-27, just prior to the establishment of Prince Albert National Park in 1928, except for brief bouts of fishing in 1943 and 1945. Initially anglers concentrated on both trout and northern pike, and took smaller numbers of walleye as well. Angling pressure has increased dramatically over the intervening years, especially on lake trout.

Recreational angling has removed enormous biological potential from the Kingsmere lake trout population, and this loss far exceeds the loss in the few years of commercial fishing prior to park creation. Anglers have removed more than 85 percent of the lake trout potential lost to fishing since 1920, while commercial netting took less than 15 percent. The loss to recreational fishing has dropped since the mid to late 1980's, but it still exceeds 85 percent of the loss during the previous fifteen years, the period of maximum catch by anglers.

3. General methods

The first-order methods used in the study are presented in detail in the Canada Country Study documents by Melville (1994, 1997). Lake herring in Kingsmere Lake had been sampled at two stations with vertical gill nets made of 25 mm stretched-mesh. This mesh size captures juvenile and early adult herring, the size most frequently eaten by predatory large fish in Kingsmere Lake.

Otherwise, the first step here was a sweeping preliminary assessment of available data potentially relevant to the study, from federal, provincial, academic and other sources, in the peer-reviewed and non-reviewed literature, institutional databases and other archival formats. Potential data sources were short-listed based on three criteria: methodological robustness, internal consistency and the readiness of availability. Examples of data sets best representing aspects of the study were selected for inclusion. The thermal habitat data came from Christie and Regier (1988), the traditional sustained yield data originated from several sources including Christie and Regier (1988), and Davidoff et al. (1973) present much of the Lake Winnipeg whitefish data. Of note, the whitefish population in Lake Winnipeg contained different adult age groups over the period studied by Davidoff et al. (1973).

All regression analyses included regression diagnostics, including examination of residuals for normal distribution, constant variance, error independence and inclusion of variables in a single linear model (Wilkenson 1985). It is important to remember in studies of this nature that the models generated are very close ‘approximations’, because they include observed data inescapably measured with statistical error, however small, as independent variables.

Specific steps in the process of formulating the adaptation approach were as follows:

1) Identification of climate linkages in practical models available to lake-ecosystem resource managers, particularly fisheries total-allowable-catch models. Sources of information included the literature and contacts.
2) Identification of the uses of climatic information in lake-ecosystem resource management on the prairies. Usage was expected to be sparse, with the exception of some fisheries catch models. Information sources included regional technical literature, resource program materials and contacts.
3) Using 1) and 2), the development of a conceptual pathway for adaptation, establishing climate linkages with key aquatic ecosystem components. This step is both deductive and inductive, and provides us with a window on how climate could affect potential management actions.
4) Using 3) and impact considerations suggest adaptation options for selected lake-ecosystem examples from the prairie provinces.
5) Assess analysis pathways, based on different adaptation possibilities. Given some of the gaps with respect to projected impacts, determining an adaptive approach is an iterative process.
6) Make recommendations with respect to the immediate applicability of the adaptation approach.

4. Habitat factors

4.1 Habitat, a basis for Total Allowable Catch (TAC)

In this section, I investigate the hypotheses that thermal habitat area (THA) and thermal habitat volume (THV) are proportional to general lake morphometric variables i.e. surface area and mean depth, relationships which one can express in simple empirical models. Management agencies can use THA and THV as direct indeces of species-specific thermal habitat, however, we lack the data required to calculate the variables for most lakes. In lieu of these data, one could calculate the indeces from more widely-known morphometric data. Alternatively, one could substitute the morphometric variables in Total Allowable Catch models, in place of thermal habitat measures, accompanied by the appropriate coefficients or correction factors.

Lake SURFACE AREA predicts lake whitefish THA for example, with more precision than MEAN DEPTH (Fig. 2), although the gap narrows to about ten percent when one outlier is dropped from the relationship (Table 1). Stepwise regression includes only SURFACE AREA when both area and MEAN DEPTH are initially included in the model statement. Single regressions for each of the two variables are probably close linear approximations of curvilinear relationships (Table 1), since the data points start to plateau slightly to the right as the independent variables increase (Fig. 2). Despite the limited thermal habitat data, less than twenty percent of the variation in the data scatter remains unexplained.

Lake MEAN DEPTH predicts lake trout THV with marginally more precision than SURFACE AREA (Fig. 3), and is included first in stepwise regression. Area is kept in the stepwise regression (Table 1) even though there is a well defined linear relationship between area and MEAN DEPTH. While distance-weighted-least-squares indicates pronounced curvilinearity in the multivariate (THV) relationship (Fig. 4), there is little suggestion that upper limits occur in regressions incorporating independent variables as polynomials. All-in-all, the variation in the data scatter remaining with respect to THV is at the level ascribed to chance, about five percent.

4.2 Climate variables as habitat indicators

Since many shallower lakes lack limnological data, we can ask whether climate variables, for example, air temperature, could serve as habitat indicators of sustainable catch directly, at least on an interim basis. Surface water temperatures are very closely associated with air temperatures, which in turn exhibit a multitude of different patterns. Air temperatures are available for Winnipeg, including the period of comprehensive scientific catch data for the whitefish fishery on Lake Winnipeg, from the 1930's to about 1970. Regression analyses of annual and seasonal mean temperatures over time revealed no significant trends for the period from 1930 to 1970, but with the exception of autumn, there was a tendency towards inverse relationships (e.g. Fig. 5, Table 2). In other words, annual, winter, spring and summer temperatures may have decreased through the four decades. I return to the role temperature as a habitat indicator in relation to fishery yields in Section 5.2.

4.3 Climate and vertical thermal habitat

Several hypotheses related to climate effects and vertical thermal responses are investigated here, specifically with respect to deeper lakes. In contrast to shallow lakes, the thermal aspects of such lakes can be far more complex, particularly with respect to vertical mixing and thermal structure during the open-water season. The main hypotheses investigated state that the vertical thermal gradient (alternatively, resistance to mixing) in Kingsmere Lake varies with the extent of atmospheric warning, and that change in the vertical thermal gradient will in turn determine a number of ecological niche characteristics directly. The factors explored include relationships driving hypolimnetic or ‘bottom’ oxygen concentrations.

Descriptively, Kingsmere Lake develops a summer thermocline, the strength of which can vary from year to year, examples of which are shown in Fig. 6. In some years, the thermocline is more gradual, while in other years change is more acute. Of note, the gradient was weaker in 1995 (Fig. 6), a year associated with a La Nina in the Pacific Ocean. A slightly steeper gradient occurred in 1994 (Fig. 6) at the tail end of the longest El Niño in the last century. Of the examples shown, the steepest gradient occurred in 1997, associated with one of the two strongest El Niño’s in the century.

Oxygen varies with depth and year as well as temperature (Fig. 6) in Kingsmere Lake. Concentrations were relatively uniform over the water column in the cool year, 1995, decreased with depth in the deepest part of the lake in 1994, and were more uniform again in 1997, but with a substantial bulge or increase in the thermocline (Fig. 6).

Analyses indicate a number of vertical habitat relationships in Kingsmere Lake (Table 3), notably the increase in the mid thermocline oxygen concentration (at 12.5m), THERMOCLINE OXYGEN, with an increase in the magnitude of the thermocline or temperature gradient (Fig. 7). The gradient is represented in two ways, the difference between the temperatures at 5.0 and 20.0m, or 5-20M TEMPERATURE DIFFERENCE, and the maximum temperature difference per metre of depth measured across the thermocline, THERMOCLINE DIFFERENCE. The oxygen concentration at 44.0m at the station 45m deep exhibits no relationships with other variables. The oxygen concentration at 34.0m, 34M OXYGEN, one metre off the bottom at the station 35m deep, is correlated with oxygen in the thermocline in a linear manner (Fig. 8).

The thermocline habitat characteristics in Kingsmere Lake correlate with climate factors, mainly the air temperature departure from the summer mean in the northwestern boreal forest, NWF-SU TEMPERATURE DEPARTURE (Table 4, Fig. 9). Mid thermocline oxygen concentrations are negatively correlated with mid thermocline temperatures, THERMOCLINE TEMPERATURE, since the solubility of oxygen declines as temperature increases. The inclusion of stations of different depth as a categorical variable, STATION (e.g. Table 3) exerts little influence on regression analyses, where stations one and two are 35 m and 45 m deep respectively.

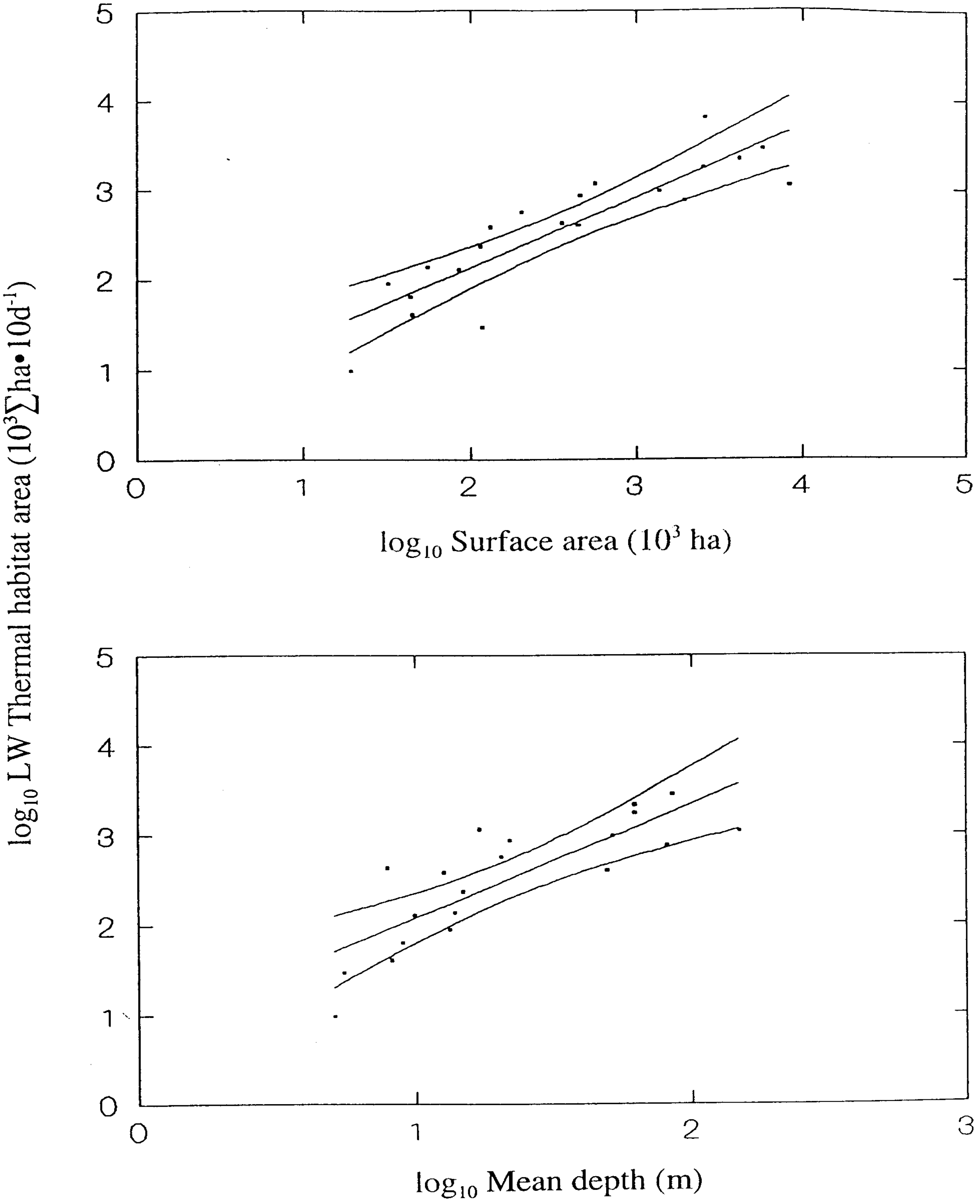

Fig. 2 Relationships between lake whitefish (LW) thermal habitat area and (top panel) lake surface area and (bottom panel) mean depth. Curved lines, 95% confidence intervals.

Table 1 Summary of regression analyses for lake whitefish THERMAL HABITAT AREA (THV) and lake trout THERMAL HABITAT VOLUME (THV) as the dependent variables versus SURFACE AREA and MEAN DEPTH (defined in text). All variables except CONSTANT log$_{10}$ transformed.

Independent variable	Coefficient	P	n	F-ratio	P	R^2
THERMAL HABITAT AREA						
CONSTANT	0.556	0.04	21	68	0	0.78
SURFACE AREA	0.788	0				
CONSTANT	-1.33	0.12	21	45.6	0	0.84
SURFACE AREA	2.37	0				
(SURFACE AREA)^2	-0.302	0.03				
CONSTANT	0.904	0.02	21	22.9	0	0.55
MEAN DEPTH	1.25	0				
CONSTANT	0.809	0.01	20	36.7	0	0.67
MEAN DEPTH	1.27	0				
CONSTANT	-1.7	0.07	20	30.4	0	0.78
MEAN DEPTH	5.2	0				
(MEAN DEPTH)^2	-1.39	0				
THERMAL HABITAT VOLUME						
CONSTANT	-1.851	0	19	199	0	0.92
MEAN DEPTH	2.76	0				
CONSTANT	-1.74	0	19	163	0	0.91
SURFACE AREA	1.45	0				
CONSTANT	-1.94	0	19	144	0	0.95
MEAN DEPTH	0.664	0.01				
SURFACE AREA	1.59	0				

Table 2 Summary of selected regression analyses with respect to air temperatures for Winnipeg, Manitoba, for 1930 to 1970. YEAR starts with 1930 as year zero

Dependent variable	Independent variable	Coefficient	P	n	F-ratio	P	R^2
MEAN ANNUAL	CONSTANT	3.52	0	41	2.17	0.148	0.05
	YEAR	-0.018	0.148				
MEAN AUTUMN	CONSTANT	4.19	0	41	0.713	0.404	0.02
	YEAR	0.017	0.404				

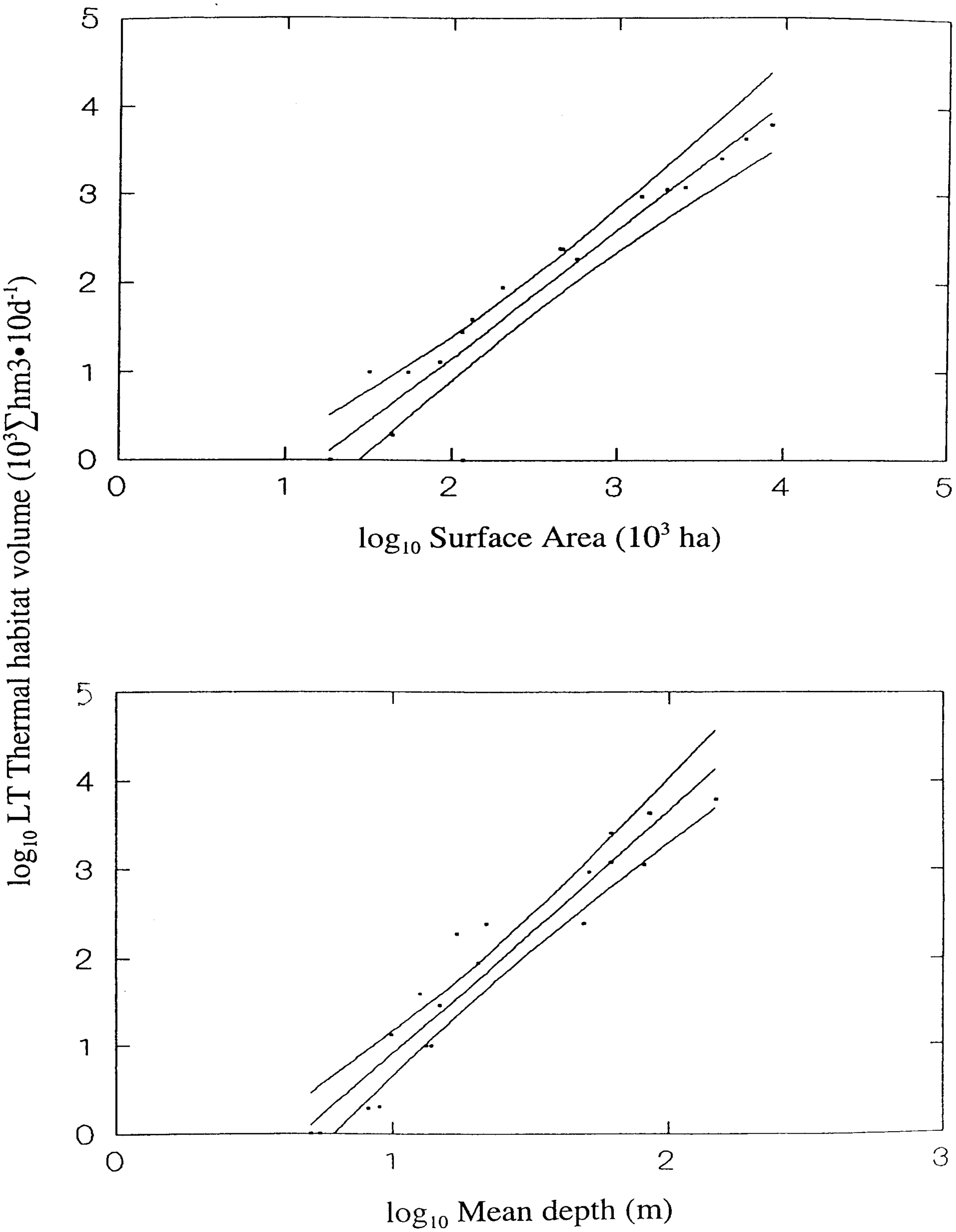

Fig. 3 Relationships between lake trout (LT) thermal habitat volume and (top panel) lake surface area and (bottom panel) mean depth. Curved lines, 95% confidence intervals.

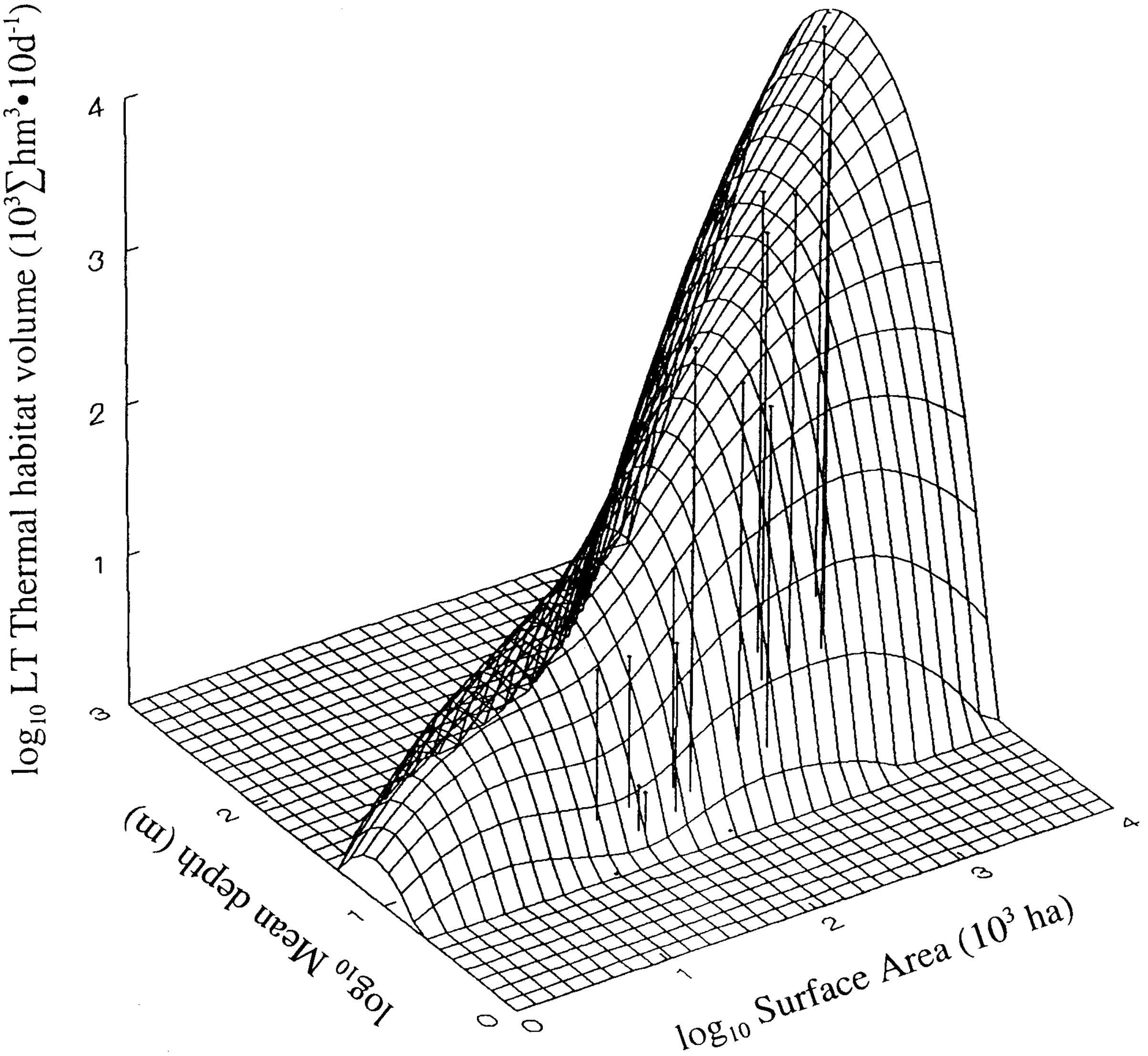

Fig. 4 Distance-weighted-least-squares response surface for lake trout (LT) thermal habitat volume versus lake surface area and mean depth.

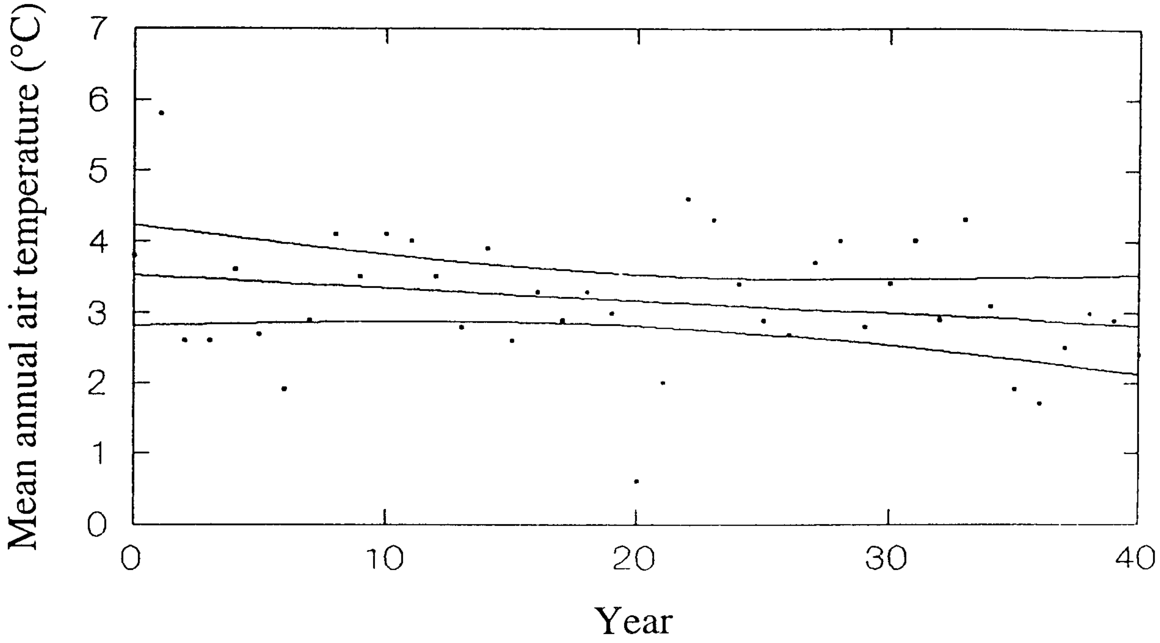

Fig. 5 Regression of mean annual air temperature for Winnipeg, Manitoba, versus year for 1930 to 1970. Year starts with 1930 as year zero. Curved lines, 95% confidence intervals.

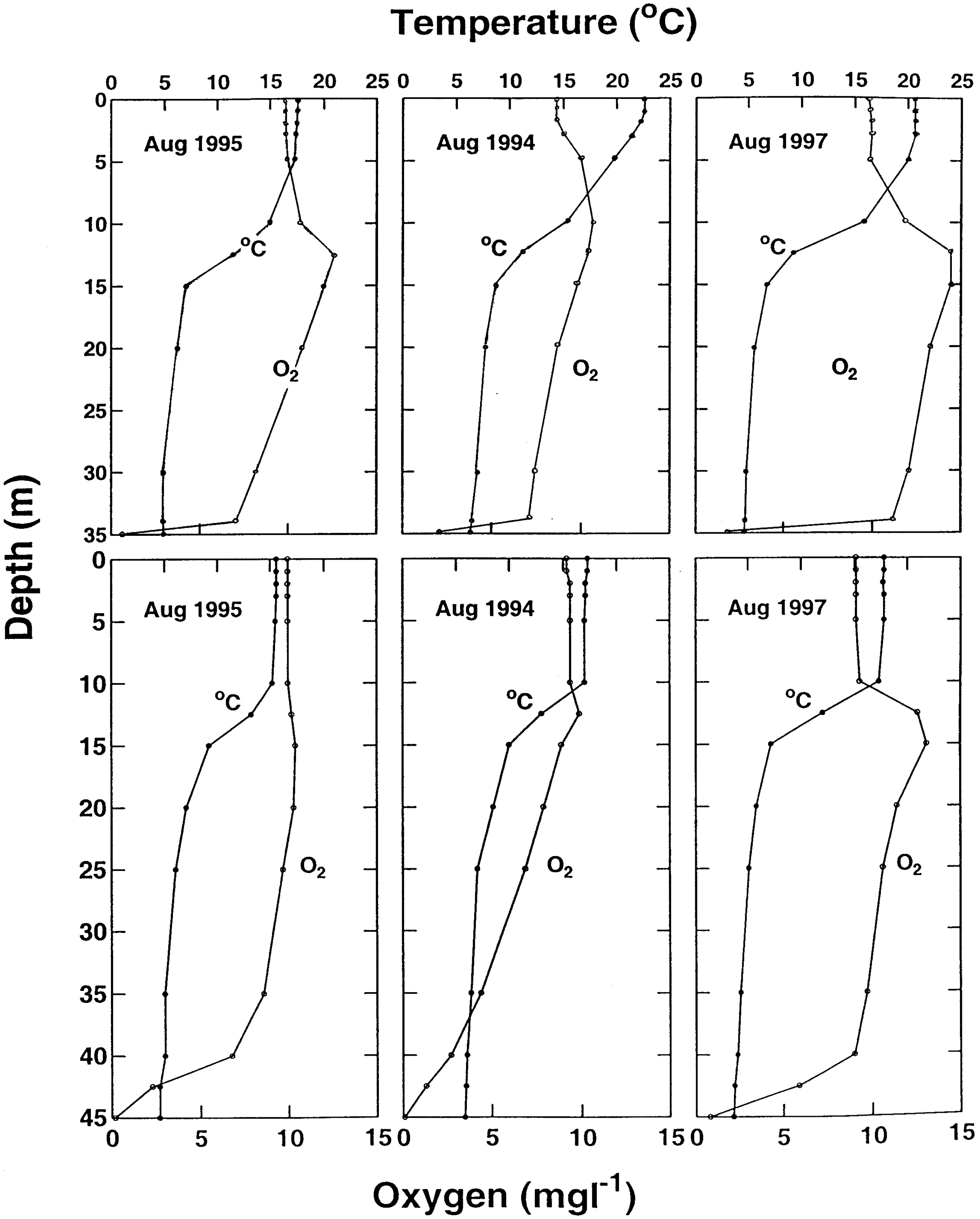

Fig. 6 Temperature and oxygen concentration versus depth in the water column, Kingsmere Lake, for (top panels) station 35m deep and (bottom panels) station 45m deep.

Table 3 Summary of regression analyses for selected vertical thermal habitat (defined in text) relationships in Kingsmere Lake. All variables except CONSTANT $\log_{10}$ transformed.

Dependent variable	Independent variable	Coefficient	P	n	F-ratio	P	R^2
5-20M TEMPERATURE DIFFERENCE	CONSTANT	-1.91	0	16	42.3	0	0.75
	5M TEMPERATURE	2.33	0				
THERMOCLINE OXYGEN	CONSTANT	1.19	0	16	12.9	0	0.67
	5-20M TEMPERATURE DIFFERENCE	0.258	0				
	THERMOCLINE TEMPERATURE	-0.383	0				
	CONSTANT	0.927	0	16	8.28	0	0.56
	THERMOCLINE DIFFERENCE	0.381	0				
	STATION	-0.033	0.1				
34M OXYGEN	CONSTANT	-0.22	0.55	8	10.4	0.02	0.63
	THERMOCLINE OXYGEN	1.07	0				

Table 4 Summary of regression analyses for selected thermal habitat (see text) characteristics in Kingsmere Lake, versus air TEMPERATURE DEPARTURE from the summer (SU) mean in the northwest boreal forest (NWF). All variables except CONSTANT $\log_{10}$ transformed.

Dependent variable	Independent variable	Coefficient	P	n	F-ratio	P	R^2
5-20M TEMPERATURE DIFFERENCE	CONSTANT	-0.387	0.228	16	21	0	0.6
	NWF-SU TEMPERATURE DEPARTURE	1.74	0				
5M TEMPERATURE	CONSTANT	0.818	0	16	10.2	0.01	0.423
	NWF-SU TEMPERATURE DEPARTURE	0.542	0.01				
THERMOCLINE OXYGEN	CONSTANT	1.32	0	16	7.22	0.01	0.526
	NWF-SU TEMPERATURE DEPARTURE	0.394	0.058				
	THERMOCLINE TEMPERATURE	-0.55	0.011				

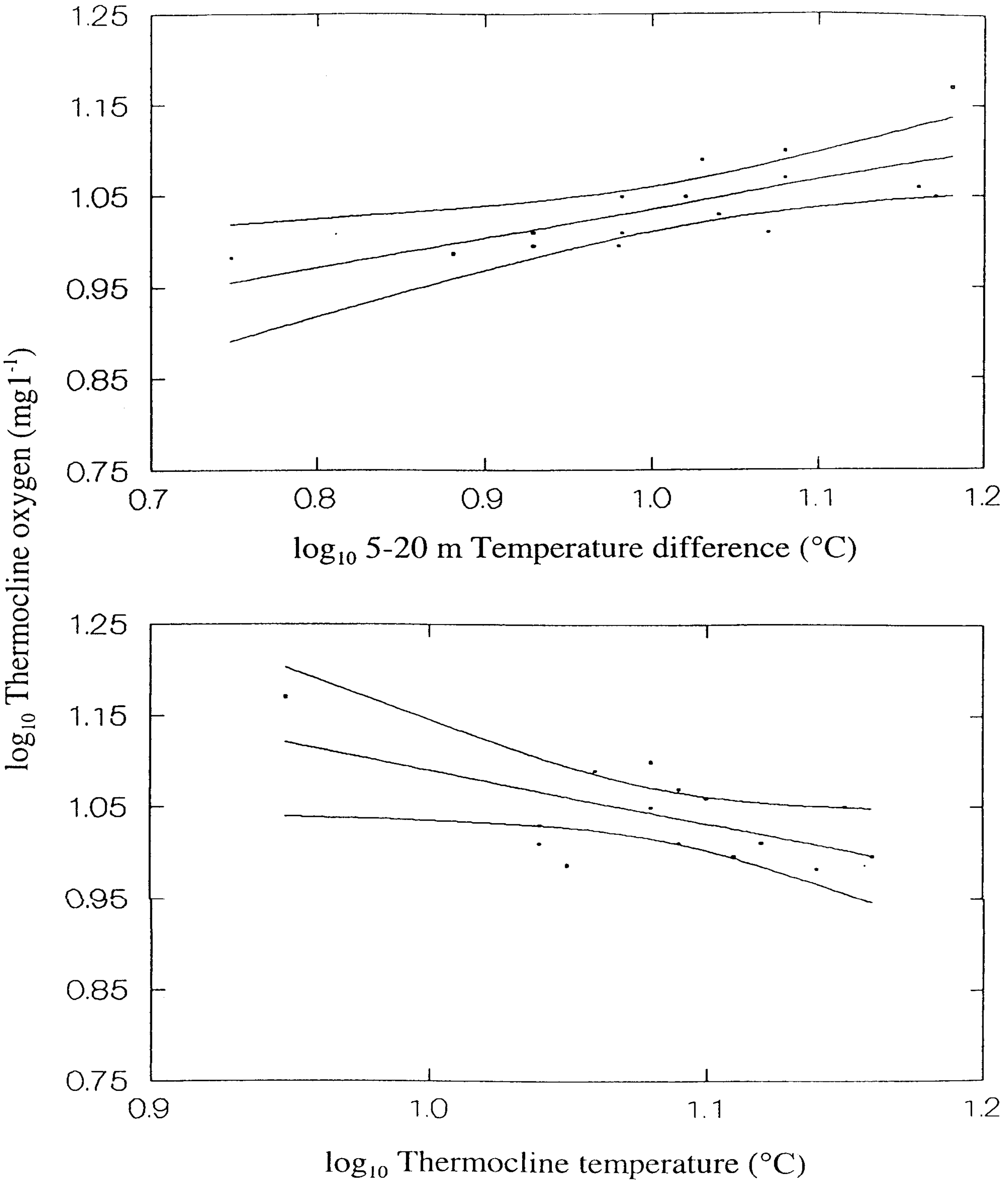

Fig. 7 Relationships between mid thermocline oxygen concentration and temperature structure in Kingsmere Lake, measured as (top panel) the difference between the temperatures at 5.0 and 20.0m and (bottom panel) mid thermocline temperature. Curved lines, 95% confidence intervals.

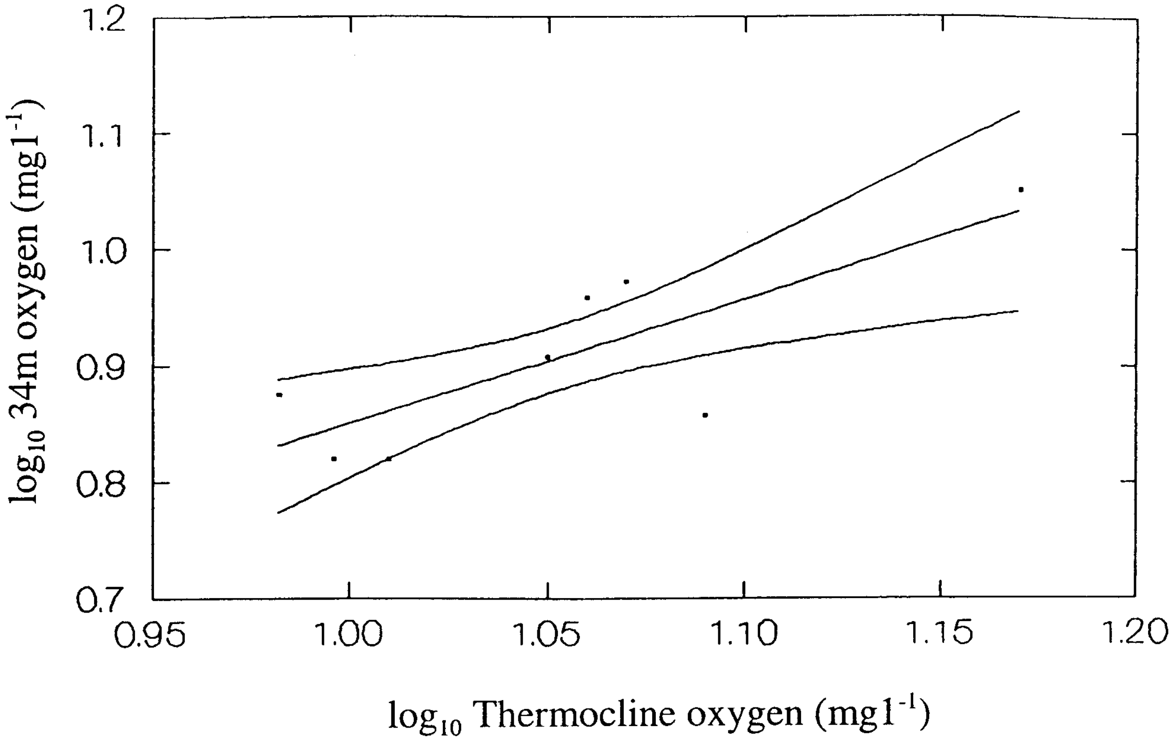

Fig. 8 Regression of oxygen concentration at 34.0m versus mid thermocline oxygen concentration in Kingsmere Lake at station 35m deep. Curved lines, 95% confidence intervals.

5. Foodweb linkages

5.1 Lake whitefish, thermal habitat and TAC

The proposed correction factor improves the precision of the relationship between thermal habitat area and the lake whitefish sustained yield, LW SUSTAINED YIELD, or the TAC (Fig. 10) by almost fifty percent (Table 5). The unexplained fraction of the variance is only five percent, the level generally allowed to account for departures from predicted values by chance. The variable LAKE CATEGORY explains about ten percent of the variation in the relationship. This variable groups lakes according to the order of magnitude of the surface area i.e. 10^n ha, where the groups are $n \geq 0$, 1, 2..etc. Analyses within groups produce similar habitat-TAC relationships, but with somewhat smaller R^2's as a result of smaller sample sizes in the subsets.

5.2 Lake whitefish, climate indicators and fishery catch

Only one comparison for Lake Winnipeg exhibits any pattern (Fig. 11), that between catch per unit effort of five year old fish and mean air temperature for the summer prior to spawning by the parent generation. It suggests that year class strength decreases as air temperature, during the parental prespawning period, increases, however the R^2 indicates the relationship is very weak (Table 6). Other analyses of year class strength and air temperature during and after parental spawning suggest no relationships.

5.3 Lake herring, vertical thermal habitat and climate

Here I hypothesize that the strength of the peak in relative abundance of lake herring at the thermocline increases with an increase in the steepness of the thermocline, and related habitat characteristics, in Kingsmere Lake. The strength of the peak should also increase with an increase in atmospheric warming. A more pronounced peak indicates that the fish are proportionately more concentrated in the depth zone of the peak, with fewer fish distributed over the remainder of the water column. I express the peak as $\log_{10} (1 + a^{-1})$, where a is the angle, in radians, of the peak of maximum abundance in the vertical profile of a sampling station.

The examples in Fig. 12 illustrate the variation in the vertical distribution of lake herring, each over an average of twelve days, by year and station depth. In some years, lake herring distribute more evenly, and in other years distributions are more restricted, particularly to depths between ten and twenty metres. The station 45m deep exhibits the latter restriction more than the 35m station. The pattern of aggregation was weakest in 1995, the year associated with La Nina. The summer of 1994, at the tail end of the longest El Niño, exhibited an intermediate pattern. The most pronounced pattern in the examples occurred in 1997, associated with one of the strongest El Niños. Over the set of examples, under some conditions, a secondary ‘peak’ seems to appear at the bottom of the lake at the station 35m deep (Fig. 12).

Analyses indicate that the overall pattern leaves little unexplained variation to chance (Table 7, Fig. 13), in the regression relating the strength of the PEAK in herring ABUNDANCE to increases in thermocline gradient, 5-20M TEMPERATURE DIFFERENCE, and STATION differences. The station differences (e.g. Fig. 12) exert a substantial influence, such that other patterns i.e. the increase in the peak with increases in THERMOCLINE OXYGEN and NWF-SU TEMPERATURE DEPARTURE, are best demonstrated by examining stations independently (e.g. Fig. 14, Table 7). Regression diagnostics eliminate two years of data for the 35m station, ultimately because herring catches were extremely low in the years, and the low catches distort the description of patterns.

The only relationship between relative herring ABUNDANCE at the BOTTOM and other variables occurs mainly with the air temperature departure from the spring mean in the prairies (Fig. 15, Table 8) at the 35m station. The relationship has a very high R^2 despite a smaller sample size.

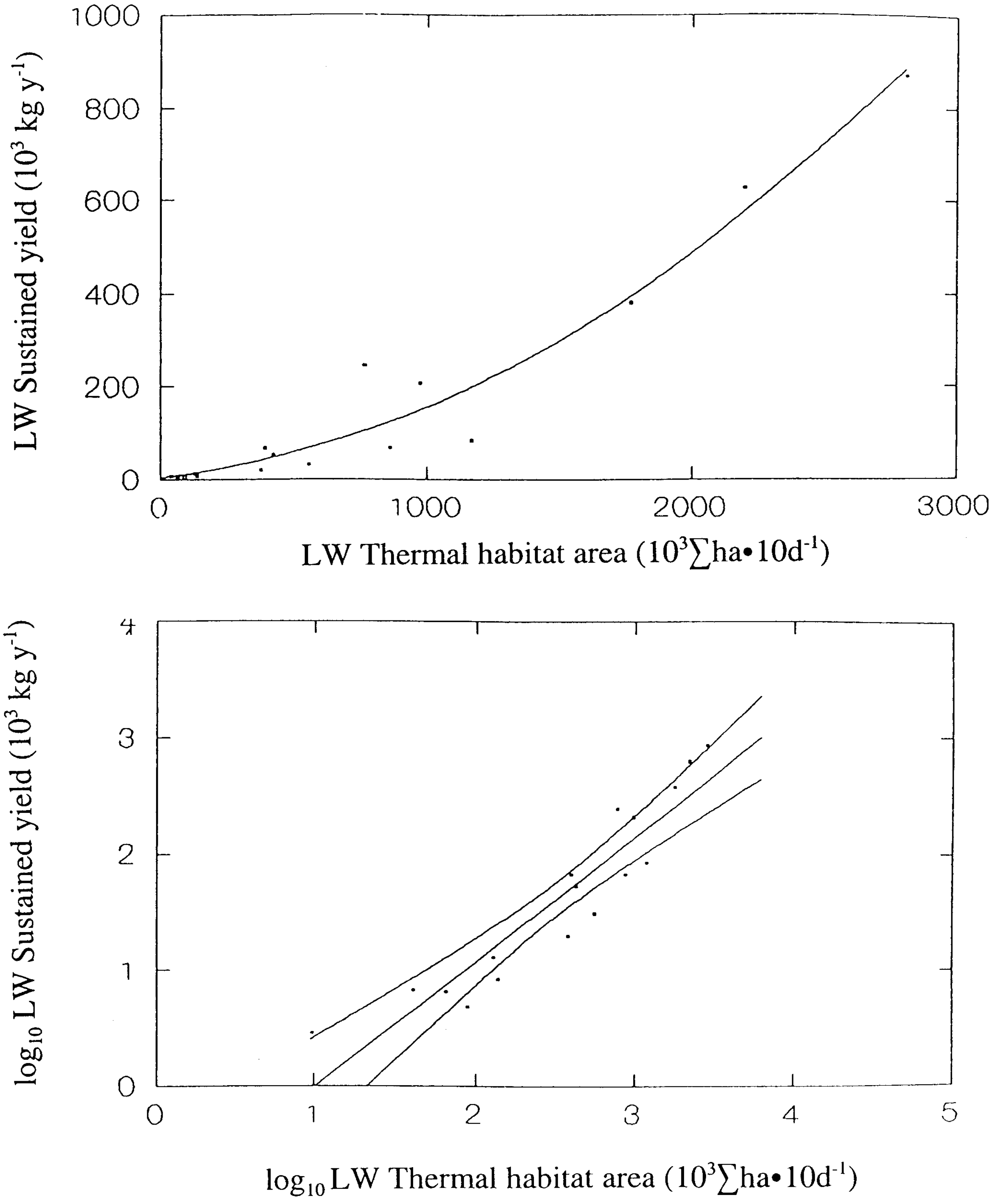

Fig. 10 Relationship between sustained yield and thermal habitat area for lake whitefish (LW). Bottom panel, curved lines 95% confidence intervals.

Table 5 Regression statistics for the relationship between lake whitefish (LW) SUSTAINED YIELD (defined in text) as the dependent variable versus THERMAL HABITAT AREA and LAKE CATEGORY. Continuous variables except CONSTANT $\log_{10}$ transformed.

Independent variable	Coefficient	P	n	F-ratio	P	R^2
CONSTANT	-1.2	0	17	135	0	0.951
THERMAL HABITAT AREA	0.453	0				
LAKE CATEGORY	0.577	0				

Table 6 Regression statistics for the relationship between catch per unit effort, or CPUE, for Lake Winnipeg whitefish as the dependent variable, versus MEAN SUMMER air temperature for Winnipeg, between 1939 and 1964. Air temperatures are those for the years in which year classes were spawned, while CPUE represents the year classes taken at five years of age. Variables except CONSTANT $\log_{10}$ transformed.

Independent variable	Coefficient	P	n	F-ratio	P	R^2
CONSTANT	15.1	0	23	8.9	0.01	0.298
MEAN SUMMER	-10.4	0.01				

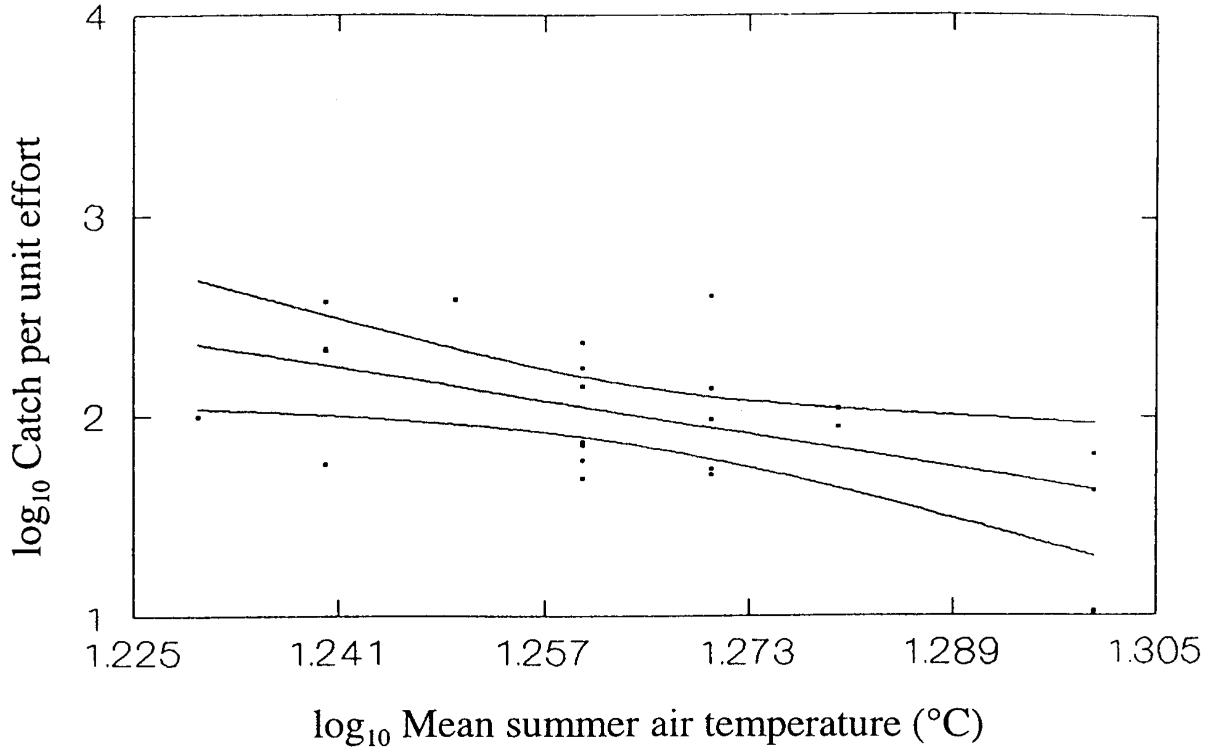

Fig. 11 Regression of catch per unit effort for Lake Winnipeg whitefish year-classes at five years of age, versus mean summer air temperatures for Winnipeg in the year spawned, between 1939 and 1964. Curved lines, 95% confidence intervals.

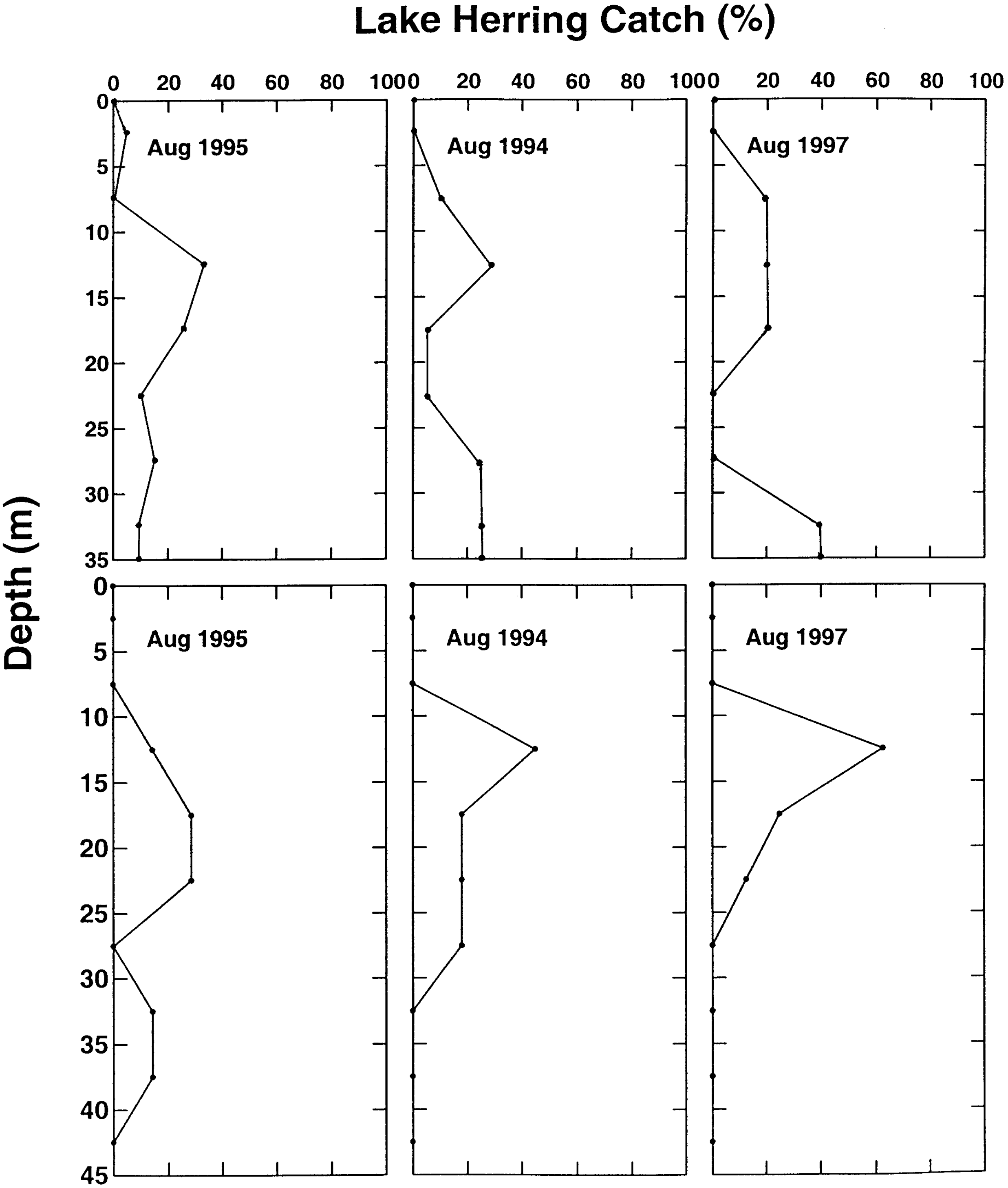

Fig. 12 Relative abundance of lake herring with depth in the water column, Kingsmere Lake, for (top panels) station at 35m and (bottom panels) station at 45m depth.

Table 7 Summary of regression analyses between strength of PEAK in relative ABUNDANCE of lake herring over water column (defined in text), as the dependent variable, versus selected climate and other factors for Kingsmere Lake. CPUE defined in text, YEAR NO starts with 1990 as year zero. All continuous variables except CONSTANT $\log_{10}$ transformed.

Independentvariable	Coefficient	P	n	F-ratio	P	R^2
Both stations						
CONSTANT	0.708	0	12	478	0	0.991
5-2OM TEMPERATURE DIFFERENCE	0.325	0.01				
STATION	-0.424	0				
Station at 45 m depth						
CONSTANT	-0.947	0	7	214	0	0.998
NWF-SU TEMPERATURE DEPARTURE	0.52	0				
THERMOCLINE OXYGEN	0.666	0				
CPUE	0.208	0				
YEAR NO	-0.004	0.04				

Table 8 Regression statistics for relationship between relative ABUNDANCE of lake herring at the BOTTOM, as the dependent variable, versus selected factors for the station 35 m deep in Kingsmere Lake. Climate factor is the air TEMPERATURE DEPARTURE from the spring (SP) mean in the prairies (P). YEAR NO starts with 1990 as year zero. BOTTOM ABUNDANCE arcsin square-root transformed, continuous variables except CONSTANT $\log_{10}$ transformed.

Independent variable	Coefficient	P	n	F-ratio	P	R^2
CONSTANT	8.88	0.218	5	46.5	0.21	0.979
P-SP TEMPERATURE DEPARTURE	35.2	0.03				
YEAR NO	-2.85	0.01				

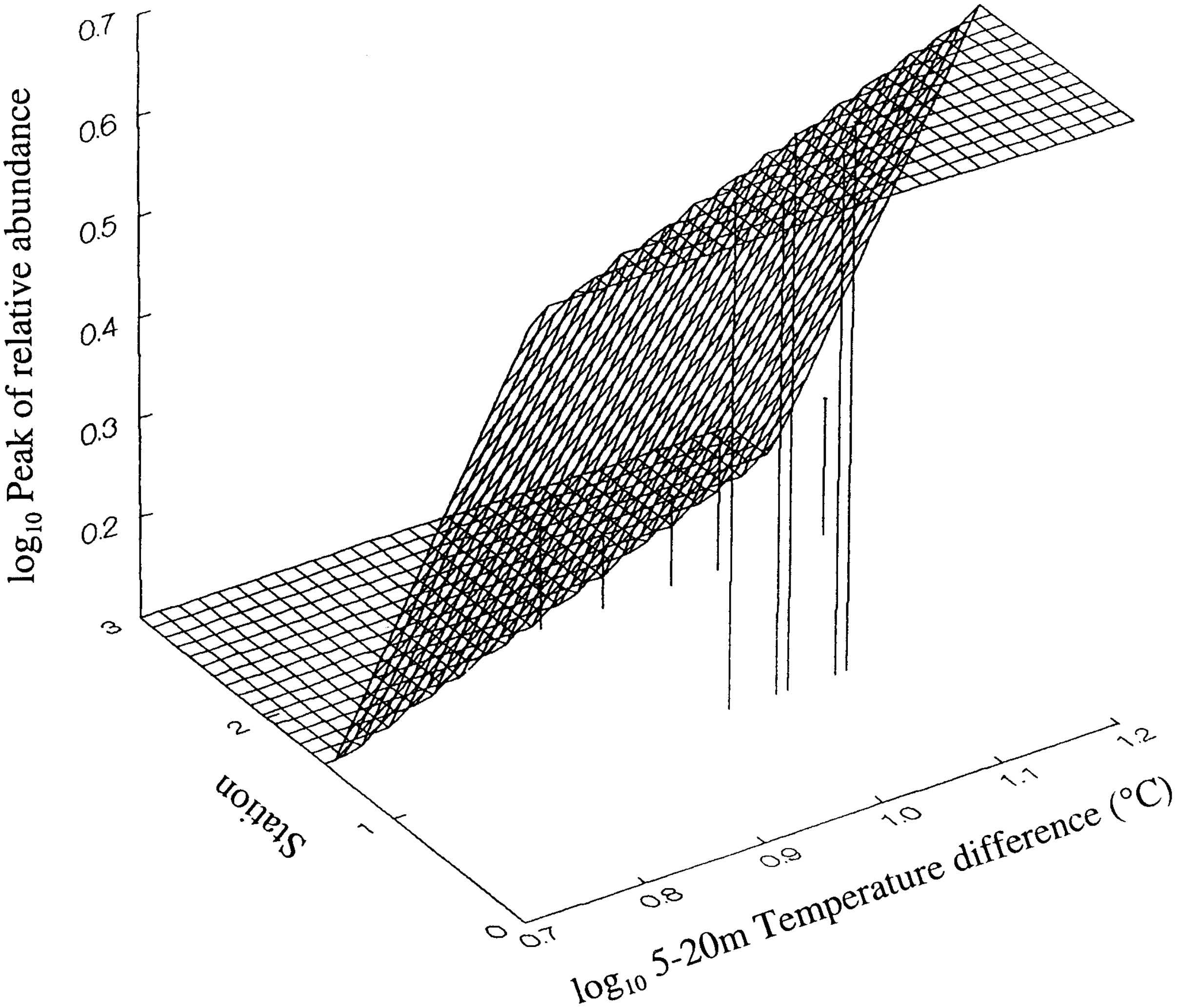

Fig. 13 Linear response surface for strength of peak in relative abundance of lake herring in the water column, versus vertical temperature gradient and station, in Kingsmere Lake. Temperature gradient is measured as the difference between the temperatures at 5.0 and 20.0m deep. Stations 1 and 2, 35m and 45m deep respectively.

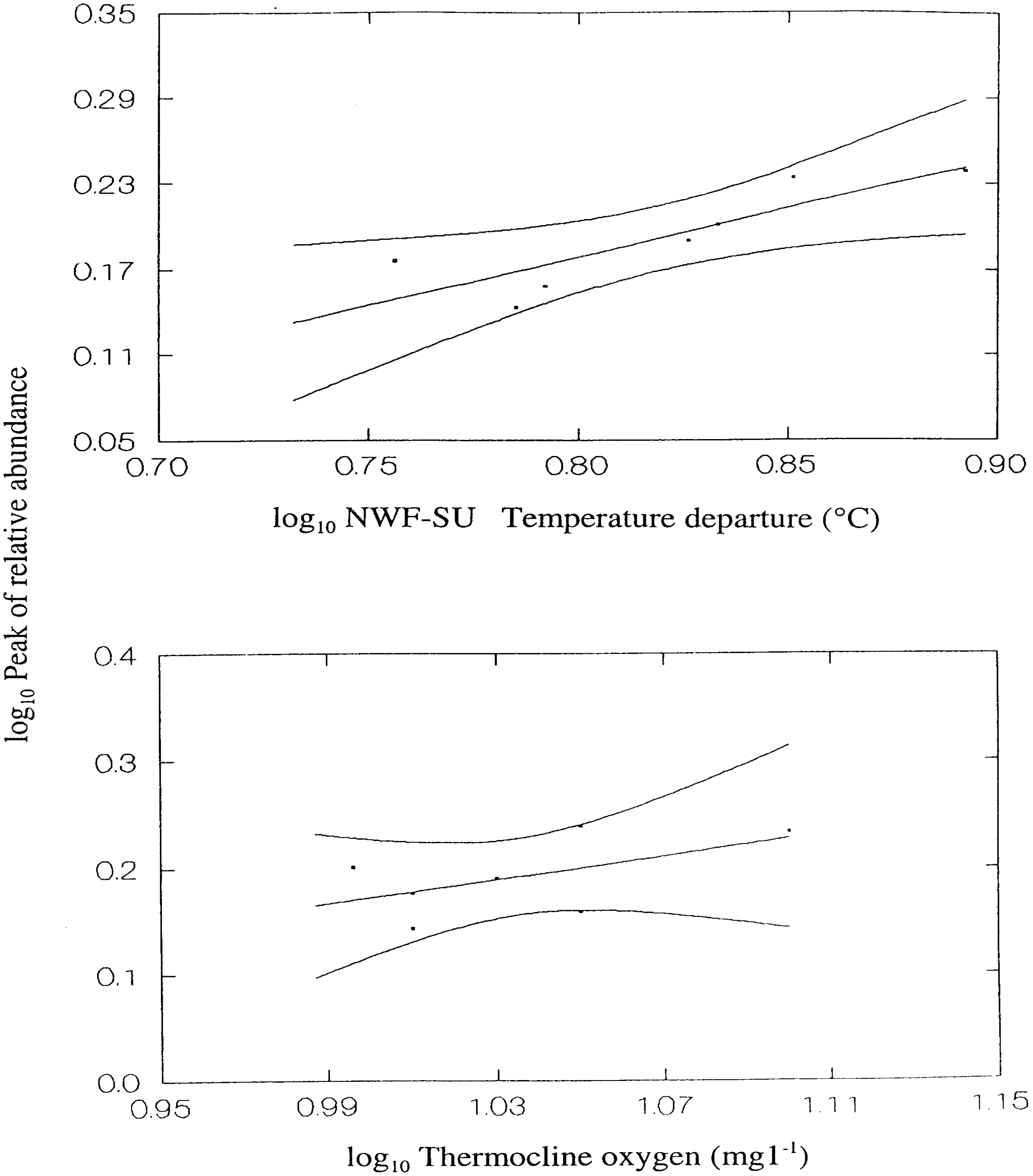

Fig. 14 Relationships between strength of peak in relative abundance of lake herring in the water column, versus (top panel) air temperature departure from the summer mean in the northwest boreal forest (NWF-SU) and (bottom panel) mid thermocline oxygen concentration, at 45m station in Kingsmere Lake. Curved lines, 95% confidence intervals.

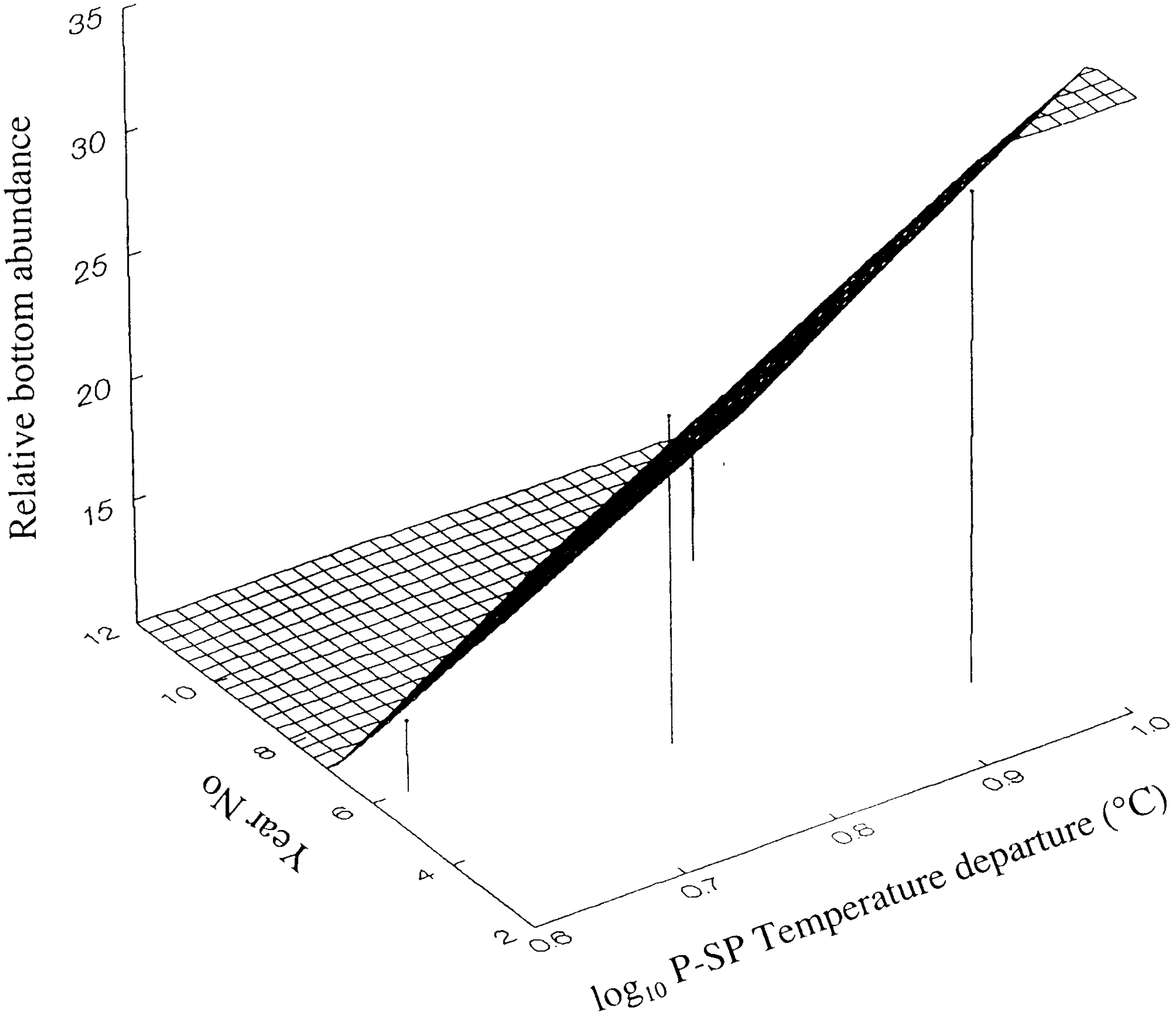

Fig. 15 Linear response surface for relative abundance of lake herring at the bottom, versus the air temperature departure from the spring mean in the prairies (P-SP) and year no., at the 35m station in Kingsmere Lake. Year no. starts with 1990 as year zero.

6. Large fish as top predators

6.1 Lake trout, thermal habitat and TAC

The conservation coefficient proposed for lake trout results in a fifteen percent increase in precision (Table 9) in the TAC-thermal habitat relationship (Fig. 16), where TAC is the sustained yield, LT SUSTAINED YIELD. While less than the increase for whitefish, the explained variation is a substantial 97.5 percent, leaving only 2.5 percent to chance. The LAKE CATEGORY variable contributes minimally to the overall regression, but is essential in indicating that lakes with surface areas <1000 km^2 probably do not fit this version of the model. Lakes with thermal habitat volumes of about $10^4 hm^3 \bullet 10d^{-1}$ are the only ones to fall outside the ninety-five percent confidence interval, and all but one with $THV \leq 10^4$ supports sustained yields of essentially zero catch. Regression analysis of this subset of lakes indicates no relationship between THV and sustained yield (Table 9).

6.2 Lake trout and vertical thermal habitat

Lake trout increase in abundance with depth below the thermocline in Kingsmere Lake, reaching maximum abundance at bottom temperatures well below (4-7˚C) the behavioural thermal ‘optimum’. Distributions varied little over the summers of 1993-95, except that trout were scarce at the bottom of the deepest or 45 m station in 1994, when oxygen concentrations at deeper depths were minimal.

6.3 Lake trout, fitness and climate considerations

Traditional measures based on WEIGHT-LENGTH relationships (Fig. 17, Table 10) suggest that the biological fitness of lake trout in Kingsmere Lake has declined substantially over the last fifteen years. Regressions for the three periods of data are highly significant, but the LENGTH coefficients (Table 10) or slopes (Fig. 18) of the regressions and the R^2s decrease substantially from one period to the next. The data were sampled in different programs, so they must be interpreted with extra caution. The middle sampling period, 1993-95, is the second half of the longest El Niño of the last century, and the most recent period follows one of the strongest El Niños.

Table 9 Regression statistics for the relationship between lake trout (LT) SUSTAINED YIELD (defined in text) as the dependent variable versus THERMAL HABITAT VOLUME and LAKE CATEGORY. Continuous variables except CONSTANT $\log_{10}$ transformed.

Independent variable	Coefficient	P	n	F-ratio	P	R^2
All lakes						
CONSTANT	-1.07	0	19	312	0	0.98
THERMAL HABITAT VOLUME	0.522	0	6	0.731	0.44	0.16
LAKE CATEGORY	0.385	0	6	0.731	0.44	0.16
Lakes < 1000 km^2			6	0.731	0.44	0.16
CONSTANT	-0.008	0.898	6	0.731	0.44	0.16
THERMAL HABITAT VOLUME	0.07	0.441				

Table 10 Regression statistics for relationships between lake trout WEIGHT as the dependent variable and lake trout LENGTH during three periods in Kingsmere Lake. Variables except CONSTANT $\log_{10}$ transformed.

Independent variable	Coefficient	P	n	F-ratio	P	R^2
1986/87						
CONSTANT	-2.4	0	80	1170	0	0.938
LENGTH	3.28	0	6	0.731	0.441	0.155
1993-95			6	0.731	0.441	0.155
CONSTANT	-1.33	0	187	758	0	0.804
LENGTH	2.66	0				
1999						
CONSTANT	-0.889	0.05	76	97	0	0.567
LENGTH	2.41	0				

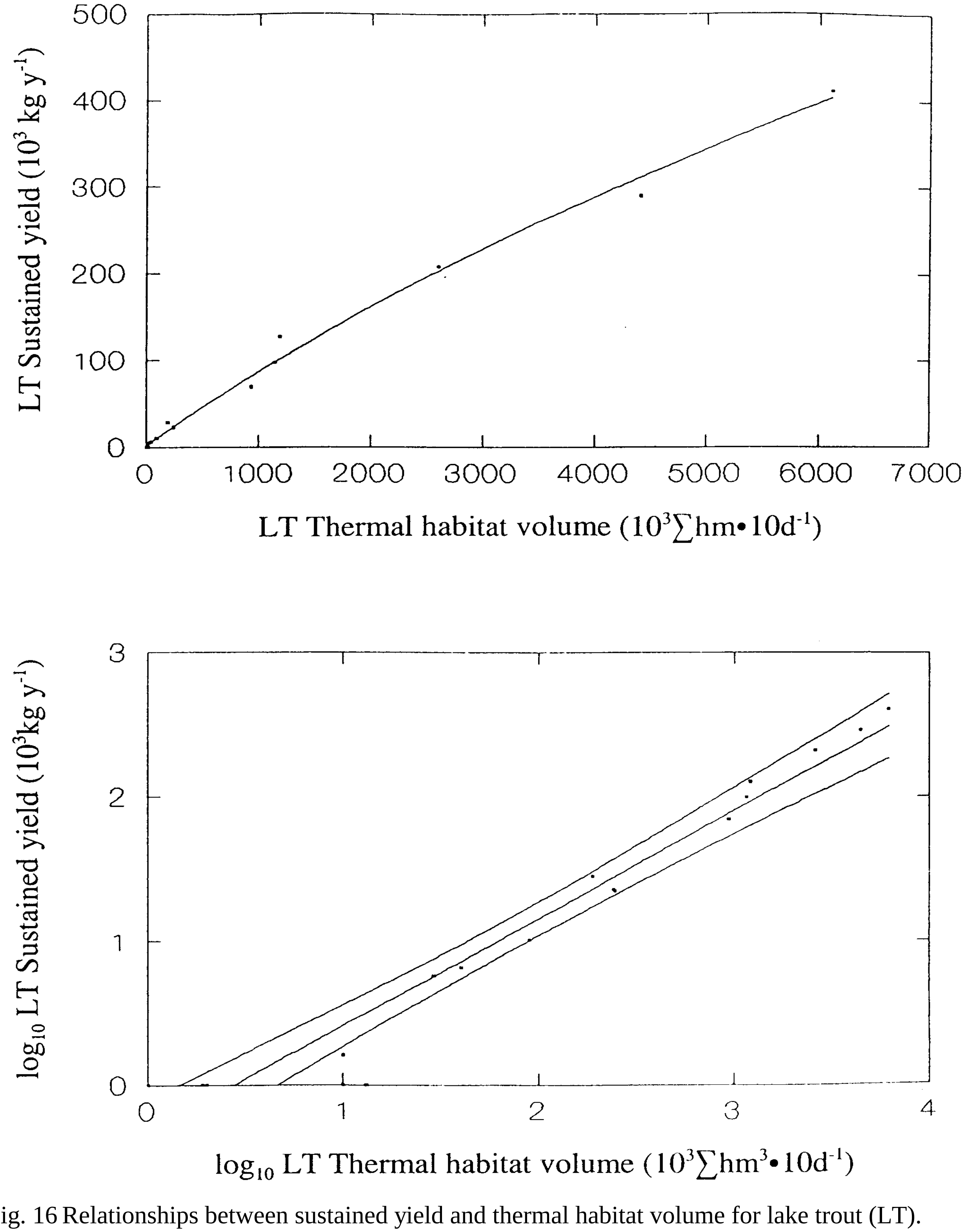

Fig. 16 Relationships between sustained yield and thermal habitat volume for lake trout (LT). Bottom panel, curved lines, 95% confidence intervals.

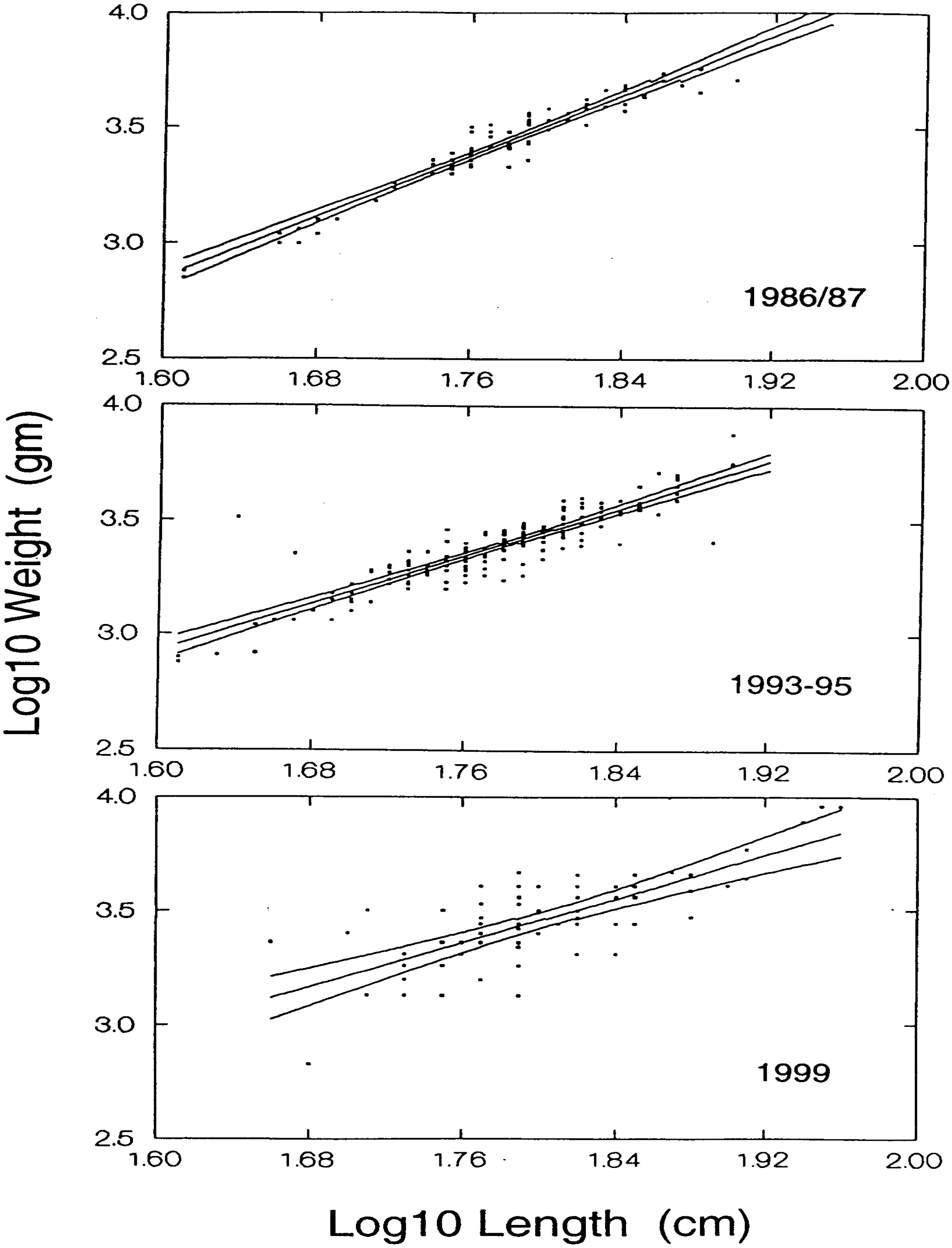

Fig. 17 Regressions between weight and length for three periods for the lake trout of Kingsmere Lake. Curved lines, 95% confidence intervals.

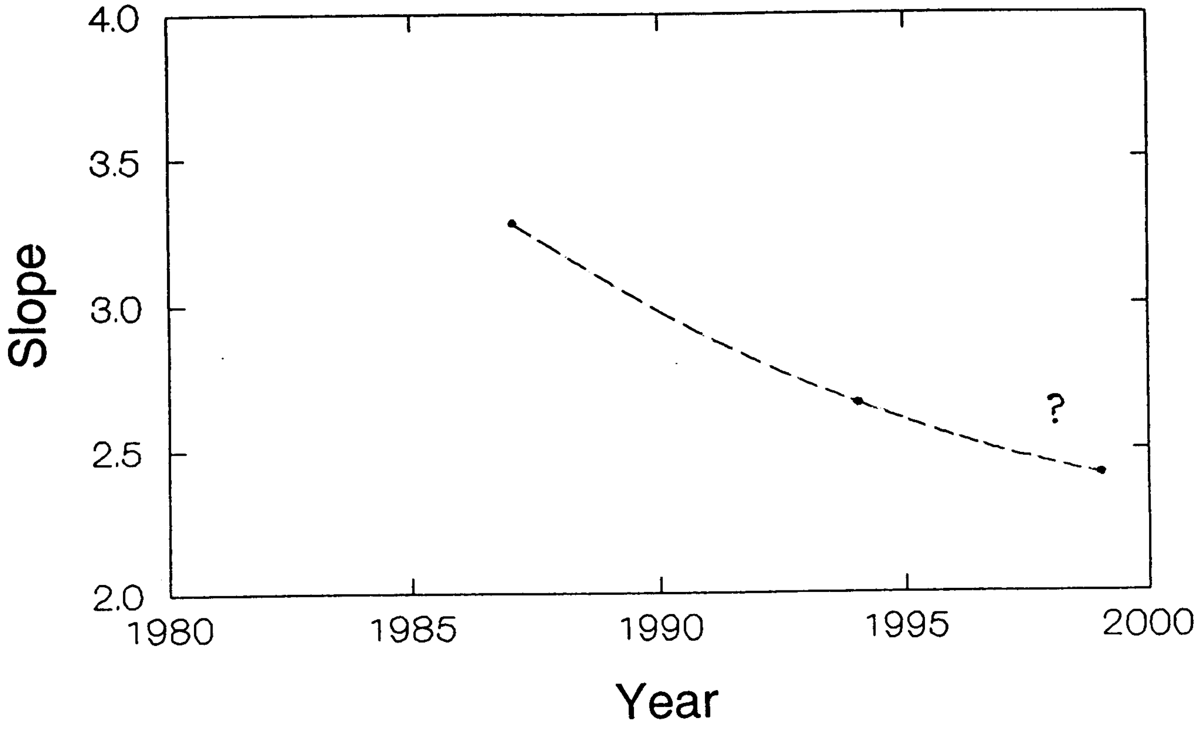

Fig. 18 Relationship between slope of the weight-length regressions for the lake trout of Kingsmere Lake, and year. ? indicates uncertainty in the relationship.

7. General conclusions and recommendations

This study offers resource managers the only set of empirical harvesting models for cold freshwater fish which will conserve population structure in the target populations. These models are based on climate-related habitat features. As a first step, fisheries managers should implement such models as soon as possible, to begin the process of adapting to climate change. These 'second-generation' models substantially improve the precision of the previous efforts (Christie and Regier 1988); more importantly however, they add accuracy through the incorporation of the conservation coefficient, CC. The models of Christie and Regier (1988) were based in the majority of cases on data from populations which were at some stage of decline, even extirpation, via fishing. In all cases, yield levels must be reduced, i.e. CC>1, and drop by as much as a factor of twenty for lake trout, and forty for lake whitefish. The TACs currently allowed are anything but sustainable, and will lead to extirpation, i.e. CC>x in many lakes. Continued use of any previous empirical models (e.g. Chen 1992) will ultimately have disastrous effects on all freshwater fisheries, if they haven't already.

The new climate-based TAC models are highly predictive for most lakes, but analyses indicate the model for lake trout may be inadequate for lakes <1000 km^2 in surface area. It follows that all other existing TAC models for lake trout are worse for lakes in this size range. The lake whitefish TAC model seems more consistent in its applicability to the full range of lakes sizes, however the conservation coefficient, CC, is more subjective than that for lake trout. More work is needed in the development of the lake whitefish TAC for all lakes, regardless of size, since sustained yields may yet be overestimated by the model developed in this study.

Sustained yields can be calculated for lakes which lack thermal habitat data, by using more basic lake morphometric data, such as surface area and mean depth. This approach excludes TACs for lake trout in lakes <1000 km^2. The use of landscape i.e. larger-scale measures (e.g. Minns and Moore 1992) with respect to individual lakes should be avoided, even in the case of huge shallow systems, for example Lake Winnipeg. Without more research, landscape measures such as the Winnipeg air temperatures have no predictive value in calculating TACs. As a great lake, we need to know far more about all aspects of Lake Winnipeg to manage it properly, regardless of the issue or context. Substitution of more immediate surrogate data, such as mean depth, in TAC calculations should be regarded as an interim measure at this point, pending further investigations with respect to contributions to error in sustained yield assessments.

Sustained yield assessments for lake trout in lakes <1000 km^2 are currently highly problematic, as the TAC analyses suggest. The Kingsmere Lake example indicates that relationships at different levels of ecological organization in individual lakes, and at different temporal and spatial scales, will factor heavily in determining TACs. In Kingsmere Lake, climate factors affect mixing processes, thus variation in vertical thermal habitat structure, which in turn determines the state of biological attributes. Increased thermocline oxygen concentrations represent increased primary production by phytoplankton, for example. Phytoplankton accumulate more at thermocline depths when the thermocline is strong, sinking at reduced rates because of the increase in density of the cooler deeper water. Lake herring move up more in the water column, perhaps in part because the phytoplankton-grazing invertebrates which they eat are more concentrated at the thermocline. Lake trout on the other hand did not seem to respond as readily, maintaining more of a presence in deeper water. Atmospheric warming may create more of a spatial gap in summer between lake trout and lake herring, prey for lake trout in lakes like Kingsmere. Increasing disjunct distributions with respect to food sources could contribute to a loss of fitness in lake trout populations, which seems to have occurred in Kingsmere Lake over the last fifteen years. Exploitation is at the root of the plight of lake trout in Kingsmere, but it may well be that climate change is the 'straw that will break the camels back'. These ecological results are in general agreement with those of Trippel and Beamish (1992) and others, who point out the importance of individual differences in the ecology of lakes to TAC's, building on a long history in the development of our understanding of these differences.

It is most probable that we can best adapt to climate change through proper management of our remaining fish stocks. For whitefish at least, this can be accomplished simply by harvesting at levels which conserve the age and size structures of harvested populations. If we maintain stocks of older large-bodied fish of all species, for example, they will help regulate the abundance of smaller fish species, since most boreal large-bodied taxa are predatory. This will help maintain elevated hypolimnetic oxygen concentrations over the long-term, regulate excessive numbers of fish-eating water birds, and help combat invasive exotic aquatic species through ecological interactions. For example, small-bodied boreal fish species eat primarily invertebrates, which consume in part phytoplankton. If greater numbers of small-bodied species were eaten by larger predatory fish in many instances, more invertebrates would survive, reducing the biomass of phytoplankton through grazing. As a consequence, there would be less hypolimnetic bacterial decomposition, which consumes oxygen, thus higher oxygen concentrations near the bottom in lakes.

Additional management adaptation requirements include the development of adequate fishery monitoring programs, few of which exist in the Boreal Plains Ecozone. Regular monitoring of total harvest, age composition and some index of exploitable abundance should accompany a typical fishery (Merritt and Quinn 2000). We also need to have a good understanding of the population dynamics, including reproduction and older-age related processes, and the ecosystem relationships of key fish species on a lake-by-lake basis.

In the short term, management agencies across the Boreal Plain Ecozone should implement a moratorium on lake trout fishing; this is the only real hope for the lake trout of the ecozone. The management agencies should also implement a comprehensive in-depth assessment of the state of surviving lake trout populations. In the case of Kingsmere Lake, PANP, the lake should be closed to fishing; as the most representative lake of its type in the park, closure is the only option which is consistent with resource management via the precautionary principle. Lake trout in the Boreal Plain are in a similar situation to that of large carnivores in the Rocky Mountains, where the fate of the "last of the last, not the last of the best" (c.f. P. Paquet) is at stake.

8. Acknowledgments

Many people contributed to small portions of this study; all their efforts are greatly appreciated. The short timeframe (13 months, 8 months from financial confirmation) unfortunately did not allow for greater participation from many contributors. The CCAF, through PARC, contributed the largest share of the funding, without which the study would not have been possible. I also thank the SRC and other funders for their contributions.

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