

# Effects of hypoxia on scope-for-activity and power capacity of lake trout (*Salvelinus namaycush*)

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**Abstract:** This study develops a quantitative model of the combined effects of temperature and ambient dissolved oxygen on metabolic scope-for-activity and power capacity of juvenile lake trout (*Salvelinus namaycush*). The model provides a framework for evaluating the effects of hypoxia on the capacity of lake trout to perform critical daily life support activities. Maximum power output for sustained swimming of yearling lake trout occurred at 12–20 °C and a dissolved oxygen concentration of >7 mg·L<sup>-1</sup>. At 4–8 °C, temperatures typical of the hypolimnetic summer habitat of juvenile lake trout, maximum power capacity was reduced by 33%, 67%, and 100% at ambient dissolved oxygen concentrations of 7, 5, and 3 mg·L<sup>-1</sup>, respectively. Analysis of power outputs, growth impairment, and recruitment success indicated that attainment of 3/4 power capacity would accommodate most daily life support activities of juvenile lake trout. At 4–14 °C, the threshold dissolved oxygen concentration for attainment of 3/4 scope-for-activity varied from 7.5 to 6.6 mg·L<sup>-1</sup>, respectively, with a mean and standard deviation of 7.04 ± 0.33 mg·L<sup>-1</sup>. A dissolved oxygen criterion of 7 mg·L<sup>-1</sup> is recommended for protection of the hypolimnetic habitat of juvenile lake trout.

**Résumé :** On trouvera ici un modèle quantitatif des effets combinés de la température et de l'oxygène dissous du milieu sur le profil métabolique et le potentiel de puissance des jeunes touladis (*Salvelinus namaycush*). Le modèle fournit un cadre pour évaluer les effets de l'hypoxie sur la capacité des touladis de remplir les activités quotidiennes essentielles à leur survie. La puissance maximale pour la nage soutenue de jeunes touladis d'un an est produite à 12–20 °C et à une concentration d'oxygène dissous de >7 mg·L<sup>-1</sup>. À 4–8 °C, des températures typiques de l'habitat d'été des jeunes touladis dans l'hypolimnion, le potentiel maximum de puissance est réduit de 33 %, 67 % et 100 % aux concentrations respectives d'oxygène dissous du milieu de 7, 5 et 3 mg·L<sup>-1</sup>. L'analyse des puissances produites, de la réduction de la croissance et du succès du recrutement indique que l'atteinte de 3/4 du potentiel de puissance suffit pour permettre la plupart des activités essentielles à la survie chez les jeunes touladis. À 4–14 °C, le seuil de la concentration d'oxygène dissous qui permet d'atteindre les 3/4 du profil métabolique varie de 7,5 à 6,6 mg·L<sup>-1</sup>, avec une moyenne et un écart type de 7,04 ± 0,33 mg·L<sup>-1</sup>. Le seuil recommandé de 7 mg·L<sup>-1</sup> assurerait la protection de l'habitat hypolimnétique des jeunes touladis.

[Traduit par la Rédaction]

## Introduction

Throughout their geographic range, lake trout (*Salvelinus namaycush*) are routinely affected by hypoxia, both naturally occurring and associated with watershed disturbances caused by human activities (Dillon et al. 1994, 2003; Ryan and Marshall 1994). Phosphorus is the limiting nutrient that controls primary production in lake trout lakes of the boreal forest ecozone (Dillon and Rigler 1974; Dillon et al. 1986; Molot and Dillon 1991). Phosphorus loading causes increased algal production (Schindler et al. 1971) and depletion of late-summer dissolved oxygen levels in the hypolimnion of lakes (Molot et al. 1992; Evans et al. 1996; Lienesch et al. 2005). Recreational and urban development of watersheds and associated impacts on natural shorelines are significant contributors to phosphorus loads and to oxygen depletion in thermally stratified lakes (Evans et al. 1996; Dillon et al. 2004). In the broader context of global climate change, lake

trout have been identified as highly vulnerable because of effects on thermal stratification and water chemistry of lakes and associated loss of summer habitat and productive capacity (Magnuson et al. 1990; Schindler 1998; Schindler and Gunn 2004). These factors are now poised to affect lake trout distribution and production across the species' range (Magnuson et al. 1997; Stefan et al. 2001; Shuter and Lester 2004). Concerns about climatic change and local impacts of human activity on the future sustainability of lake trout are driving the need for improved quantitative models of the habitat requirements of this species.

Lake trout is a stenothermal species that inhabits relatively deep, cold lakes spanning the North American continent from Alaska to Labrador (Lindsey 1964), with the southern limits of the primary range extending into Minnesota, Wisconsin, Michigan, New York, Vermont, New Hampshire, and Maine. Across this range, lake trout seek thermal refuge in the cooler waters of the hypolimnion of

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thermally stratified lakes during summer (Evans et al. 1991, 1996). During this time, an adequate supply of dissolved oxygen is essential to meet the metabolic demands of life support activities, including swimming, feeding, avoidance of predators, growth, and reproduction. Adult lake trout inhabit temperatures of 4–18 °C (Martin and Olver 1980) but during summer are most often found at 8–12 °C (Christie and Regier 1988), although Sellers et al. (1998) have reported that warmer temperatures up to 20 °C are frequented during the night in small boreal forest lakes. During early summer, lake trout move to deeper water and are found near the base of the thermocline during the day. Lake trout continue to occupy this habitat during summer, gradually moving to greater depths as the thermocline deepens (Martin and Olver 1980). Young-of-the-year and older juvenile lake trout inhabit greater depths and cooler temperatures than adults (Elrod and Schneider 1987; Evans et al. 1991; Davis et al. 1997). As surface waters cool during early fall, adult lake trout again move shoreward and are widely dispersed prior to spawning, which occurs on shallow rocky shorelines during September and October (Martin and Olver 1980; Sly and Evans 1996).

Dissolved oxygen also directs the vertical movements of lake trout, but field observations of responses to low dissolved oxygen are relatively rare. The dissolved oxygen avoidance threshold in Lac la Ronge was about 3.6–4.3 mg·L<sup>-1</sup> (Martin and Olver 1980). In Lake Simcoe, a general upward movement of lake trout occurred in response to dissolved oxygen <4 mg·L<sup>-1</sup> (Evans et al. 1996). In small lakes in northwestern Ontario, 75%–90% of lake trout were found at >6 mg·L<sup>-1</sup> and the daytime avoidance threshold appeared to be 2–4 mg·L<sup>-1</sup> (Sellers et al. 1998). Dissolved oxygen concentrations of 1.4–2.9 mg·L<sup>-1</sup> were observed to be lethal in Swan Lake, Alberta (Martin and Olver 1980). The laboratory response threshold to reduced dissolved oxygen for salmonids, measured as increased random swimming, occurs at about 6 mg·L<sup>-1</sup> and the avoidance threshold is about 4 mg·L<sup>-1</sup> (Davis 1975; Spoor 1990).

The energetic consequences of temperature and oxygen variation for lake trout can be defined within the metabolic framework of scope-for-activity and quantified in terms of power output or energy flow required to support critical daily life support activities. On balance, adequate power output must be maintained to support the necessary daily work load. Temperature and oxygen operate as directive, controlling, and limiting factors (Fry 1971; Brett and Groves 1979; Evans and Neill 1990) that ultimately affect survival, growth, abundance, and sustainability at the population level (Ricker 1975; Shuter et al. 1998).

This study develops a quantitative model of the combined effects of temperature and ambient dissolved oxygen on metabolic scope-for-activity and power capacity of juvenile lake trout and links these to requirements for critical life support activities including routine and maximal swimming activity and energy costs for maintenance and maximum feeding rates. The purpose is to provide a quantitative metabolic model that can effectively inform management decisions concerning temperature and dissolved oxygen requirements for the protection of lake trout habitat under the emerging pressures of climate change, water regulation,

forest harvesting, shoreline development, and nutrient loading in lakes across the species' range (Steedman et al. 2004).

## Materials and methods

### Metabolic scope-for-activity and response to hypoxia

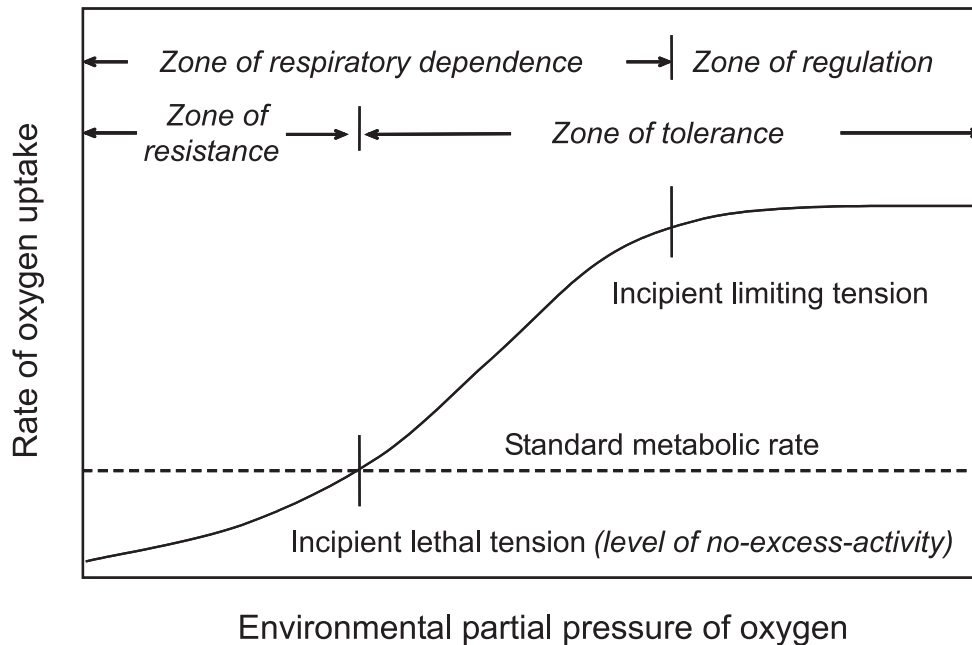
This paper provides a new and extended analysis of data originally published in Gibson and Fry (1954) and integration of more recent metabolism data for lake trout, with emphasis on scope-for-activity and power outputs for critical daily activities under the influence of hypoxia. Scope-for-activity is defined as the difference between standard (resting, postabsorptive) metabolic rate and the maximum sustained metabolic rate (Fry 1947, 1971), the latter being measured during laboratory swimming trials (e.g., Brett 1964; Beamish 1978). Scope-for-activity therefore defines the range of metabolic energy that is potentially available for capture of prey, avoidance of predators, diurnal vertical movements, spawning migration, aggressive behaviour, and all other types of volitional activity, including the increased energy demands of the heart, respiratory muscles, and kidneys during exercise (Jones and Randall 1978). Scope-for-activity offers an effective measure of the aerobic capacity to perform work and provides a quantitative, physiological construct for characterizing the effects of hypoxia on fish activity.

The general analytical construct for the limiting effect of dissolved oxygen on active metabolic rate of aquatic species (Fig. 1) was described by Fry (1947) and Hughes (1964) and later elaborated by Davis (1975). The limiting effects of reduced dissolved oxygen occur within the zone of respiratory dependence (Fig. 1), which is bounded at its upper limit by the partial pressure of dissolved oxygen at which the transport of oxygen across the gill membrane first begins to be dependent on ambient dissolved oxygen. The zone of respiratory dependence is intersected by the incipient lethal dissolved oxygen level, which corresponds to the postabsorptive oxygen consumption rate that is required to maintain the basic integrity of the organism (referred to as standard metabolic rate; Fry 1971). This threshold also corresponds to the level of no-excess-activity, meaning that there is no surplus energy available for volitional activities (Fry 1971). The incipient lethal level therefore marks the boundary between the zone of tolerance and the zone of resistance, death being a simple function of exposure time within the latter. Lake trout and other species can enter their zone of resistance, but only temporarily and at high risk (Priede 1977).

### Standard and active metabolic rates

Published information on the metabolism of lake trout has been used to derive the effects of reduced ambient dissolved oxygen on scope-for-activity and power capacity. The only published study on the effects of hypoxia on the metabolism of lake trout is Gibson and Fry (1954). The initial step in my analysis was to compare the metabolic data in Gibson and Fry (1954) with those from more recent studies (Stewart et al. 1983; Beamish et al. 1989; Rottiers 1993) to establish the consistency of the data. The latter studies provided independent measures of standard and active metabolic rates of juvenile lake trout under normoxic conditions.

**Fig. 1.** Metabolic response of fish to reduced partial pressure of dissolved oxygen showing the zones of respiratory regulation and dependence and the zones of tolerance and resistance. The standard metabolic rate intersects the response curve at the incipient lethal threshold for dissolved oxygen (modified after Davis 1975).



Standard and active metabolic rates of yearling and 2-year-old lake trout were determined in laboratory trials by Gibson and Fry (1954). They used Erlenmeyer flask respirometers to determine standard rates of quiescent fish and a rotating annular swimming chamber to determine active rates (Smit 1965; Beamish 1978). Figure 2 in Gibson and Fry (1954) was digitized to recapture the original standard and active metabolic rates. Data for yearling and 2-year-old lake trout were included in comparisons of standard and active metabolic rates with more recent published data. The hypoxia data for yearlings were analyzed here but the data for 2-year-olds were too incomplete for further analysis.

Metabolic rates were converted from  $\text{mL}\cdot\text{L}^{-1}$  in the original study (Gibson and Fry 1954) to  $\text{mg}\cdot\text{L}^{-1}$ , and for comparison with other studies, oxygen consumption was adjusted to  $\text{mg}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$  for a 100 g lake trout using a weight exponent of 0.85 based on Job (1955) and Beamish et al. (1989). The body weights of the yearlings and 2-year-olds were 16.4–37.9 g (mean = 27.7 g) and 57.6–120.6 g (mean = 82.8 g) and their estimated mean total lengths, based on length-weight relationships for Ontario hatchery stock (Haliburton strain) at the same ages, were 14.8 and 20.9 cm, respectively (D.O. Evans, unpublished data). These mean body weights were used to correct the standard metabolic rate data in Gibson and Fry (1954) to a body weight of 100 g. A weight exponent of 0.85 was also applied to adjust the metabolic data in Beamish et al. (1989) and Rottiers (1993) to correspond to a 100 g fish.

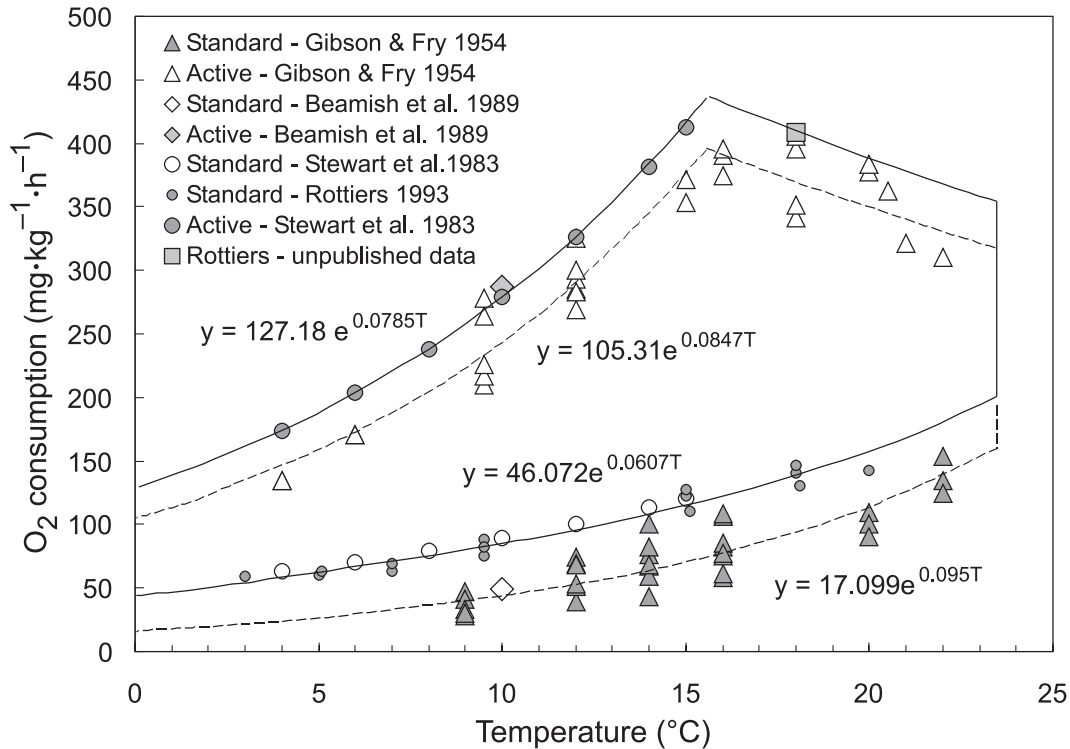
The respiration model of Stewart et al. (1983), which included weight, temperature, and swim speed coefficients, was used to calculate standard and active metabolic rates for that study. Swimming speed is strongly influenced by fish size (Brett 1965; Beamish 1978). Small fish swim at higher relative speed ( $\text{L}\cdot\text{s}^{-1}$ ) but attain lower absolute speed than

larger fish. The actual maximum swimming speed of a 100 g lake trout at each of the five test temperatures, 3.5, 5, 7, 10, and 15 °C, reported in Stewart et al. (1983) was much lower than the maximum speed ( $50\text{--}60\text{ cm}\cdot\text{s}^{-1}$ ) reported by those authors for fish of larger average size. Mean body weight of fish in their study was 486 g (range 20–1835 g). The original data set, provided by D.V. Rottiers (7540 Dexter Pickney Road, Dexter, MI 48130-9608, USA), was used to estimate the maximum swim speed of fish of various lengths by fitting a regression model of maximum  $\text{L}\cdot\text{s}^{-1}$  versus total length at each temperature and estimating speed for a 100 g fish with total length of 22.8 cm. The relationship between temperature and estimated maximum speed for a 100 g fish was then fitted and speeds were calculated at 4, 6, 8, 10, 12, and 14 °C. These speeds, 44.0, 45.6, 47.3, 49.0, 50.7, and 52.4  $\text{cm}\cdot\text{s}^{-1}$ , respectively, were used in the Stewart et al. (1983) model to calculate the active metabolic rates for a 100 g lake trout (Fig. 2). Standard metabolic rates at temperatures from 4 to 20 °C were estimated for all studies by fitting exponential regression functions. Brett and Groves (1979) concluded that this transformation effectively characterizes the relationship between standard metabolic rate and temperature for fish. The ascending and descending limbs of the active metabolic rate versus temperature relationships were also fitted using exponential functions.

### Response to hypoxia

Metabolic rates at 1/4, 1/2, and 3/4 scope-for-activity levels were obtained for yearling lake trout at 4, 6, 8, 10, 12, 14, 16, 18, 20, and 22 °C by partitioning the scope-for-activity envelope (Fig. 3) derived from equations fitted to the original data in Gibson and Fry (1954). These arbitrary scope-for-activity horizons were selected to provide a structured metabolic framework to relate energy costs for various

**Fig. 2.** Active and standard metabolic rates of lake trout (*Salvelinus namaycush*) derived from the published literature as indicated. Rates from Gibson and Fry (1954) are for yearlings and 2-year-olds and have been adjusted to a body weight of 100 g using a weight exponent of 0.85 as were the rates from Beamish et al. (1989). Data from Stewart et al. (1983) and Rottiers (1993) have been adjusted to 100 g body weight using their weight exponents. Active rates for Gibson and Fry (1954) at 4 and 6 °C are based on their estimated swim speeds using the respiration model in Stewart et al. (1983). The vertical line connecting the standard and active metabolic rates at 23.5 °C is the upper incipient lethal temperature level, i.e., the level that causes 50% mortality of a sample of thermally acclimated fish.



activities to the limiting effects of hypoxia on oxygen consumption. The framework required the following steps and calculations: (i) determination of the active rate of oxygen uptake over a wide range of temperatures and limiting ambient dissolved oxygen conditions from Gibson and Fry (1954), (ii) determination of oxygen consumption over a range of temperatures for each scope-for-activity horizon, (iii) determination of the ambient dissolved oxygen levels on each temperature response curve that correspond to oxygen consumption rates of 1/4, 1/2, and 3/4 scope-for-activity, and (iv) compilation of the metabolic costs for various daily life support activities including maintenance, routine and maximum feeding, aggressive behaviour, and excitability that would occur during predator avoidance to determine critical thresholds of ambient dissolved oxygen.

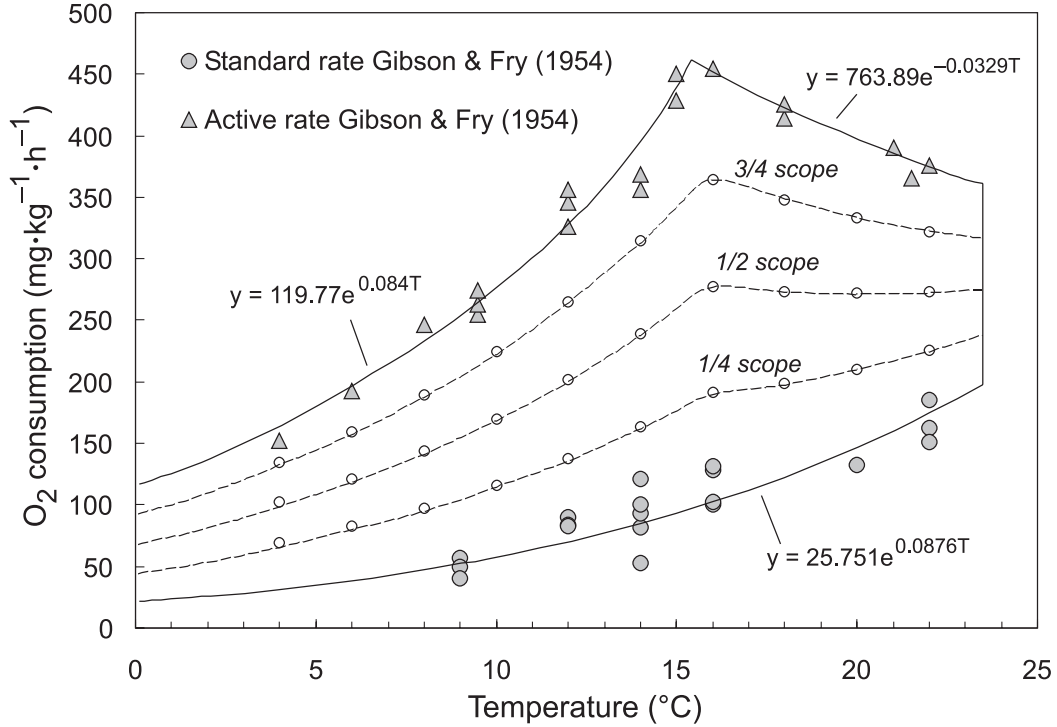
#### Limiting effect of dissolved oxygen on active metabolic rate

Gibson and Fry (1954) determined the effect of low dissolved oxygen on juvenile lake trout. I have digitized and replotted their fig. 3, active metabolic rate versus oxygen pressure, at 9.5–18 °C for yearling lake trout. Analyses of metabolic rates and responses of yearling lake trout to hypoxia were completed using the original data unadjusted for body weight because the individual weights of fish in each experiment were not reported. Also, given the variation

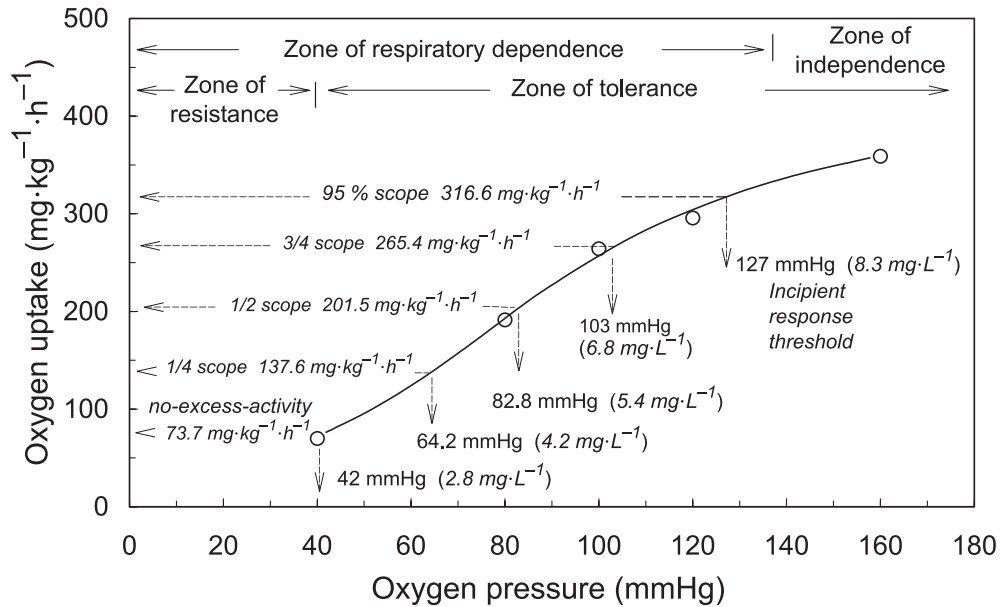
in the oxygen consumption – body size exponent reported among species and studies (Fry 1971; Brett and Glass 1973; Clarke and Johnston 1999), it was deemed best to minimize adjustments of the original data used in the hypoxia analyses. Therefore, I used the original values for normoxic standard and active metabolic rates. Similarly, the active metabolic rate response to hypoxia for yearling lake trout was adjusted directly to  $\text{mg}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ . Partial pressures of atmospheric oxygen, reported in the original paper, were converted to dissolved oxygen concentrations in  $\text{mg}\cdot\text{L}^{-1}$  using standard solubility tables (e.g., Davis 1975) for atmospheric pressure at 243.8 m above sea level at Maple, Ontario, where the original experiments were performed. Oxygen partial pressures reported in the original paper (Gibson and Fry 1954, their fig. 3) were adjusted from measured concentrations to fractions of 100% air saturation. I have used the same approach in converting partial pressures reported in the paper back to concentrations, except to adjust the concentration at full saturation for elevation as noted.

The detailed derivation of ambient dissolved oxygen concentrations that limit lake trout yearlings to 1/4, 1/2, and 3/4 scope-for-activity is illustrated for experiments conducted at 12 °C (Fig. 4). I used the derived values for 1/4, 1/2, and 3/4 scope from Fig. 3 to utilize the strength of the whole data set to obtain the best estimates rather than simply using the individual response curves to identify the cut points. The curves

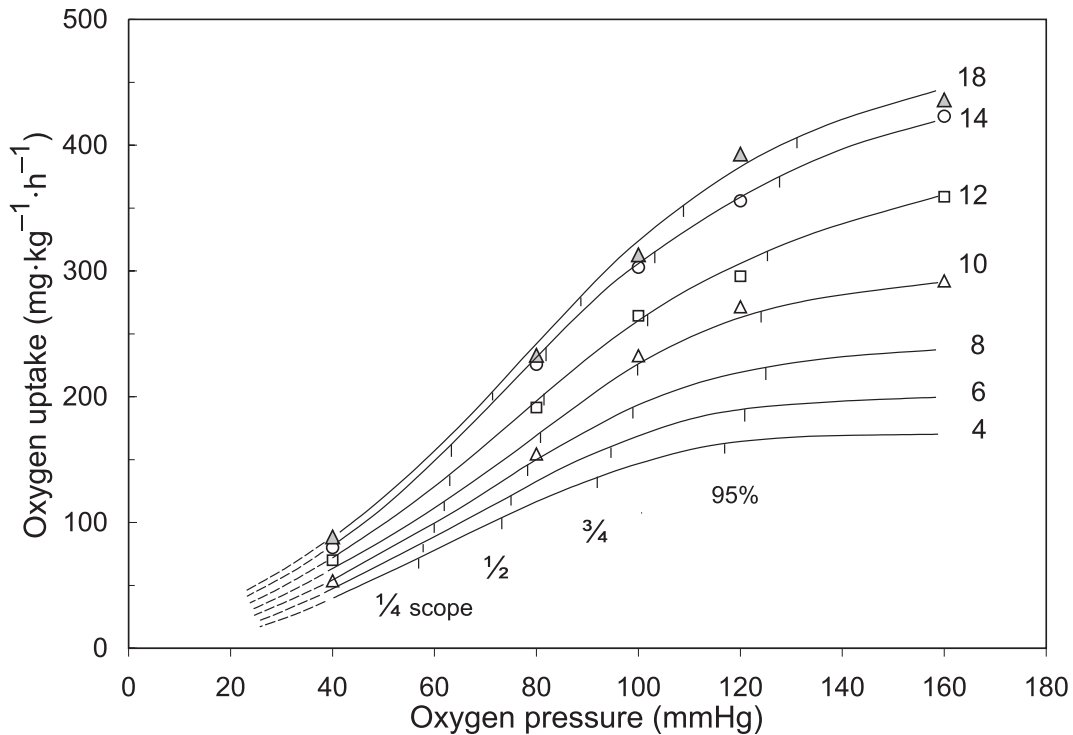
**Fig. 3.** Active and standard metabolic rate of yearling lake trout at a body weight of 27.7 g. Scope-for-activity is defined by the active and standard metabolic rate boundaries. Intermediate boundaries are shown at 1/4, 1/2, and 3/4 scope-for-activity defining progressively increasing potential power available for life support activities. The standard and metabolic rates are derived from fitted exponential functions based on the original data and the intermediate scope-for-activity values were calculated at each temperature based on the fitted equations for standard and active rates. Active rates at 4, 6, and 8 °C were modeled using Stewart et al. (1983) and swim speeds estimated from Gibson and Fry (1954).



**Fig. 4.** Response of active metabolic rate of yearling lake trout to declining partial pressure of oxygen at 12 °C to illustrate the derivation of dissolved oxygen thresholds for scope-for-activity. Oxygen pressures and dissolved oxygen consumption rates corresponding to the level of no-excess-activity, 1/4, 1/2, and 3/4 scope for activity (from Fig. 3), and the incipient response threshold at 95% oxygen saturation are indicated by arrows on each response curve. The symbols are observed values reported by Gibson and Fry (1954). Oxygen consumption rates at 1/4, 1/2, and 3/4 scope-for-activity were taken from Table 2 to establish the associated ambient oxygen pressures.



**Fig. 5.** Response of active metabolic rate of yearling lake trout to reduced partial pressure of dissolved oxygen at 4, 6, 8, 10, 12, 14, and 18 °C. The incipient response thresholds of respiratory dependence are indicated by the vertical tick marks at the upper right of each curve. Tick marks on each curve also indicate 1/4, 1/2, and 3/4 scope-for-activity thresholds. The symbols are observed data from Gibson and Fry (1954). The curves at 4, 6, and 8 °C were drawn by eye between the estimated standard and active metabolic rates shown in Fig. 3 and Table 1.



for 10, 12, and 14 °C were fitted by eye and the response curves at 4, 6, and 8 °C were interpolated using the standard and active rates from Fig. 1 to fix the upper and lower ends of the curves (Fig. 5). For each temperature curve, the intercept is shown for the oxygen consumption rates that correspond to 1/4, 1/2, and 3/4 scope-for-activity (as in Fig. 4). The threshold of respiratory dependence is also indicated on each curve as is the point of significant initial respiratory decline set arbitrarily at the 95% scope-for-activity response level. It should be noted that the analyses are based on the original data of Gibson and Fry (1954) and that any potential limitations of the original data remain. The integrity of the original data set has been maintained with the added benefit that the standard and active metabolic rate versus temperature curves are now based on fitted regressions that make no specific assumptions about the data. The data have also been integrated with the more recent published literature to test for any inconsistencies that might potentially introduce bias into the present analyses.

### Power capacity

Power capacity was calculated at 1/4, 1/2, 3/4, and full scope-for-activity at temperatures from 4 to 23.5 °C. Power is defined as the rate of energy flow per unit time in watts ( $1 \text{ W} = 1 \text{ J}\cdot\text{s}^{-1}$ ). Scope-for-activity expressed as  $\text{mg O}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$  for yearling lake trout was converted to energy units using an oxycaloric equivalent of  $3.241 \text{ cal}\cdot\text{mg oxygen}^{-1}$  (Elliott and Davison 1975; Brett and Groves 1979) or  $13.6 \text{ J}\cdot\text{mg oxygen}^{-1}$  (Prieditis 1985). Power capacity was calculated for temperatures from 4 to 23.5 °C and partial pressures of oxygen from

30 to 160 mmHg at 20 mmHg intervals by interpolation of the metabolic rate – oxygen partial pressure response curves at 4, 6, 8, 10, 12, 14, and 18 °C (Fig. 5) and converting oxygen consumption to milliwatts. Power capacity at each oxygen saturation level was then plotted versus temperature. These curves were fitted by eye and interpolated to construct a response surface of power capacity over the temperature range 4–23.5 °C and 30–160 mmHg partial pressure of oxygen.

### Results

There is general consistency among the published studies of lake trout metabolism (Fig. 2), but the standard and active metabolic rates in Stewart et al. (1983) are higher than reported by Gibson and Fry (1954) and Beamish et al. (1989). The higher standard rates reported by Stewart et al. (1983) are consistent with those of Rottiers (1993), the latter two studies being based on the same experimental data. Their standard rates were for 1-, 2-, and 3-year-old lake trout tested in a tunnel respirometer. In those experiments, lake trout were forced to swim at initial speeds of  $10\text{--}20 \text{ cm}\cdot\text{s}^{-1}$  up to maxima of  $50\text{--}60 \text{ cm}\cdot\text{s}^{-1}$  and swimming speed was increased in increments of  $10 \text{ cm}\cdot\text{s}^{-1}$  after 90 min swimming intervals. Standard metabolic rates were estimated for individual fish or groups of small fish using the intercept of the oxygen consumption versus swimming speed relationships. Typically, in tunnel respirometers, fish express spontaneous swimming at lower speeds especially when tested in groups (Brett and Sutherland 1965; Fry 1971; Beamish 1978).

**Table 1.** Standard and active metabolic rates, scope-for-activity, the level of no-excess-activity corresponding to standard metabolic rate, and the threshold of respiratory dependence corresponding to 95% of full scope-for-activity for yearling lake trout (*Salvelinus namaycush*) at 4–18 °C based on data in Gibson and Fry (1954).

Temperature (°C)	Metabolic rate		Scope-for-activity at 100% O <sub>2</sub> saturation (mg·kg <sup>-1</sup> ·h <sup>-1</sup> )	Level of no-excess-activity (incipient lethal threshold)		Threshold of respiratory dependence (95% scope-for-activity)	
	Standard (mg·kg <sup>-1</sup> ·h <sup>-1</sup> )	Active (mg·kg <sup>-1</sup> ·h <sup>-1</sup> )		O <sub>2</sub> partial pressure (mmHg)	O <sub>2</sub> concentration (mg·L <sup>-1</sup> )	O <sub>2</sub> partial pressure (mmHg)	O <sub>2</sub> concentration (mg·L <sup>-1</sup> )
4	36.6	167.8	131.2	39.5	3.2	118.0	9.4
6	43.6	198.6	155.0	40.0	3.1	122.0	9.2
8	51.9	235.1	183.2	41.0	3.0	126.3	9.1
10	61.8	278.3	216.5	41.5	2.9	124.8	8.6
12	73.7	329.4	255.7	42.0	2.8	126.8	8.3
14	87.8	389.9	302.1	42.5	2.7	129.2	8.1
18	124.6	422.5	297.9	52.0	3.0	132.7	7.7

Spontaneous activity at slow speeds might explain the elevated standard metabolic rates in Stewart et al. (1983). The standard rate reported by Beamish et al. (1989) at 10 °C was identical to that of Gibson and Fry (1954) and the latter authors provide the best estimates of standard metabolic rate for this species over a wide range of temperatures.

The higher active metabolic rates in Stewart et al. (1983) might be due to higher swimming speeds being attained in the tunnel-type respirometer versus the rotating annular chamber used by Gibson and Fry (1954). Direct comparison of fish of the same size, however, revealed that swimming speeds attained in the annular chamber and tunnel respirometer were similar. At 10 °C, fish averaging 14.9 cm total length attained a maximum mean speed of 38.1 cm·s<sup>-1</sup> in the rotating annular respirometer (Gibson and Fry 1954) compared with 10 fish of 15.0 cm mean total length that attained a sustained maximum speed of 36.7 cm·s<sup>-1</sup> in the tunnel respirometer. Similarly, at 18 °C, lake trout of 20.7 cm total length swam at 63.8 cm·s<sup>-1</sup> in the annular chamber versus 50.1 cm·s<sup>-1</sup> for 10 fish of mean length 24.7 cm in the tunnel respirometer. Juvenile lake trout, therefore, swam as fast or faster in the Gibson and Fry (1954) annular chamber compared with the tunnel respirometer of Stewart et al. (1983). The active metabolic rate at 10 °C measured by Beamish et al. (1989) was 17% higher than that estimated by Gibson and Fry (1954). Similarly, the estimated active rate at 10 °C from Stewart et al. (1983) was 13.5% higher than that from Gibson and Fry (1954), but scope-for-activity at 10 °C was estimated as 201.4 mg·L<sup>-1</sup> by Gibson and Fry (1954) versus 189.4 mg·L<sup>-1</sup> by Stewart et al. (1983) and 237.9 mg·L<sup>-1</sup> at 10 °C by Beamish et al. (1989). The active metabolic rates in the annular chamber were slightly lower than those in the tunnel respirometers but well within the range of variation normally seen among studies (Beamish 1978, 1980). The overall similarity of scope-for-activity for lake trout among these studies validates use of the data from Gibson and Fry (1954) in the present study.

Standard metabolic rates of yearling lake trout increased monotonically with temperature, whereas active metabolism peaked at 15–16 °C, as did scope-for-activity (Fig. 2). The level of no-excess-activity varied from about 2.7 to 3.2 mg·L<sup>-1</sup> over the range 4–18 °C (Table 1). The incipient response threshold, indicating the boundary of the zone of

respiratory dependence, defined herein as the 95% scope-for-activity threshold, varied from 9.4 to 8.1 mg·L<sup>-1</sup> at temperatures of 4–18 °C, respectively (Fig. 5; Table 1). Above these thresholds, full scope-for-activity is attainable. Full scope-for-activity was 3.5 times standard at 4–14 °C but decreased to 2.4 times standard at 18 °C. These ratios define the upper limit for the costs of activity in lake trout.

The selected scope-for-activity thresholds (1/4, 1/2, and 3/4 scope) partitioned the scope into four equal segments (Fig. 3). The active metabolic rate at various ambient partial pressures of oxygen is illustrated in detail for tests at 12 °C (Fig. 4). The selected thresholds, i.e., 1/4, 1/2, and 3/4 scope-for-activity, the level of no-excess-activity, and the incipient response threshold are indicated on the dissolved oxygen response curves for all test temperatures (Fig. 5). These curves revealed the limiting effect of hypoxia on active metabolic rate at various temperatures. As a general rule, hypoxia caused a more precipitous decline in active metabolic rate at the higher temperatures, 14–18 °C.

The ambient dissolved oxygen concentrations that limited performance to 1/4, 1/2, and 3/4 scope-for-activity varied from 4.1 to 4.6, from 5.2 to 5.9, and from 6.3 to 7.5 mg·L<sup>-1</sup>, respectively (Table 2). The mean dissolved oxygen thresholds for 1/4 and 3/4 scope-for-activity at 10 °C, 4.4 and 7.0 mg·L<sup>-1</sup>, were separated by only 2.6 mg ambient dissolved oxygen·L<sup>-1</sup>, revealing that relatively small changes in oxygen content of the natural environment can have major implications for metabolism and activity of yearling lake trout. This range defines the scale from avoidance and maintenance feeding at about 4.3 mg·L<sup>-1</sup> to a relatively high level of metabolic performance at 7.0 mg·L<sup>-1</sup>. At 4–14 °C and 1/4, 1/2, and 3/4 scope, the activity component of the total metabolic rate averaged 0.89 ± 0.01, 1.76 ± 0.03, and 2.63 ± 0.04 times standard metabolic rate, respectively. These ratios, i.e., multipliers of standard metabolic rate, define the maximum upper limits for activity at the corresponding ambient dissolved oxygen levels shown in Table 2.

### Effect of hypoxia on power capacity

Hypoxia and temperature had a dramatic effect on net power capacity, i.e., the power available for all volitional activities. The net power capacity is illustrated per kilogram of yearling lake trout at various partial pressures of oxygen

**Table 2.** Scope-for-activity of juvenile lake trout at 1/4, 1/2, and 3/4 scope-for-activity.

Temperature (°C)	1/4 scope			1/2 scope			3/4 scope		
	O <sub>2</sub> uptake (mg·kg <sup>-1</sup> ·h <sup>-1</sup> )	O <sub>2</sub> partial pressure (mmHg)	Ambient O <sub>2</sub> (mg·L <sup>-1</sup> )	O <sub>2</sub> uptake (mg·kg <sup>-1</sup> ·h <sup>-1</sup> )	O <sub>2</sub> partial pressure (mmHg)	Ambient O <sub>2</sub> (mg·L <sup>-1</sup> )	O <sub>2</sub> uptake (mg·kg <sup>-1</sup> ·h <sup>-1</sup> )	O <sub>2</sub> partial pressure (mmHg)	Ambient O <sub>2</sub> (mg·L <sup>-1</sup> )
4	69.4	58.0	4.62	102.2	74.5	5.94	135.0	93.6	7.46
6	82.3	59.0	4.47	121.1	76.3	5.78	159.9	96.0	7.27
8	97.7	61.0	4.40	143.5	79.5	5.73	189.3	100.2	7.22
10	115.9	63.2	4.35	170.1	82.0	5.64	224.2	101.0	6.95
12	137.6	64.2	4.22	201.5	82.8	5.44	265.4	103.0	6.77
14	163.3	64.5	4.06	238.8	83.0	5.23	314.3	104.5	6.58
18	199.1	71.3	4.13	273.6	88.7	5.13	348.0	108.6	6.29

**Note:** Scope values at each temperature were derived from Fig. 3 for yearling lake trout at a mean body weight of 27.7 g.

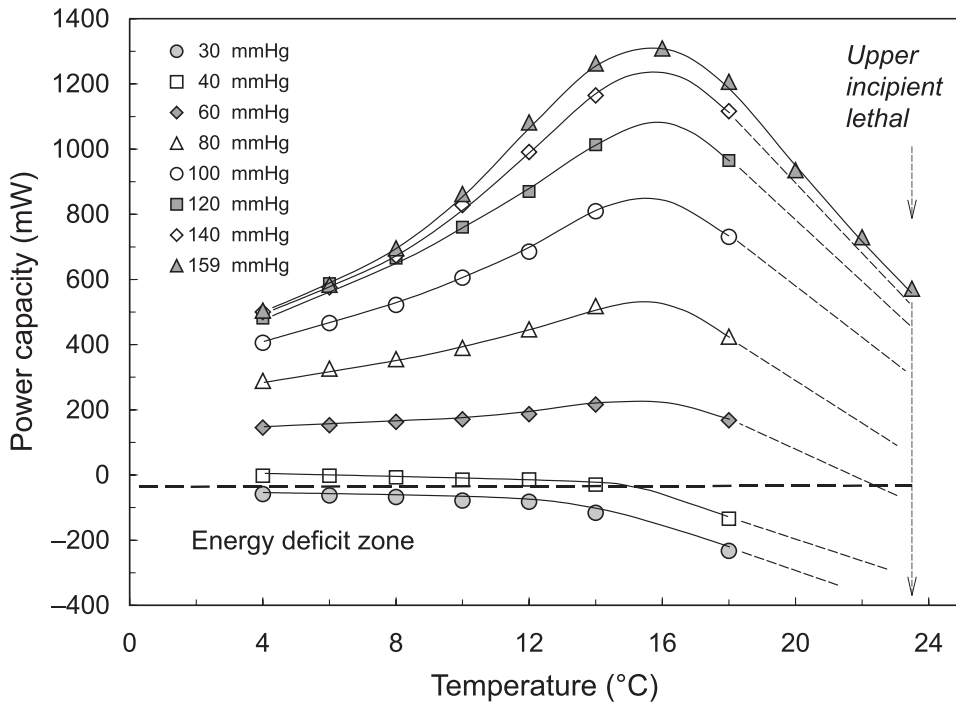
(Fig. 6). Power capacity is maximal at 14–18 °C and declines to zero as ambient partial pressure of oxygen declines to 40 mmHg. At 66 mmHg, which is equivalent to about 4.0 mg dissolved oxygen·L<sup>-1</sup> at 16 °C, power capacity fell to about 25% of full power. Hence, there is a dramatic decline in power available for various work activities as dissolved oxygen falls from air saturation to the avoidance threshold near 4.0 mg·L<sup>-1</sup>. At temperatures >16 °C, lake trout were operating at an aerobic power deficit at 40 mmHg partial pressure of oxygen and at 30 mmHg were in a deficit position at all temperatures. The chronic lethal threshold for lake trout survival would therefore be expected to be about 40 mmHg partial pressure (Fig. 6). The mean ± SD incipient lethal threshold corresponding to the level of no-excess-activity was estimated to be 40.8 ± 3.5 mmHg at 4–18 °C (Table 1). Interpolation of Fig. 6 provided a rectangular matrix of power capacity across the range of temperatures and oxygen pressures normally experienced by lake trout in the natural environment. This matrix was used to generate a two-dimensional response surface of power capacity (Fig. 7; the points are the interpolated values from Fig. 6). The temperature range exploited by lake trout during summer, 4–20 °C, provides for a potential power capacity of about 500–1300 mW·kg<sup>-1</sup> at 100% oxygen saturation, declining to zero near 40 mmHg (Fig. 7). The response surface has been partitioned to include the habitats associated with juveniles and adults (Fig. 8). The maximum power capacity of lake trout occurred at oxygen concentrations exceeding 7 mg·L<sup>-1</sup> and temperatures of 12–20 °C (Fig. 8, shaded area). Juvenile lake trout that inhabit the hypolimnion and frequent temperatures of about 4–8 °C during the summer months (Davis 1997) clearly have greatly reduced power capacity (500–700 mW) compared with 700–1300 mW·kg<sup>-1</sup> at temperatures of 8–20 °C, i.e., the thermal habitat routinely frequented by adult lake trout. Within the thermal zone occupied by juvenile lake trout, it is also clear that a decline in oxygen pressure from air saturation to 120 mmHg would have relatively little impact on power capacity of the juveniles. A further decline in oxygen pressure to 86–96 mmHg corresponding to a concentration of about 7 mg·L<sup>-1</sup> at 4–8 °C, however, would reduce net power capacity by about 33%, and further declines in oxygen pressure to 66 mmHg (5 mg·L<sup>-1</sup>) and 40 mmHg (3 mg·L<sup>-1</sup>) would result in dramatic declines in net power capacity of 67% and 100%, respectively (Fig. 8).

## Discussion

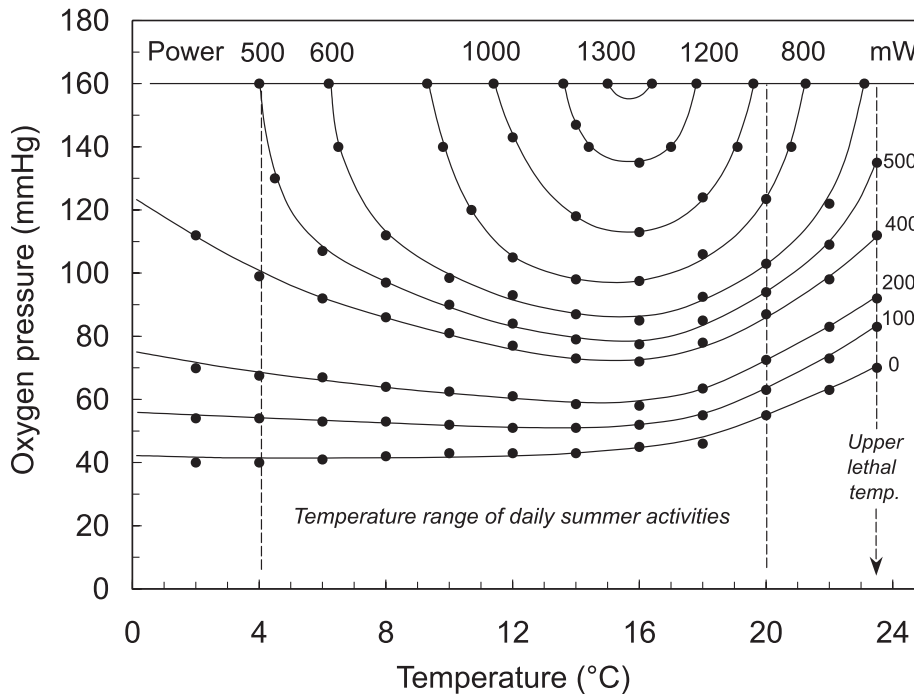
### Habitat, life history, and dissolved oxygen

Using a remotely operated vehicle, Davis (1997) and Davis et al. (1997) directly observed juvenile lake trout in the hypolimnion of four study lakes at temperatures of 4–8 °C. The deep distribution of juvenile lake trout at physiologically suboptimal temperatures (McCauley and Tait 1970; Edsall and Cleland 2000) is probably maintained by the predation pressure of cannibalistic adults, which inhabit shallower depths (Evans and Willox 1991; Evans et al. 1991). The juveniles are confined to the hypolimnion during the summer months, making this habitat a potential bottleneck for lake trout recruitment because of the limiting effect of low dissolved oxygen that commonly occurs in stratified lakes. A recent whole-lake fertilization experiment in a

**Fig. 6.** Net power capacity of yearling lake trout per kilogram of fish at various oxygen pressures and ambient temperatures. Power was derived from oxygen consumption at each oxygen pressure taken directly from Fig. 5 minus standard metabolic rate at each temperature. The broken horizontal line corresponds to the level of no-excess-activity or lethal threshold below which lake trout would be in a deficit energy state.



**Fig. 7.** Response surface of net power capacity for yearling lake trout per kilogram of fish derived from Fig. 6. The points indicate the interpolated values. The vertical broken lines at 4 and 20 °C represent the potential operational temperature range for all life stages of lake trout.

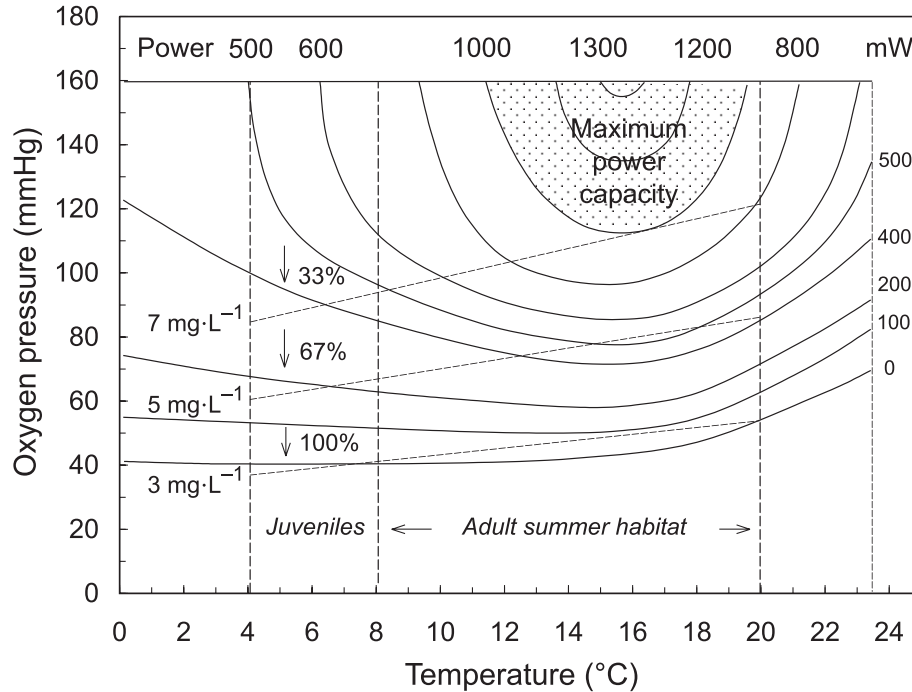


small Arctic lake has clearly demonstrated the linkages between phosphorus loading, primary production, hypolimnetic dissolved oxygen depletion, and lake trout recruitment (Lienesch et al. 2005).

**Standard and active metabolic rates of lake trout**

Standard metabolic rates are difficult to obtain because of the effects of handling stress (Fry 1971) and the need to account for spontaneous activity (Evans 1972, 1984, 1990). In

**Fig. 8.** Net power capacity of yearling lake trout illustrating the zone of optimal performance (shaded area) and selected dissolved oxygen thresholds at 3, 5, and 7 mg·L<sup>-1</sup>. The primary temperature ranges frequented by juvenile (4–8 °C) and adult lake trout during summer (8–20 °C) are indicated by vertical broken lines. The solid curves indicate the power capacity for yearling lake trout of 27.7 g mean body weight expressed per kilogram. The sloping broken lines are the dissolved oxygen concentrations at 3, 5, and 7 mg·L<sup>-1</sup> corresponding to temperatures and oxygen partial pressures across the surface. The percentages shown in the juvenile zone indicate approximate power losses of 33%, 67%, and 100% at the dissolved oxygen boundaries of 7, 5, and 3 mg·L<sup>-1</sup>, respectively.



this study, standard metabolic rates adjusted to a 100 g fish varied from 25.5 to 114.3 mg·kg<sup>-1</sup>·h<sup>-1</sup> for yearling lake trout at 4–20 °C, which are similar to standard rates reported for sockeye salmon (*Oncorhynchus nerka*) (Brett 1964), Atlantic salmon (*Salmo salar*) (Peterson and Anderson 1969), and rainbow trout (*Oncorhynchus mykiss*) (Dickson and Kramer 1971) over the same temperature range. Beamish et al. (1989) reported a standard metabolic rate of 50.7 mg·kg<sup>-1</sup>·h<sup>-1</sup> at 10 °C for yearling lake trout adjusted to a body weight of 100 g that was essentially identical to the rate 51.0 mg·kg<sup>-1</sup>·h<sup>-1</sup> determined for yearling lake trout at 10 °C by Gibson and Fry (1954).

Standard metabolic rates estimated for lake trout by Rottiers (1993) and Stewart et al. (1983), however, were consistently higher than those reported by Gibson and Fry (1954). Webb (1997) suggested that a change in swimming gait at slower speeds results in J-shaped speed–cost curves, oxygen consumption rising at lower speeds. Extrapolation of this type of relationship to zero activity would tend to overestimate standard metabolic rate. Brett and Sutherland (1965) first noted the marked effect of spontaneous activity at slow speeds on oxygen consumption in tunnel respirometers. Beamish et al. (1989) observed similar behaviour in lake trout and omitted measurements of oxygen consumption for fish swimming at 20 cm·s<sup>-1</sup> when extrapolating to zero activity. Spontaneous start-and-stop swimming compared with swimming at a constant speed has also been shown to have dramatically increased costs (Smit 1965). Variation in swimming gait or mode at low speeds might in part explain the higher standard rates reported by Rottiers (1980, 1993)

and Stewart et al. (1983) compared with Gibson and Fry (1954) and Beamish et al. (1989). Gibson and Fry (1954) used the lowest measured rates of quiescent fish over a 24 h cycle to characterize standard metabolic rate, which also explains their lower estimates.

The active metabolic rate of lake trout at 10 °C from Gibson and Fry (1954) was 14.5% lower than that from Beamish et al. (1989) and 11.9% lower than that from Stewart et al. (1983). Differences of this magnitude can easily be accounted for by variation in study-specific oxygen consumption – body weight exponents used to adjust to a common fish size (Fry 1971). In contrast, the scope-for-activity for lake trout from Gibson and Fry (1954) is 4–10% higher than scope-for-activity values from Stewart et al. (1983) at 4–15 °C and within 2% of values calculated for brown trout (*Salmo trutta*) at 15 °C (Priede 1985), indicating consistency between metabolic scope reported by Gibson and Fry (1954) and the more recent literature.

### Response to hypoxia

The response of lake trout to hypoxia was similar to that observed for brook trout (*Salvelinus fontinalis*), active metabolic rate declining from the highest oxygen partial pressures to the level of no-excess-activity with little or no zone of oxygen independence (Graham 1949; Job 1955; Basu 1959). For brook trout at 10 and 15 °C, 1/2 scope occurred at about 87 and 95 mmHg (Basu 1959) compared with 82 and 86 mmHg, respectively, for lake trout. Similarly, 3/4 scope for brook trout at 10 and 15 °C occurred at 120 and 125 mmHg (Basu 1959) compared with 101 and 105 mmHg,

respectively, for lake trout. The acute lethal threshold for brook trout fry was  $1.58 \text{ mg}\cdot\text{L}^{-1}$  (Sheppard 1955), but a comparable value is not available for lake trout. Carlson and Seifert (1974) did find that all lake trout larvae incubated at  $1.9\text{--}3.2 \text{ mg}\cdot\text{L}^{-1}$  at  $7^\circ\text{C}$  and  $3.0\text{--}4.2 \text{ mg}\cdot\text{L}^{-1}$  at  $10^\circ\text{C}$  died at or prior to first-feeding.

An important question with reference to the ability to compensate for the effects of hypoxia on metabolic scope is whether exposure to low oxygen results in acclimation with the benefit of improved survival and swimming performance. Bushnell et al. (1984) found that acclimation of rainbow trout to hypoxia (oxygen partial pressure = 40 and 60 mmHg at  $15^\circ\text{C}$ ) did not increase maximum swimming speeds in normoxic or hypoxic swim trails. Similarly, Kutty (1968) found no evidence of enhanced swimming capacity in hypoxia-acclimated goldfish (*Carassius auratus*).

Standard metabolic rates of rainbow trout were not significantly affected by acclimation to hypoxia when tested under normoxic or hypoxic conditions, oxygen partial pressure of 40 mmHg (Bushnell et al. 1984), although control fish tended to have higher standard rates under hypoxia. The latter observation is consistent with Beamish (1964) who reported elevated standard metabolic rate of brook trout at 80 mmHg when tested at 10 and  $15^\circ\text{C}$ . In contrast with Bushnell et al. (1984), Beamish (1964) also found that hypoxia-acclimated brook trout showed a noticeable, but smaller, increase at 80 mmHg than the normoxic controls. This suggested that acclimation to low oxygen reduced the cost of ventilation at low ambient dissolved oxygen. Beamish (1964) attributed the 40%–50% increase in standard metabolic rate of normoxic control fish at 80 mmHg to the cost of increased respiratory volume needed to meet standard metabolic costs. Standard oxygen consumption did not rise to the level of active metabolic rate and swimming continued until the oxygen partial pressure reached 30–40 mmHg. Beamish (1964) speculated that anaerobiosis might be engaged to help meet the metabolic demands at low oxygen partial pressure. If a similar mechanism occurs in lake trout, the current values of scope-for-activity would be overestimated at ambient oxygen levels near 80 mm Hg, i.e., near the level of 1/2 power capacity. In effect, an aerobic power reduction would appear at the 1/2 scope threshold when costs of elevated heart rate and increased respiratory volume become engaged, thereby increasing standard costs and reducing metabolic scope (Saunders 1962). There would be an apparent slight recovery of scope when second-stage biochemical mechanisms and anaerobic pathways come on line (Heath et al. 1980; Dunn and Hochachka 1986). This possible increase in standard metabolic rate and associated decline in scope at about 60–80 mmHg oxygen partial pressure would have no effect on the ambient oxygen required to attain 3/4 scope-for-activity because this would be well above the oxygen partial pressure that causes elevation of the standard rate.

### Scope-for-activity and net power capacity

Scope-for-activity defines the amount of energy available for activity, whereas power is the flow of energy per unit time in  $\text{J}\cdot\text{s}^{-1}$ . While these measures can be converted from one to the other, they have distinctive meanings. Scope is the range of aerobic metabolism available for volitional activi-

ties and power is the output of energy associated with a specific workload. The limiting effect of hypoxia on oxygen uptake directly constrains scope-for-activity and the power output that can be achieved during performance of various activities. Maintenance of power outputs comfortably within the boundaries set by standard and active metabolic rates (Fry 1971; Priede 1977, 1985), while at the same time providing surplus energy for somatic growth, requires a balancing of energy intake and the metabolic costs of capturing prey and avoiding predators (Brett 1979; Brett and Groves 1979). The latter activities of lake trout would be severely constrained by hypoxia because of the limits imposed on oxygen uptake (Jones 1971; Davis 1975). There would also be elevated foraging risks associated with reduced quality and availability of summer nursery habitat (Molot et al. 1992; Evans et al. 1996; Dillon et al. 2003).

Feeding metabolism at levels from maintenance to maximum ration includes the cost of standard metabolism, swimming activity, and heat increment associated with handling and processing ingested food, all of which can be expressed as a fraction of the available scope-for-activity (Table 3). These activities are additive and their relative contributions to total metabolism are continually under adjustment during the activity trade-offs of a normal day (Brett and Groves 1979; Priede 1985). Hypoxia has the potential to limit or completely interdict some or all of these activities, which in the latter case could cause an energy deficit with metabolic power falling below the level of no-excess-activity. If persistent, this would result in mortality.

### Cost of daily life support activities with reference to hypoxia

Knowledge of the actual daily costs of critical activities would allow the significance of hypoxia on scope-for-activity to be quantified for wild fish. Energy intake (prey) minus energy expenditures for standard metabolism, locomotory activity, heat increment, and excretion determines the energy available for growth and production (Brett and Groves 1979). Hence, quantification of the actual level of swimming activity and associated energy expenditure of free-ranging fish has been the subject of much scientific enquiry (Boisclair and Leggett 1989; Rowan and Rasmussen 1996; Rennie et al. 2005). Metabolic costs of daily activities have not been published for free-ranging lake trout, but costs for various activities are available from laboratory studies for lake trout and other salmonids, including sockeye salmon (Brett 1964, 1965) and brown trout (Elliott 1976; Priede 1985). Sockeye salmon attain sustained active metabolic rates that are 10 times the standard metabolic rate compared with lake trout at five times and brown trout at 4.3 times standard (Table 3). Sockeye salmon, brown trout, and lake trout, however, have similar standard metabolic baselines.

Standard metabolism for lake trout in Table 3 is from Gibson and Fry (1954), active metabolism is from Stewart et al. (1983), maintenance, routine, and maximum feeding metabolism were derived from Rottiers (1993) and maximum aggression or excitability metabolism was estimated as one-half active metabolic rate (Fry 1971). The oxygen consumption – feeding ration relationship at  $15^\circ\text{C}$  derived from Rottiers (1993) was used to estimate metabolic rates of lake trout at maximum and maintenance feeding levels. The maximum

**Table 3.** Comparison of metabolic rates ( $\text{mg}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ ) of sockeye salmon (*Oncorhynchus nerka*), brown trout (*Salmo trutta*), and lake trout (*Salvelinus namaycush*) and costs of various activities adjusted to a body weight of 100 g at 15 °C.

Species	Standard rate, $R_s$	Active rate, $R_{act}$	Scope-for-activity, $R_{act} - R_s$	Feeding maintenance, $R_{fmin}$	Feeding routine, $R_{fr}$	Feeding maximum, $R_{fmx}$	Aggression or excitability	Migration maximum
Sockeye salmon	75	790	715	140	250	360	310–420	640
			<i>100</i>	<i>9</i>	<i>24</i>	<i>40</i>	<i>32–48</i>	<i>79</i>
Brown trout	98	421	323	175	229	368	210	na
			<i>100</i>	<i>24</i>	<i>41</i>	<i>84</i>	<i>35</i>	
Lake trout	71	413	342	116	253	370	207	na
			<i>100</i>	<i>13</i>	<i>53</i>	<i>87</i>	<i>40</i>	

**Note:** Standard and active metabolic rates of brown trout and lake trout were adjusted using a weight exponent of 0.85. The data for sockeye salmon are from Brett and Groves (1979) and for brown trout are from Elliott (1976) and Priede (1985). Lake trout data: standard from Gibson and Fry (1954), active rate from Stewart et al. (1983), and maintenance and maximum feeding from Rottiers (1993). Aggression or excitability for brown trout and lake trout was calculated as 0.5 of the active metabolic rate (Fry 1971). The percentage of scope-for-activity required by each activity is shown in italics. The cost of standard metabolism is included in all values except scope-for-activity. na, not available.

feeding rate ( $78.1 \text{ cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) was the mean at the observed maximum ration at 15 °C (Rottiers 1993). Maintenance ration ( $22.03 \text{ cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) was the intercept of the growth–ration curve at 15 °C ( $y = 22.026e^{0.0528x}$ , where  $y$  is ration ( $\text{cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) and  $x$  is growth ( $\text{cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ )). Elliott (1976) reported similar maximum ( $65.5 \text{ cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) and maintenance ( $18.6 \text{ cal}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) feeding rations for brown trout at 15 °C. Routine field metabolism of lake trout was based on observed field growth of juvenile lake trout at 7.25 °C (Rottiers 1993). The estimated routine ration in the field, 2.0% body weight·day<sup>-1</sup> (Rottiers 1993), was adjusted to an expected ration at 15 °C of 4.39% body weight·day<sup>-1</sup> using the slope ( $b = 0.308$ ) of the optimal ration–temperature curve in Brett (1979, their fig. 10A). Using Rottiers' (1993) relationship between oxygen consumption and ration expressed as % body weight·day<sup>-1</sup>, the routine field metabolic rate was  $252.7 \text{ mg}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$  for a 100 g fish, which was equivalent to 53% of full scope-for-activity. Priede (1985) provided a power estimate of 340 mW for a 500 g randomly feeding, free-ranging brown trout in a Scottish loch. This equates to oxygen consumption of  $229 \text{ mg}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$  or 41% of full scope-for-activity for a 100 g fish (Table 3). Lake migration of juvenile sockeye in Babine Lake, British Columbia (Johnson and Groot 1963; Groot and Wiley 1965), required 380–640  $\text{mg O}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$  or 53%–79% of the available scope-for-activity (Brett and Groves 1979).

Under laboratory conditions at 15 °C, maintenance, routine, and maximum feeding and excitability of sockeye consumed 9%, 24%, 40%, and 34%–48%, respectively, of the maximum scope-for-activity (Brett and Groves 1979) (Table 3). Brown trout utilized 24%, 41%, 84%, and 35% of available scope for maintenance, routine, and maximum feeding and excitability, respectively (Elliott 1976; Priede 1985), compared with lake trout at 13%, 53%, 87%, and 40% for the same activities (Table 3). Similar daily activity costs of lake trout and brown trout reflect their well-matched lacustrine life histories and corresponding low power capacities. Sockeye power capacity is much higher, reflecting a more demanding life history that includes extensive ocean and freshwater migrations. Somatic energy reserves are accumulated in ocean-feeding sockeye in proportion to the distance and difficulty of migration routes of various stocks (Hendry and Berg 1999). These and similar observations

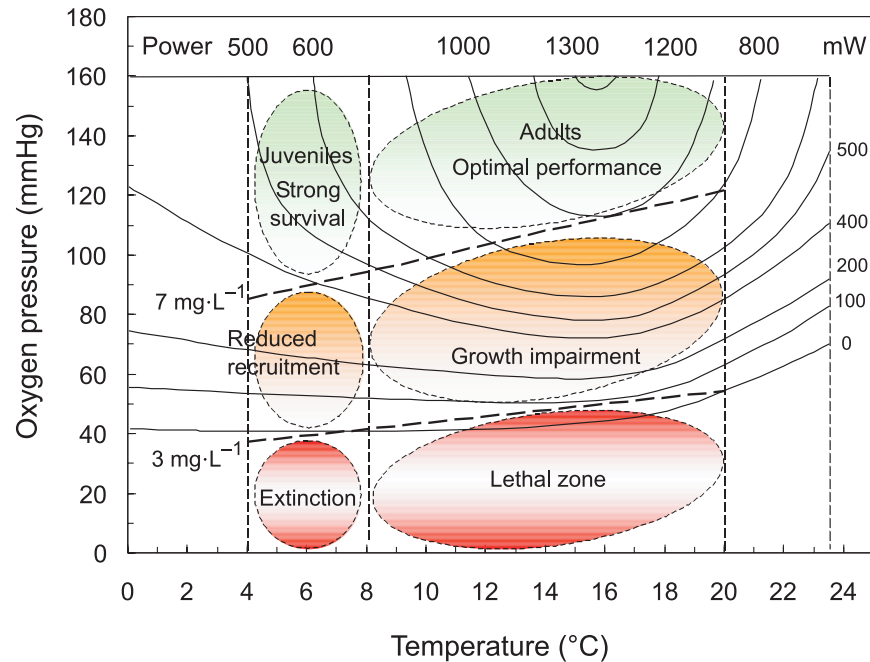
(e.g., Rand and Hinch 1998; Cooke et al. 2006) suggest that physiological mechanisms are well adapted to satisfy but not greatly exceed the functional requirements of the whole organism (Lindstedt and Jones 1987). Accordingly, lake trout have limited physiological capacity to compensate for hypoxia, and because of the tight coupling between oxygen uptake, power capacity, swimming activity, and feeding, both acquisition and consumption of energy are directly affected.

The present laboratory estimates of costs (Table 3), with the exception of excitement, must be minimal estimates of the normoxic energy expenditures of wild fish because of the additional costs of searching for and capturing living prey, competition for resources, and avoiding and escaping predators in the natural environment (e.g., Pazzia et al. 2002; Rennie et al. 2005). Nevertheless, routine feeding by lake trout at 53% of available scope means that the routine metabolic rate would be 1.88 times standard (Table 3). This compares with mean activity multipliers of  $1.51 \pm 0.54$  (SD) times resting metabolic rate for immature lake trout from Great Slave Lake and 2.27 for Lake Michigan based on analysis of mass balances of growth and <sup>137</sup>Cs (Rowan and Rasmussen 1996). These independent estimates of mean activity expenditures are similar and consistent with the idea that the probability of mortality is minimized when an organism operates well within its maximal metabolic range with a mean power output near 1/2 scope (Priede 1977, 1985).

#### A quantitative model for protection of lake trout summer habitat

Viable habitats for lake trout must provide adequate oxygen to meet the energy demands of standard and active metabolism. Based on telemetry studies, Priede (1985) concluded that for most of the time, brown trout operated conservatively at about 1/2 power capacity and that maximum power capacity occurred only about 1% of the time. Half scope of lake trout can be attained at oxygen partial pressures of 74.5–88.7 mmHg or 5.1–5.9  $\text{mg}\cdot\text{L}^{-1}$  at 4–18 °C. Half scope would not be an effective threshold for protection of brown trout or lake trout, however, considering that daily activity levels would routinely vary between 1/4 and 3/4 scope and occasionally approach 100%. Maximal feeding of lake trout and brown trout requires about 84%–87% of full scope. The upper range of normal power output correspond-

**Fig. 9.** Net power capacity response surface showing the spatial distribution of juvenile and adult lake trout segregated by temperature and dissolved oxygen and the physiological and population consequences of exposure to hypoxia by life stage. Juvenile and adult ovals are shown within their usual daytime summer thermal distributions, 4–8 and 8–20 °C, respectively.



ing to 3/4 scope-for-activity, which is attainable by lake trout at an ambient dissolved oxygen concentration of about  $7 \text{ mg}\cdot\text{L}^{-1}$ , would be a better criterion for protection of their summer habitat.

Effects of hypoxia on growth are especially relevant because of the high aerobic energy demands of capturing and processing prey (Brett and Groves 1979). The total metabolic costs will determine the amount of energy available for growth after accounting for the costs of activity, heat increment, and losses in feces and urine. The limiting effect of hypoxia on oxygen uptake will constrain activity that is required for searching for and capturing prey and escaping capture by predators. Processing of the prey that is captured will in turn impose a feedback limit on further activity. In the case of extreme hypoxia at 40 mmHg, there is zero capacity for capture of prey or avoidance of predators. Growth would cease at a somewhat higher oxygen concentration set by power requirements for activities needed to sustain basic maintenance. A conservative estimate of this threshold corresponds to 1/4 scope-for-activity or an ambient dissolved oxygen concentration of about  $4.4 \text{ mg}\cdot\text{L}^{-1}$ .

The response threshold for growth impairment in laboratory experiments at high feeding rates for six species of salmonid was  $7\text{--}8 \text{ mg}\cdot\text{L}^{-1}$  (British Columbia Ministry of Environment, Lands and Parks 1997) and growth impairment increased exponentially at oxygen concentrations below  $7 \text{ mg}\cdot\text{L}^{-1}$ , reaching 20%–30% at  $4 \text{ mg}\cdot\text{L}^{-1}$ . Complete impairment of growth at this level of hypoxia would be expected in the natural environment where searching and capturing prey would be energetically much more costly than in laboratory tanks.

A recent compilation of recruitment success in 81 lake trout lakes in south-central Ontario (D.O. Evans, unpublished data) revealed good to excellent recruitment in lakes with

late-summer (15 August – 15 September) mean hypolimnetic oxygen concentrations exceeding  $7 \text{ mg}\cdot\text{L}^{-1}$ . Lakes with average to poor recruitment had hypolimnetic oxygen concentrations of  $5\text{--}6 \text{ mg}\cdot\text{L}^{-1}$  and lakes with very poor recruitment were at  $4 \text{ mg}\cdot\text{L}^{-1}$  or lower. These results showed that prolonged exposure to ambient dissolved oxygen of  $<7 \text{ mg}\cdot\text{L}^{-1}$  during late summer had a negative effect on lake trout recruitment. This is consistent with the effects of hypoxia on power capacity and the published effects of hypoxia on growth of salmonids (Davis 1975; Jensen et al. 1993; Barton and Taylor 1996).

Most daily life support activities of lake trout appear to be accommodated within bounds set by 3/4 scope-for-activity. Ambient dissolved oxygen of  $7.13 \pm 0.27 \text{ mg}\cdot\text{L}^{-1}$  corresponding to oxygen partial pressures of 95–105 mmHg enabled juvenile lake trout to attain 3/4 power capacity at 4–12 °C, temperatures that conservatively span their summer habitat. Population responses of lake trout to combinations of temperature and oxygen partial pressures are illustrated in Fig. 9. No negative effects would be expected at dissolved oxygen concentrations above  $7 \text{ mg}\cdot\text{L}^{-1}$ . Growth and recruitment impairment would be expected at ambient dissolved oxygen concentrations between 7 and  $3 \text{ mg}\cdot\text{L}^{-1}$  and mortality and local extinctions would be expected at conditions below 40 mmHg or  $3 \text{ mg}\cdot\text{L}^{-1}$ .

Davis (1975) identified three levels of dissolved oxygen protection for freshwater and marine fishes in Canada corresponding to low, medium, and high risk thresholds. He recommended a low risk criterion of  $7.75 \text{ mg}\cdot\text{L}^{-1}$  for the protection of freshwater salmonids (rainbow trout, brown trout, brook trout, including steelhead) and a moderate risk level for this group of  $6.0 \text{ mg}\cdot\text{L}^{-1}$ . The moderate risk category was defined as “the oxygen value where the average member of a population would begin to exhibit symptoms of

oxygen distress". At the moderate risk level, he further noted that "some degree of risk to a portion of fish populations exists at this level if the oxygen minimum period is prolonged beyond a few hours". In the context of the no-net-loss concept (Department of Fisheries and Oceans 1986; Minns 1997), it is obvious that a short-term response threshold would not meet the requirements for long-term maintenance of productive capacity and that a moderate risk criterion that accepts some distress to a portion of a fish population is not acceptable. Davis (1975) set the low risk levels at 1 SD above the mean dissolved oxygen response threshold. The responses that he considered for postlarval life stages included the effect of hypoxia on respiratory dependence of metabolic processes and swimming ability, respiratory functions (breathing amplitude, buccal pressures, oxygen saturation of the blood), circulatory functions (heart rate, stroke volume), growth rate, and avoidance. I have shown that a decline of only  $1 \text{ mg}\cdot\text{L}^{-1}$  from 7 to  $6 \text{ mg}\cdot\text{L}^{-1}$  can have significant negative effects on power capacity, growth, and recruitment success of lake trout and that a minimum of  $7.0 \text{ mg}\cdot\text{L}^{-1}$  is required for the protection of lake trout summer habitat. Davis' (1975) level B protection at  $6.0 \text{ mg}\cdot\text{L}^{-1}$  for freshwater salmonids is definitely not adequate for protection of lake trout summer habitat, while his level A protection at  $7.75 \text{ mg}\cdot\text{L}^{-1}$  appears to be more conservative than required for this purpose.

### Resource management implications

Long-term sustainability of lake trout populations requires regulatory measures to ensure healthy aquatic ecosystems for this species. In small inland lakes, dissolved oxygen is critically important from a regulatory perspective because of the influence of land-use activities on phosphorus loading and lake trophic state (Evans et al. 1996; Hutchinson 2002; Steedman et al. 2004). Municipal sewage, cottage septic systems, and surface runoff from developed landscapes are potential sources of phosphorus. The linkage between phosphorus and lake trout habitat is mediated by the annual cycle of algae production and decomposition (Schindler et al. 1971; Dillon and Rigler 1974), the latter process placing a significant demand on the fixed supply of dissolved oxygen in the hypolimnion (Molot et al. 1992; Clark et al. 2004; Lienesch et al. 2005). Quantitative models are now available to predict the consequences of shoreline development and associated phosphorus loading for algal production and hypolimnetic oxygen depletion in Precambrian Shield lakes (Hutchinson et al. 1991; Dillon et al. 1994; Paterson et al. 2006).

Given that juvenile lake trout inhabit the hypolimnion during the summer months (Davis 1997; Davis et al. 1997), the recommended  $7 \text{ mg}\cdot\text{L}^{-1}$  criterion should be applied to the hypolimnetic volume. Evans et al. (1996) characterized the mean volume-weighted hypolimnetic dissolved oxygen concentration (MVWHDO) to provide a measure specific to the summer habitat utilized by coldwater species. Correction of MVWHDO to a fixed date, 15 September, using estimated or observed oxygen depletion rates provides consistent estimates for interannual and interlake comparisons. Lake trout lakes having late-summer MVWHDO at or below the  $7.0 \text{ mg}\cdot\text{L}^{-1}$  criterion would have no further capacity for anthropogenic phosphorus loading without negatively affect-

ing lake trout habitat. Lake trout populations in lakes below the threshold would also be more susceptible to other stressors (Evans and Wilcox 1991) and should be identified as requiring a high level of stock protection. The data requirements for application of this criterion are described in Quinlan et al. (2005) and standard calculations in Evans et al. (1996) and Clark et al. (2002).

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