Thermal histories, stress, and metabolic rates of chinook salmon (*Oncorhynchus tshawytscha*) in Lake Ontario: evidence from intra-otolith stable isotope analyses

C.M. Wurster, W.P. Patterson, D.J. Stewart, J.N. Bowlby, and T.J. Stewart

Abstract: We describe thermal histories for Lake Ontario chinook salmon (*Oncorhynchus tshawytscha*) as determined from otolith $\delta^{18}O$ thermometry using computer-controlled micromilling techniques to recover otolith aragonite at subseasonal resolution. We find that during the summer months chinook salmon inhabited epilimnetic waters with temperatures of ~19–20 °C as far back as the late 1980s. Chinook would approach but rarely exceed their reported upper incipient lethal limit of approximately 22 °C, which suggests that these fish were seeking water with temperatures as high as was tolerable while otolith growth occurred. These results contrast with expected midsummer temperatures for this cold-water salmonine. Bioenergetic simulations indicate significant stress imposed upon chinook salmon. We estimate consumption to be up to 20% more and gross conversion efficiency 18% less annually relative to nominal simulations where chinook salmon are modeled nearer their preferred temperature, reinforcing previous inferences that the chinook salmon population may be near the limits of sustainability. We also find a strong negative correlation between $\delta^{18}O$ and $\delta^{13}C$ values. Therefore, seasonal and ontogenetic variation in $\delta^{13}C$ values of chinook salmon otoliths appear to be related to metabolic rate during pelagic residence and may provide an indirect method for evaluating field activity and other aspects of fish life history.

Résumé : Nous décrivons l'histoire thermique des saumons quinnat (*Oncorhynchus tshawytscha*) du lac Ontario d'après la thermométrie $\delta^{18}O$ des otolithes à l'aide de techniques de moulinage sous contrôle d'ordinateur pour récupérer l'aragonite des otolithes à une échelle de résolution inférieure à une saison. Durant les mois d'été, les saumons quinnat habitent les eaux épilimnétiques de température ~19–20 ºC depuis la fin des années 1980. Les saumons quinnat s'approchent du seuil de leur limite thermique létale supérieure connue qui est d'environ 22 ºC, mais la dépassent rarement, ce qui laisse croire que les poissons recherchent des eaux de la plus haute température tolérable durant la période de croissance des otolithes. Ces résultats tranchent avec les températures attendues en mi-été pour ce salmoniné d'eau froide. Des simulations bioénergétiques indiquent qu'il se produit un important stress chez le saumon. Nous estimons que la consommation est de 20 % supérieure et que l'efficacité brute de conversion est de 18 % inférieure à l'échelle annuelle par rapport à des simulations nominales dans lesquelles les saumons quinnat sont traités plus près de leur température préférée; cela renforce les déductions antérieures voulant que la population de saumons quinnat soit près de ses limites de maintien. Il y a aussi une forte corrélation négative entre les valeurs de $\delta^{18}O$ et de $\delta^{13}C$. Ainsi, les variations saisonnières et ontogéniques des valeurs de $\delta^{13}C$ des otolithes des saumons quinnat semblent être reliées au taux de métabolisme durant leur temps de résidence pélagique et cela peut fournir une méthode indirecte d'évaluer l'activité en nature et d'autres aspects du cycle biologique des poissons.

[Traduit par la Rédaction]

Introduction

There is considerable concern that Lake Ontario's salmonine sport fishery is reaching the limits of sustainability (e.g., Rand et al. 1994; Rand and Stewart 1998*a*; Mills et al. 2003). Chinook salmon (*Oncorhynchus tshawytscha*; hereinafter referred to as chinook) were estimated to generate five times as much lake-wide production than either coho salmon (*Oncorhynchus kisutch*) or lake trout (*Salvelinus namaycush*) in Lake Ontario (Rand and Stewart 1998*b*) and, therefore,

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chinook were the top predators, with the highest forage demand of all stocked salmonines (Jones et al. 1993). Because the diet of chinook in Lake Ontario during their pelagic residence is composed almost entirely of alewife (*Alosa pseudoharengus*) (Brandt 1986; Rand and Stewart 1998*b*; Lantry 2001), chinook energetics are key to understanding ecological stress in this system. Originally introduced in the 1970s to control a burgeoning population of non-native alewife, chinook have subsequently been found, in a number of studies, to rely predominantly on alewife, despite the latter's decreasing abundance and quality (e.g., Mason et al. 1995; Rand and Stewart 1998*b*; Lantry 2001). The presence of chinook subsequently allowed the development of an important recreational fishery that generates considerable economic activity for many coastal districts (Talhelm 1988; Mills et al. 2003). This substantial economic resource stimulated the growth of salmonine hatcheries around the lake (Hartig et al. 1991). However, prey fish production may be inhibited by significant reductions in total phosphorus concentrations and nutrient loading in Lake Ontario (Johengen et al. 1994), and subsequent zebra and quagga mussel invasions (e.g., Mills et al. 2003). In addition to the increase in predatory pressure (e.g., O'Gorman and Stewart 1999), these conditions in Lake Ontario may have contributed to the observed rapid reduction in prey availability and quality (e.g., Mills et al. 2003), and the concern that chinook cannot maintain current growth and survival rates (e.g., Rand and Stewart 1998*a*).

Bioenergetic simulations suggest that consumption by chinook is near the maximum rate for the current environment in Lake Ontario (e.g., Rand and Stewart 1998*b*), although consumption may be limited more by thermal stress than by production itself. Rand et al. (1994) originally predicted that chinook would have to triple their ingestion of prey fish to make up for decreases in prey size and condition, an inference that was subsequently supported (e.g., Rand and Stewart 1998*a*; Lantry 2001). Chinook in Lake Michigan, undergoing similar stress due to reduction in prey abundance and quality, have already been observed to undergo a reduction in growth and survival, coupled with an increase in disease (Stewart and Ibarra 1991; Rand and Stewart 1998*a*). Bioenergetic simulations were conducted with the assumption that chinook occupy water at 11 °C during midsummer. However, the highest alewife biomass density in Lake Ontario is in the epilimnion at temperatures of 21 °C (Mason et al. 1995), and there is some evidence that chinook may move to warmer water to obtain increasingly scarce food resources (e.g., Olson et al. 1988; Goyke and Brandt 1993). Higher temperatures require higher food intake to compensate for the increased energetic cost of respiration. We can now reconstruct individual thermal-history records preserved in sagittal otoliths of chinook to test the hypothesis that chinook in Lake Ontario are now found in warmer water than in the past.

Otoliths are aragonitic biominerals produced in the inner ear of teleost fish and used in hearing and balance (Campana 1999). This structure grows sequentially, without resorption, and often displays yearly and daily banding patterns that provide age and growth information for most fish species (e.g., Panella 1980). Therefore, high-resolution $\delta^{18}O$ and $\delta^{13}C$ subseasonal records can be acquired from these biominerals. Because $\delta^{18}O$ values of otoliths have been determined to form at or near equilibrium with the ambient water (e.g., Patterson et al. 1993; Thorrold et al. 1997; Høie et al. 2004*a*), the temperature experienced by the fish can be tracked throughout its life if the $\delta^{18}O$ value of the ambient water is known, and variations in this value are unlikely (in a large lake with relatively constant $\delta^{18}O$ values, for example). Conversely, widely disparate $\delta^{18}O_{(H_2O)}$ values can be used to track migration patterns (tributary-to-lake migrations, for example).

The $\delta^{13}C$ values of otoliths were originally thought to reflect the $\delta^{13}C$ values of dissolved inorganic carbon (DIC) only (Degens et al. 1969). However, otolith $\delta^{13}C$ values are considerably lower than those predicted assuming equilibrium with ambient water, suggesting that there is a metabolic contribution of respiratory carbon to the otolith (e.g., Kalish 1991). Recent studies clearly indicate a relationship between metabolic rate and incorporation of otolith carbon (Tohse and Mugiya 2002; Høie et al. 2003), and intra-otolith $\delta^{13}C$ values have been shown to record ontogenetic variations in metabolic rate (Schwarcz et al. 1998; Wurster and Patterson 2003; Høie et al. 2004*b*). Although more work is necessary to evaluate intra-otolith $\delta^{13}C$ values, given the confounding influences of environment, diet, and tissue turnover, $\delta^{13}C$ values may become a powerful proxy for fish physiology and (or) environment once relative controls are quantified. So $\delta^{13}C$ values may provide a unique proxy for individual energetic behavior, such as the cost of activity (Sherwood and Rose 2003; Wurster and Patterson 2003), especially in fishes whose diet is relatively stable and whose reproduction is reserved for the end of life, such as adult chinook. Therefore, intra-otolith $\delta^{18}O$ and $\delta^{13}C$ values may provide both an indirect record of the most fundamental variable, temperature (He and Stewart 1998), and, arguably the most difficult parameter to estimate, respiration of activity in free-ranging fishes (e.g., Rowan and Rasmussen 1996; Trudel et al. 2004).

The primary goal of this study is to track temperatures that chinook experience during their pelagic residence in Lake Ontario. Temperatures are estimated from an otolith-specific aragonite temperature–fractionation relationship for freshwater fish (Patterson et al. 1993), using intra-otolith $\delta^{18}O$ values and measured $\delta^{18}O$ values of Lake Ontario water. Intra-otolith $\delta^{18}O$ and $\delta^{13}C$ values are analyzed for a suite of otoliths collected in 1991 (archived group) and in 1997 (Salmon River group) to compare potential changes in temperature of waters occupied as prey fish abundance and quality declined after 1991. We coupled this new information with a chinook bioenergetic model (Stewart and Ibarra 1991) to evaluate the level of stress within the Lake Ontario pelagic food web using specific growth rate and gross conversion efficiency (GCE; gross production/prey consumption) as a measure of that stress. We examined rates of exploitation of prey fish and compared the results with earlier simulations that modeled chinook at preferred temperatures in midsummer (Rand et al. 1994; Rand and Stewart 1998*b*). A secondary goal of this study is to evaluate intra-otolith $\delta^{13}C$ values as a potential indicator of metabolic rate.

Methods

Field collection, micromilling, and analysis of $\delta^{18}O$ and $\delta^{13}C$ values

Archived otoliths were obtained from angler-caught chinook from Ontario waters of Lake Ontario in 1991 (Stewart

et al. 2003). Chinook were also taken during their spawning run into the Salmon River, New York, on 7 October 1997. Sex and total length were noted, and both otoliths were removed and stored in an envelope. Six archived otoliths collected in 1991 and a subset of nine otoliths collected in 1997 were chosen for application of micromilling techniques. Chinook otolith lengths were generally 9–10 mm for a sagittal section. The monthly trend in body condition was determined as the mean weight of a 600 mm long chinook after adjusting for differences in length and year using analysis of covariance. Fork length and wet weight of chinook were measured in angler surveys during 1988–1992 (Stewart et al. 2003). Fork lengths ranged from 300 to 780 mm. Body condition was not significantly different between ages 1 and 2, so these fish were combined for this analysis.

The detailed methodology for micromilling is described by Wurster et al. (1999). Specimens were polished to reveal growth annuli, attached to a stage beneath a fixed dental drill, and viewed on a computer monitor via a color digital video camera. Annuli were subsequently digitized in real time as a series of three-dimensional coordinates, while intermediate coordinates were interpolated using a cubic spline algorithm. An array of intermediate sampling paths was calculated between digitized curves. Sample path arrays guided three high-precision actuators, which positioned the sample stage relative to the fixed dental drill. Approximately 30 to 50 μg aliquots of sample carbonate were recovered for routine analysis.

Once extracted, samples were roasted in vacuo for 1 h at 200 °C to remove volatiles that may have interfered with $\delta^{18}O$ and $\delta^{13}C$ measurement. Samples were reacted in a Kiel III automated carbonate preparation device directly coupled to a Finnigan MAT 252 or a MAT 253 stable isotope ratio mass spectrometer. Carbon dioxide was generated by the reaction of carbonate with 3–4 drops of anhydrous phosphoric acid in individual reaction vessels at 70 °C. Individual samples were analyzed using a micro-inlet, which reduces sample "memory" and permits analysis of ~20 μg of carbonate. Carbonate samples were analyzed with a precision of ±0.08‰ (1σ), determined by analysis of international carbonate standards NBS-18 and NBS-19, and reported relative to Vienna Pee Dee Belemnite (VPDB).

Water samples were collected from the surface of the Salmon River and Lake Ontario in Nalgene™ containers, which were sealed until analyzed for $\delta^{18}O_{(H_2O)}$. Most samples were measured using a Finnigan HDO-II water-equilibration device directly coupled to a Finnigan MAT 252 gas ratio mass spectrometer. For measuring $\delta^{18}O_{(H_2O)}$, standard carbon dioxide gas was equilibrated with water samples for 6 h at 25 °C and then analyzed sequentially. Values are reported to ±0.1‰ for $\delta^{18}O_{(H_2O)}$ relative to Vienna Standard Mean Ocean Water (VSMOW). Replicate analyses of water samples were better than ±0.1‰. A few additional Lake Ontario $\delta^{18}O_{(H_2O)}$ values were analyzed on a Finnigan high temperature conversion/elemental analyzer via high-temperature pyrolysis. Samples analyzed for $\delta^{18}O_{(H_2O)}$ via both high-temperature pyrolysis and water-equilibrator methods agreed within ±0.1‰. Carbonate and water stable isotope analyses were performed at the isotope laboratories of Syracuse University, Syracuse, New York, and the University of Saskatchewan, Saskatoon.

Estimation of chinook temperatures

Temperature can be calculated from otolith aragonite with a precision and accuracy better than 1 °C (Thorrold et al. 1997; Høie et al. 2004*b*). Several otolith-specific aragonite temperature–fractionation relationships have been determined from well-constrained environments (e.g., Patterson et al. 1993; Thorrold et al. 1997; Høie et al. 2004*a*). These relationships have slopes that are statistically indistinguishable from each other and from Kim and O'Neil's (1997) theoretical temperature–fractionation relationship for inorganic aragonite, although the intercepts may differ significantly (Campana 1999; Thorrold and Hare 2002). Because of the similar slopes, we calculated chinook temperatures from the aragonite temperature–fractionation relationship of Patterson et al. (1993) (which included freshwater salmonid otoliths) using the measured otolith $\delta^{18}O$ value and the Lake Ontario $\delta^{18}O$ value. We used –6.8‰ VSMOW as the $\delta^{18}O$ value of Lake Ontario water (e.g., Hodell et al. 1998; Coplen and Kendall 2000; this study).

Because of differing growth rates and size of otoliths, not all the specimens were microsampled at the same resolution. To compare seasonal values, we assume limited otolith growth for winter months. We matched each calculated minimum temperature to the average Lake Ontario water temperature to estimate both the spring and the fall Julian day that the minimum temperature represents. We then assumed equal growth through the growing season to determine the day of the year each temperature estimate represents. Therefore, we are not accounting for seasonal growth changes within and among otoliths; nonetheless, this is a relatively unbiased way to transform data and compare individual years. Estimates of Lake Ontario water temperature are derived from Hodell et al. (1998) and from the National Oceanic and Atmospheric Administration's Great Lakes Environmental Research Laboratory (http://coastwatch.glerl.noaa.gov).

Chinook energetics

We used the chinook bioenergetics model of Stewart and Ibarra (1991), implemented with the "Fish Bioenergetics 3.0" computer application (Hanson et al. 1997), to evaluate production, predation, and stress for chinook in Lake Ontario. Detailed inputs to the model differ from those used by Rand and Stewart (1998*b*) in temperature only, therefore we do not include a detailed description of the energetics model or the inputs. Energy density of predator and prey, and diet proportions (including invertebrates and prey fish), can be found in other publications (Elrod and O'Gorman 1991; Stewart and Ibarra 1991; Rand et al. 1993).

Most chinook in Lake Ontario spawn in their third or fourth year, and discounting age 0+ and the year of spawning, most chinook have spent 1 or 2 "full" summers as offshore residents (e.g., Rand and Stewart 1998*b*). We therefore modeled the dominant life forms of chinook for an average fish from 1989 to 1991 and an average fish from 1995 to 1997 to compare with a nominal simulation by Rand and Stewart (1998*b*). From the bioenergetic model outputs we estimated specific growth rate, GCE, and prey consumption of an average individual chinook in Lake Ontario as a measure of stress. This modeling exercise was repeated using assumed preferred temperatures (nominal simulation) to

Table 1. Covariation between intra-otolith $\delta^{18}O$ and $\delta^{13}C$ values of individual Lake Ontario chinook salmon (*Oncorhynchus tshawytscha*).

Specimen	Equation	R^2
Salmon River group		
CHK1	$\delta^{13}C = 1.3 \cdot \delta^{18}O + 1.5$	0.73
CHK4	$\delta^{13}C = 1.3 \cdot \delta^{18}O + 1.7$	0.73
CHK7	$\delta^{13}C = 1.3 \cdot \delta^{18}O + 1.5$	0.73
CHK13	$\delta^{13}C = 1.8 \cdot \delta^{18}O + 4.6$	0.78
CHK14	$\delta^{13}C = 1.3 \cdot \delta^{18}O + 2.6$	0.84
CHK15	$\delta^{13}C = 1.4 \cdot \delta^{18}O + 2.8$	0.90
CHK23	$\delta^{13}C = 1.5 \cdot \delta^{18}O + 2.7$	0.81
Pooled	$\delta^{13}C = 1.2 \cdot \delta^{18}O + 1.5$	0.71
Archived group		
SAM12	$\delta^{13}C = 1.7 \cdot \delta^{18}O + 3.3$	0.87
SAM54	$\delta^{13}C = 1.9 \cdot \delta^{18}O + 4.9$	0.85
SAM84	$\delta^{13}C = 2.2 \cdot \delta^{18}O + 4.6$	0.87
SAM92	$\delta^{13}C = 1.6 \cdot \delta^{18}O + 4.0$	0.84
SAM93	$\delta^{13}C = 1.6 \cdot \delta^{18}O + 2.5$	0.87
SAM108	$\delta^{13}C = 1.6 \cdot \delta^{18}O + 3.4$	0.70
Pooled	$\delta^{13}C = 1.4 \cdot \delta^{18}O + 1.8$	0.57
All data pooled	$\delta^{13}C = 1.3 \cdot \delta^{18}O + 1.1$	0.55

compare bioenergetic outputs with chinook temperatures found via the otolith thermometry technique.

Results

Intra-otolith $\delta^{18}O$ and $\delta^{13}C$ values

Specimens from the archived group, collected in 1991 from Lake Ontario, display cyclic patterns in $\delta^{18}O$ values that range from –7.4 ± 0.3‰ to –5.3 ± 0.6‰ VPDB (±SD). The $\delta^{13}C$ values covary with $\delta^{18}O$ values (Table 1; Fig. 1). Specimens collected in 1997 from the Salmon River (Salmon River group) also display cyclicity; however, both $\delta^{18}O$ and $\delta^{13}C$ values in the first and last years are much more negative than the other values (Fig. 2). We assume that each cycle represents 1 year of otolith growth, and pelagic residence is assumed to include all cycles except the first, which corresponds to age 0+, and the last half-year of growth in the Salmon River group, which corresponds to the spawning run. Intra-otolith $\delta^{18}O$ and $\delta^{13}C$ values of specimen CHK20 (CHK is a sample code for chinook from the Salmon River group) are unique relative to the other 14 otoliths sampled (Fig. 2*g*). This specimen's $\delta^{18}O$ values are generally more negative and show a much greater seasonal range. Because no distinct pelagic-residence years could be interpreted from CHK20, we did not consider this data set in analyses requiring Lake Ontario residence, but it should be noted as an example of alternative behavior; perhaps this fish spent a year in a river before smolting.

Minimum $\delta^{18}O$ values for all pelagic-residence years were remarkably consistent for both the archived group and the Salmon River group (–7.4 ± 0.3‰ and –7.5 ± 0.1‰ VPDB, respectively), and mean values did not differ significantly between groups (*t* test, $p < 0.05$). However, maximum $\delta^{18}O$ values for individual pelagic-residence years did vary somewhat more among specimens, yet they had the same mean value, –5.3 ± 0.6‰ and –5.3 ± 0.5‰ VPDB for the archived group and Salmon River group, respectively. Mean maximum $\delta^{18}O$ values for pelagic-residence years also did not differ significantly between the groups (*t* test, $p < 0.05$).

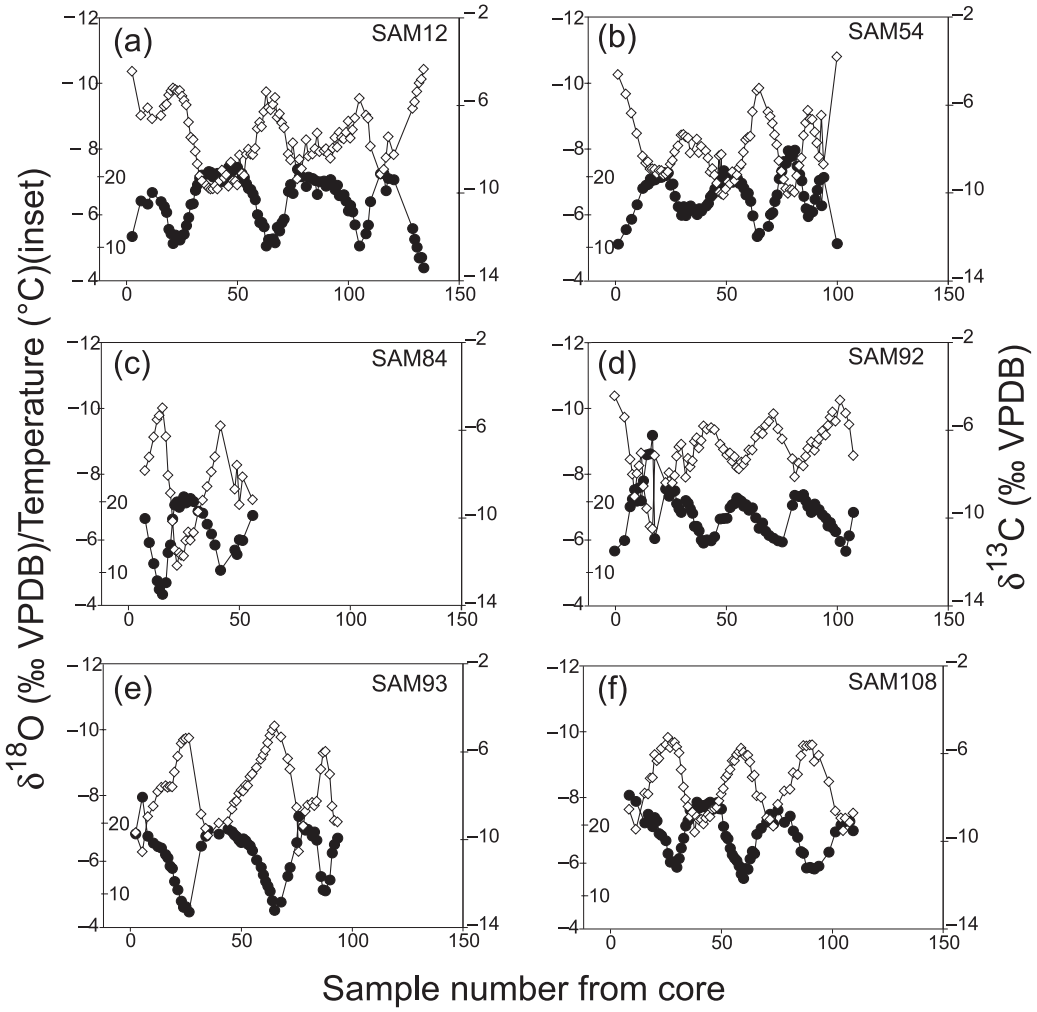
In contrast to the remarkable consistency in seasonal minimum $\delta^{18}O$ values among individual chinook otoliths, seasonal minimum $\delta^{13}C$ values are inconsistent despite strong covariations between $\delta^{13}C$ and $\delta^{18}O$ values (Table 1; Figs. 1 and 2). Both groups have notable covariation between $\delta^{18}O$ and $\delta^{13}C$ values, with CHK15 having the highest correlation coefficient ($R^2 = 0.90$; Table 1). Least squared linear regressions are significantly different and cannot be considered to have the same relationship between $\delta^{13}C$ and $\delta^{18}O$ values for any of the populations — archived, Salmon River, or grouped. However, linear regressions for specimens in the archived group, except specimen SAM84 (SAM is a sample code for chinook from the archived group), are not significantly different, based on analysis of covariance ($\alpha = 0.05$, $F_{[4,375]} = 2.26$).

Chinook thermal histories and energetics

We measured $\delta^{18}O_{(H_2O)}$ values of –6.9 ± 0.05‰ VSMOW for Lake Ontario in 1998 and 2000 ($n = 4$) that are consistent with Hodell et al.'s (1998) $\delta^{18}O_{(H_2O)}$ values of –6.7 ± 0.13‰ VSMOW from Rochester basin surface waters and a depth transect during the years 1993–1995 ($n = 37$). Those authors concluded that Lake Ontario showed relatively little variation with depth, time, or space. Additionally, these values agree well with that of the Niagara River (–6.8‰ VSMOW; Gat et al. 1994; Coplen and Kendall 2000), which is considered characteristic of the eastern portion of the Great Lakes system (Gat et al. 1994). We used a value of –6.8‰ VSMOW to calculate chinook temperatures and consider this value stable through space, depth, and time for Lake Ontario's water.

Midsummer temperatures calculated using this $\delta^{18}O_{(H_2O)}$ value (–6.8‰ VSMOW) and Patterson et al.'s (1993) temperature–fractionation relationship are consistently near 20 °C (Fig. 3), and exceed 22 °C in two specimens (Figs. 1*b* and 1*f*). The lowest maximum temperature calculated was 18 °C from SAM93 in the archived group (Fig. 3*a*). Most specimens appear to reach and stay within a narrow temperature range in midsummer for 2 or 3 weeks (Fig. 3). Several pelagic-residence years show evidence of a two-step temperature change, where the chinook remain at one temperature for a period of time and then move into water that is 1–2 °C warmer or colder for the remainder of the midsummer period (for examples, see Figs. 1*a* and 2*g*). We do not know the extent to which deviation from this dominant pattern is merely a result of differences in seasonal growth in the otolith or in fish movement in Lake Ontario. We then averaged temperatures for the Salmon River group and archived group separately (Fig. 3). To weight each specimen equally we interpolated daily temperatures for each specimen using a cubic spline. Averages for both groups show a similar pattern, reaching relatively stable temperatures at about 19 °C in midsummer. Despite the similarity, mean temperatures of each group from day 210 to day 250 (midsummer) are significantly different (*t* test, $p < 0.05$), with the mean temperature of the Salmon River group +0.4 °C higher than that of the archived group. Additionally, we find that linear regres-

Fig. 1. Intra-otolith $\delta^{18}O$ values and calculated temperatures (●) and $\delta^{13}C$ values (◇) relative to Vienna Pee Dee Belemnite (VPDB) for the archived group of chinook salmon (*Oncorhynchus tshawytscha*) in Lake Ontario. Archived specimens were collected in 1991 from offshore waters of Lake Ontario. Each subplot represents one otolith from an individual fish. The $\delta^{18}O$ and $\delta^{13}C$ values are plotted according to the number of the sample from the core of the otolith; note that $\delta^{18}O$ values are plotted with more negative values toward the top. The temperature scale (inset on *y* axis) is calculated using a Lake Ontario $\delta^{18}O$ value of –6.8‰ Vienna Standard Mean Ocean Water (VSMOW) and Patterson et al.'s (1993) temperature–fractionation relationship for otolith aragonite of freshwater fish.



sions between estimated pelagic temperatures and $\delta^{13}C$ values are homogeneous for otoliths within the archived group (except SAM84), the Salmon River group, and between these two groups, which suggests that given the same Lake Ontario environment, the relationship between $\delta^{13}C$ and $\delta^{18}O$ values is the same. SAM84 displays unusually negative $\delta^{13}C$ values during pelagic residence (Fig. 1*c*), resulting in a much greater slope (Table 1).

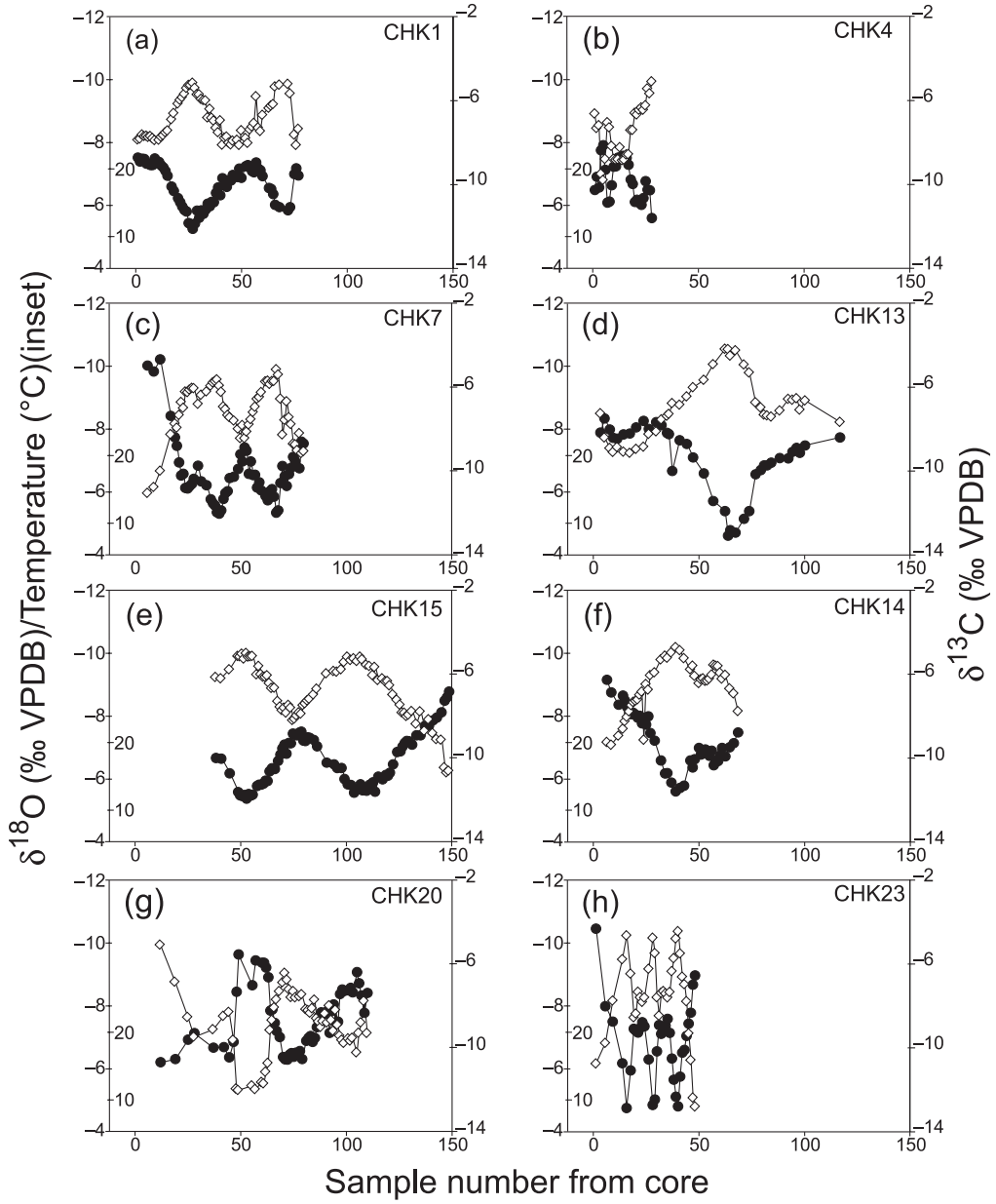
Otolith thermometry of the archived and Salmon River groups suggests that chinook are reaching and staying for some time in ~19 °C water. We therefore re-ran the bioenergetic simulation of Rand and Stewart (1998*b*) assuming that chinook inhabited the warmest available water, up to but not exceeding 11 °C (nominal simulation) or 19 °C (otolith thermometry simulation). Energetic comparisons between the nominal and otolith thermometry simulations indicate significant stress imposed upon Lake Ontario chinook in midsummer (Fig. 4). The specific growth rate declines to near zero in midsummer for the otolith thermometry simulation and is nearly six times lower than for the comparative nominal simulation in midsummer (Fig. 4). However, the specific growth rate is higher for the otolith thermometry simulation relative to the nominal simulation just prior to and just after the growth depression in midsummer. GCE imitates this pattern, declining in midsummer to less than 0.1 (Fig. 4). To maintain observed growth, in the otolith-based simulation chinook are consuming prey fish near the maximum rate, and annually consume 18% more prey by weight relative to the nominal simulation (Table 2). Since chinook must eat more to attain the same growth at higher temperatures, annual GCE is estimated to be 18.2% lower than in the nominal simulation (Table 2).

Discussion

Derivation of temperature histories of adult chinook

Before further interpreting chinook temperature histories, we must first qualify uncertainties associated with the use of

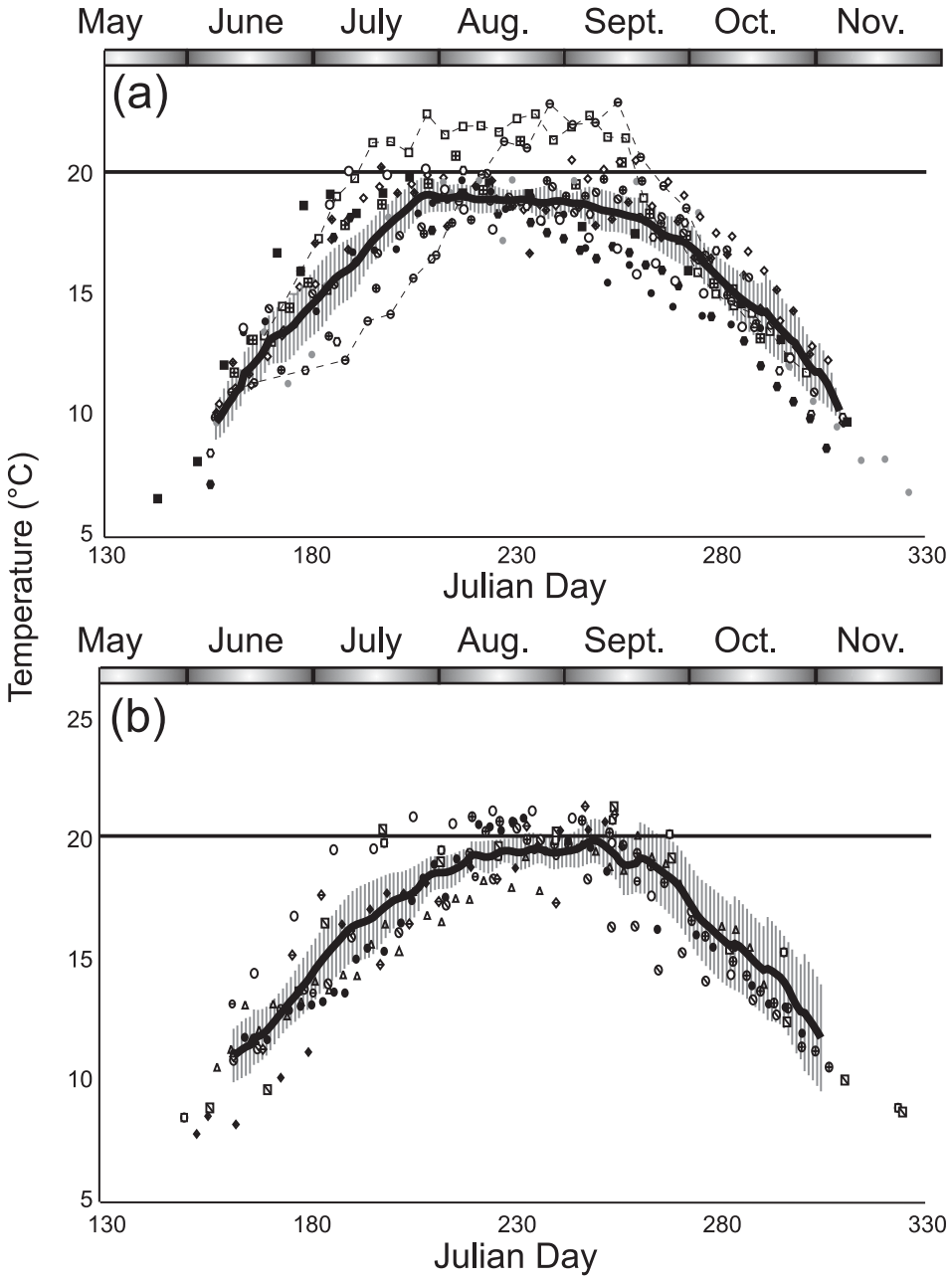
Fig. 2. Intra-otolith $\delta^{18}O$ values and calculated temperatures (●) and $\delta^{13}C$ values (◇) relative to VPDB for chinook from the Salmon River group collected on 7 October 1997 during the annual Salmon River, New York, spawning run. Each subplot represents one otolith from an individual fish. The $\delta^{18}O$ and $\delta^{13}C$ values are plotted by the number of the sample from the core of the otolith; note that $\delta^{18}O$ values are plotted with lower values toward the top. The temperature scale (inset on *y* axis) is calculated using a Lake Ontario $\delta^{18}O$ value of –6.8‰ VSMOW and Patterson et al.'s (1993) temperature–fractionation relationship for otolith aragonite of freshwater fish.



the otolith thermometry technique. This requires discussion of two key elements: (1) the temperature–fractionation relationship and (2) the appropriate $\delta^{18}O_{(H_2O)}$ value used in the selected temperature–fractionation relationship. We therefore begin our discussion by addressing these key issues.

Although it is well established that otoliths produce aragonite at least close to equilibrium with the ambient water (Campana 1999) with a temperature precision and accuracy better than 1 °C (Thorrold et al. 1997; Høie et al. 2004*b*), there may still be species-dependent temperature–fractionation relationships (Høie et al. 2004*a*). Therefore, we must choose the appropriate temperature–fractionation relationship if direct estimation of environmental temperatures is to be done accurately. We chose to calculate temperatures using Patterson et al.'s (1993) equation because it was specifically developed for freshwater fishes in natural systems and includes freshwater salmonids from the Great Lakes. We consider this equation representative of those calculated using the equations of Radtke et al. (1996), Høie et al. (2004*a*), and Kim and O'Neil (1997) because the temperatures calculated are all within 1 °C. Thorrold et al.'s (1997) equation, however, produces temperatures ~4 °C higher than the other

Fig. 3. Estimated seasonal temperatures during pelagic residence of chinook in (*a*) the archived group and (*b*) the Salmon River group in Lake Ontario calculated via otolith thermometry. Minimum calculated temperature was used to determine the Julian day for the first day of growth (spring) and the last day of growth (fall) for each yearly profile. Invariant growth rates were assumed within one growing season to reconstruct and compare chinook seasonal temperature variation. Average seasonal temperature profiles and confidence intervals were determined from cubic spline interpolations of each specimen's temperature profile to ensure equal representation of each year. Each symbol represents one pelagic-residence year.



equations. Thorrold et al.'s (1997) equation therefore predicts temperatures beyond lethal limits for chinook and is thus not appropriate.

The slope of the temperature–fractionation relationship is such that an error in $\delta^{18}O_{(H_2O)}$ value of ~0.25‰ results in a temperature error of 1 °C, and it is therefore critical to have accurate $\delta^{18}O$ values of Lake Ontario water. In addition to Hodell et al.'s (1998) values, which are in close agreement with our own measured values for Lake Ontario, we plot seasonal values for Sodus Bay and Lake Ontario (this study), the Niagara River and St. Lawrence River (Gat et al. 1994; Yang et al. 1996; Coplen and Kendall 2000) at Lake Ontario's outflow to address variability in Lake Ontario $\delta^{18}O_{(H_2O)}$ values (Fig. 5). Also plotted are seasonal $\delta^{18}O$ values for the Salmon River (this study) and Genesee River (Coplen and Kendall 2000) as an example of potential river inputs to the Lake Ontario system. River waters have lower and more seasonally variable $\delta^{18}O$ values than Lake Ontario and the Niagara River and St. Lawrence River systems. Although there is distinct seasonality to the larger Niagara and St. Lawrence river systems, this is modified to a high degree from the original precipitation input, as they are dominantly

Fig. 4. Energetic output for pelagic residence of age 3+ chinook comparing nominal (shaded line) and otolith thermometry (solid line) bioenergetic simulations. Model parameters were kept constant, and only temperature and associated p value (i.e., the proportion of maximum consumption estimated by iterative fit to growth) differed between the two simulations. The nominal simulation assumes that chinook stay at 11 °C in midsummer, whereas in otolith-based simulations, temperatures indicate chinook swimming at up to 19 °C during midsummer.

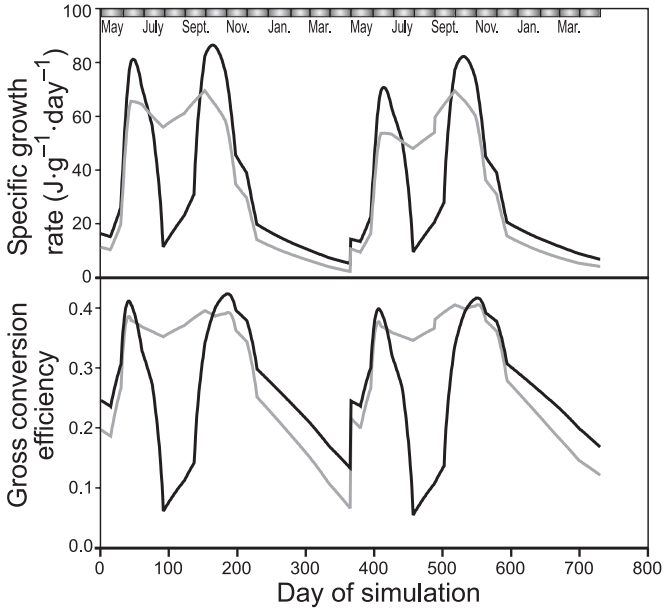


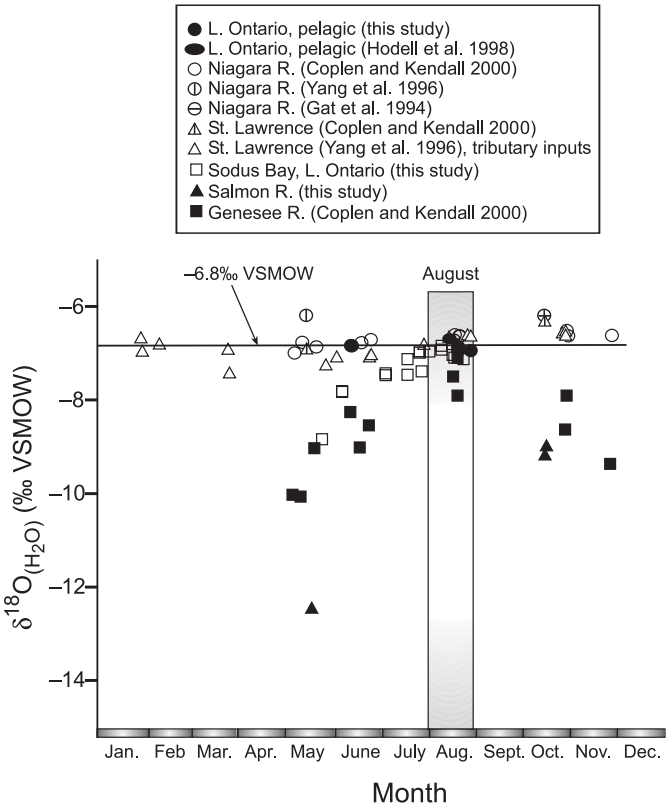
Table 2. Comparison of bioenergetic simulation (otolith thermometry and nominal) output of total consumption and gross conversion efficiency (GCE) of adult chinook during pelagic residence in Lake Ontario.

	Year 1	Year 2	Total	GCE
Consumption (g)				
Otolith, age 3+	5323	24 128	29 451	0.27
Nominal, age 3+	4742	19 400	24 142	0.33
Difference (%)	11	20	18	18
Consumption (g)				
Nominal, age 2+	7546	*	7 546	0.27
Otolith, age 2+	6656	*	6 656	0.33
Difference (%)	12	*	12	18

*No estimate.

outflow from stable sources (Lakes Erie and Ontario). These rivers show variations of –6.7 ± 0.14‰ and –6.9 ± 0.26‰ VSMOW, respectively. However, Lake Ontario proper shows no seasonal variation in isotope values. Ignoring the Genesee and Salmon rivers and focusing on Lake Ontario and the Niagara and St. Lawrence rivers, $\delta^{18}O$ values are more variable in the fall and early summer, but converge on –6.8 ± 0.19‰ VSMOW, the value used in our calculations, in July and August. We therefore consider this value appropriate to use in determining at least maximum temperatures in midsummer using our otolith thermometry technique; we estimate the precision to be approximately 1 °C. However, spring and early-summer $\delta^{18}O$ values may be more variable, possibly because of snowmelt, especially near river inputs (L.I. Wassenaar, National Hydrology Research Centre, Environment Canada, Saskatoon, SK S7N 3H5, Canada, personal communication). Additionally, we will overestimate temperatures for chinook that migrate toward a tributary. It is important to recognize that Lake Ontario's $\delta^{18}O_{(H_2O)}$ value does not vary spatially (including with depth) in August, and is not dependent on temperature changes in the lake.

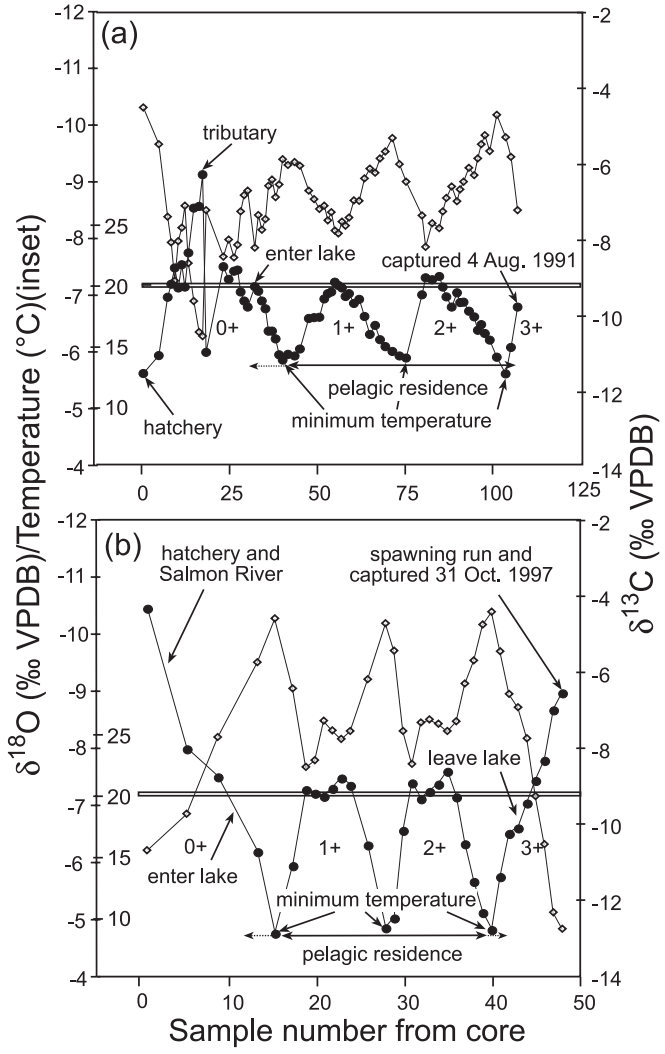
Fig. 5. Seasonal $\delta^{18}O_{(H_2O)}$ values relative to VSMOW for Lake Ontario, Niagara River, and St. Lawrence River (at Lake Ontario outflow) and smaller tributaries. The $\delta^{18}O_{(H_2O)}$ values represented are from various years. Data sources are represented on the plot.



Chinook pelagic residence: temperature histories and energetics

The interpretive character of chinook intra-otolith $\delta^{18}O$ and $\delta^{13}C$ values is illustrated using two exemplary figures, one specimen from each group, both micromilled from the core to the edge of the otolith (Fig. 6). SAM92 displays a cyclic (seasonal) pattern ranging from approximately –5.5‰ to about –7.3‰ VPDB after an initial decrease in $\delta^{18}O$ values to as low as –9‰ VPDB in the first year of growth (Fig. 6*a*). There are just over three seasonal patterns, which is consistent with an independent age count of 3+. Otolith growth is negligible during the winter, therefore maximum $\delta^{18}O$ values record a spring and (or) fall minimum temperature. This young of the year is interpreted as moving in or near a tributary (recorded as relatively low $\delta^{18}O$ values), permitting inference of juvenile migration to Lake Ontario (Fig. 6). For example, a temperature of 12 °C is calculated using a Salmon River tributary $\delta^{18}O_{(H_2O)}$ value of –10‰ VSMOW (Fig. 5). Age 1+, 2+, and 3+ represent pelagic residence in Lake Ontario. Converting $\delta^{18}O$ value to tempera-

Fig. 6. Example plots of intra-otolith $\delta^{18}O$ values and calculated temperatures (●) and $\delta^{13}C$ (◇) values relative to VPDB from two chinook otoliths, one from specimen SAM92 from the archived group (*a*) and the other from specimen CHK23 from the Salmon River group (*b*). The temperature scale (inset on *y* axis) is calculated using a Lake Ontario $\delta^{18}O$ value of –6.8‰ VSMOW and Patterson et al.'s (1993) temperature–fractionation relationship for otolith aragonite of freshwater fish. Pelagic residence indicates the time the chinook spent in Lake Ontario proper. We modeled 2 full years of growth, indicated by the solid line. Chinook may also be Lake Ontario residents during the fall of their first year and just prior to spawning, indicated by the dotted lines. Otolith growth decreases or ceases in winter, so winter temperatures are not recorded. Only a minimum temperature just prior to cessation of otolith growth can be determined; this is noted on the plot. Assuming that otoliths grew during days above the minimum seasonal temperature calculated, the average resolution is 4 days per sample for specimen SAM92 and 14 days per sample for CHK23. The double horizontal lines mark 20 °C temperature.



ture using the Lake Ontario $\delta^{18}O_{(H_2O)}$ value, we plot the thermal history of this fish from age 1+ to age 3+, when it was captured offshore on 18 August 1991 (Fig. 6*a*). Maximum seasonal temperatures are very near 20 °C, and remain stable just above 20 °C during year 2+, before decreasing. The temperature estimated nearest the time of capture was 18 °C, consistent with the season of capture. We estimate a resolution that averages less than 4 days per sample for this specimen, typical for specimens in this study.

CHK23 from the Salmon River group displays four seasonal cycles, indicating that this fish was also aged 3+ at the time of capture (Fig. 6*b*). Age 1+ and age 2+ display a similar pattern to the same age class for SAM92, and calculated midsummer temperatures appear to remain stable at 20 °C during this fish's pelagic residence. Lower $\delta^{18}O$ values in the first and last year of growth are representative of the lower $\delta^{18}O$ values of Salmon River water experienced in the hatchery and during the spawning migration, respectively (Fig. 5). We estimate a resolution of 14 days per sample, which is the lowest sample resolution in this study. Although intra-otolith $\delta^{18}O$ and $\delta^{13}C$ values agree with known life-history traits of chinook, this technique should be validated by using otoliths from fish fitted with archival tags that provide an independent measure of temperature.

Our otolith thermometry results indicate that adult chinook inhabit water with temperatures considerably higher than those they prefer (e.g., McCullough 1999). We estimate that chinook commonly occupied water at temperatures near 19 °C in midsummer. We also suggest that chinook are actively seeking water at this temperature through midsummer, as most pelagic-residence years for nearly all specimens with adequate resolution show evidence of a temperature plateau for at least 2 weeks. Because Lake Ontario stratifies in the summer and surface temperatures are often above 20 °C, chinook must occupy the epilimnion of Lake Ontario near to but not at the surface, even though the presumed optimal temperature for this species was always available near the thermocline. The highest mean alewife densities are found in the epilimnion (at temperatures above 17 °C), and the highest prey fish biomass is found near 20 °C (Mason et al. 1995). Therefore, it is likely that chinook must search epilimnetic water in Lake Ontario to find prey. It may be that as prey production has become limiting, chinook have had to search the warmer epilimnion more often for food, or it may be that chinook have always foraged here since they were first stocked. The absence of a strong alewife year class from 1992 to 1997, with year classes in 3 of these years amongst the smallest from 1977 to 1997, indicates that alewife numbers decreased after 1991 (e.g., Mills et al. 2003). However, we found no corresponding change in chinook thermal orientation over the same period of time.

We find very little difference between chinook maximum temperatures calculated for the archived group and Salmon River group, in contrast to our hypothesis that thermal orientation of the chinook would change with prey quality and quantity. Interestingly, Haynes and Keleher (1986) found one chinook in 19.7 °C water in the beginning of September as early as 1984. Although it was the only chinook (out of three) found at a temperature this high in the summer/fall, they were unable to closely track the other tagged fish during midsummer, owing to the methodology used (no fish were found in August). They assumed that this was due to chinook moving into deeper waters. However, they were only able to track fish near the shore, and the other chinook may have moved offshore. Our results appear to contradict other

reports of these fish being captured closer to the thermocline. Olson et al. (1988) found 82% of chinook above the thermocline and offshore, although they were vertically distributed widely and averaged 14.4 ± 2.9 °C at depths where they were captured using nets set overnight for 12–28 h. Using similar methods, Stewart and Robertson (1991) also found chinook at a similar median temperature, 13.2 °C, and did not capture chinook in 19 °C water. To calculate temperatures nearer to these observations, the Lake Ontario $\delta^{18}O_{(H_2O)}$ value must be 1.5‰ more negative than those we and others have measured.

A possible interpretation that would allow the results of these capture studies to be correlated with ours is that chinook migrate vertically to warmer water to catch prey, and then seek thermal refugia nearer the thermocline. To be consistent with this interpretation, otolith growth must be greatly reduced when chinook are not occupying warmer epilimnetic waters. Otolith growth has been highly correlated with metabolic rate (Wright 1991; Tohse and Mugiya 2002) and metabolic rate increases with temperature, indicating that there would be a bias toward higher temperature estimates. However, even with this bias, some carbonate accretion should occur while chinook inhabit water near the thermocline. Therefore, our temperature estimates suggest that chinook would experience near-lethal temperatures for limited periods if this vertical migration occurred.

Based on a literature review, McCullough (1999) concluded that 21–22 °C was the upper incipient lethal level for adult chinook. Although Bjorn and Reiser (1991) noted an upper incipient lethal level for adult chinook as high as 26.2 °C, they reported that environmental temperatures from 23 to 25 °C could be lethal and were actively avoided. Finally, Eaton et al. (1995) reported 23.7 °C as the upper habitat temperature limit for chinook. The remarkable consistency in minimum $\delta^{18}O$ values (maximum temperatures) for pelagic residence regardless of the group (where group members vary both with lake location and time), and the close agreement between maximum calculated temperatures and the chinook's upper incipient lethal limit, suggest that chinook in Lake Ontario are seeking alewife prey in water of temperatures as high as are tolerable. We found only 2 years out of a total of 22 where chinook were recorded at temperatures above 22 °C. Such exceedingly high temperature estimates may result if the fish entered waters with more negative $\delta^{18}O_{(H_2O)}$ values than those typical of the open lake, indicating that the true temperature experienced is less than that estimated. For example, the fish may have resided in a harbor or near a major tributary input to seek food. Forays into warm littoral habitats are likely to be uncommon because Lake Ontario has very little of such habitat outside the eastern basin and few small embayments (Mason et al. 1995). However, if chinook do migrate to littoral regions, they are still likely to encounter high water temperatures that are not optimal for growth.

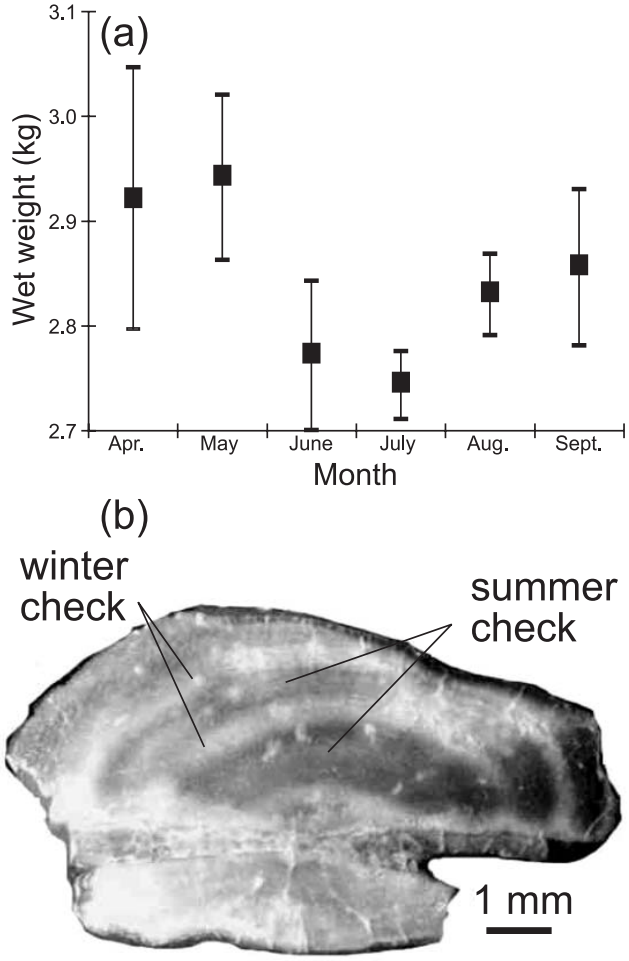
Maximum seasonal $\delta^{18}O$ values (minimum temperatures) are considerably more variable. Interestingly, temperatures are often nearer the preferred temperature of chinook (McCullough 1999). It is tempting to speculate that chinook are moving to high-temperature waters in search of food for as long as can be tolerated, then moving into water at preferred temperatures, where body and otolith growth are reduced, so these are the minimum temperatures recorded via otolith thermometry. However, calculated temperatures may be elevated artificially by more negative and more variable $\delta^{18}O_{(H_2O)}$ values measured in the fall and spring (L.I. Wassenaar, National Hydrology Research Centre, Environment Canada, Saskatoon, SK S7N 3H5, Canada, personal communication). Finally, we note that mean midsummer temperatures for the archived and Salmon River groups are significantly different, although mean temperatures differed by just 0.4 °C. Although this "increased temperature" may be a reflection of ecological adaptation or environmental warming, the observed temperature difference might also be a result of slightly different mean $\delta^{18}O$ values for Lake Ontario. In fact, Hodell et al. (1998) reported a mean Lake Ontario $\delta^{18}O_{(H_2O)}$ value of –6.7‰ VSMOW for 1993–1995, while we measured a mean $\delta^{18}O_{(H_2O)}$ value of –6.9‰ VSMOW for 1998 and 2001. Mean calculated temperatures would be within 0.2 °C using Hodell et al.'s (1998) value for the archived group and our measured $\delta^{18}O_{(H_2O)}$ value for the Salmon River group. Regardless, such small differences are unlikely to be ecologically significant for chinook.

Adult chinook thermal histories determined from intra-otolith $\delta^{18}O$ values indicate that Lake Ontario's chinook population could be under energetic stress during midsummer. Bioenergetic modeling simulations predict severe growth reductions to near zero in midsummer, and slightly negative growth is predicted for chinook inhabiting water at 20 °C (unpublished data). GCE is also reduced during midsummer, providing further evidence of stress. Corresponding to reduced GCE, total annual consumption by chinook is estimated to be up to 20% higher in the otolith thermometry simulation relative to the nominal simulation. This growth stress is corroborated by an observed decrease in condition factor in chinook captured by anglers (Fig. 7*a*). Additionally, summer stress marks are often observed in chinook scales and otoliths. Summer stress marks on chinook scales from Lake Ontario preclude accurate aging, and otolith or fish length is used instead (J.N. Bowlby and T.J. Stewart, Ontario Ministry of Natural Resources, Glenora Fisheries Station, Picton, unpublished data). Many otoliths from Lake Ontario chinook show summer growth checks, opaque regions in the otolith that are less distinct than opaque regions associated with winter growth checks (Fig. 7*b*).

There is recent evidence that modeled respiration, a key component of the bioenergetic model, is in error (Trudel et al. 2004). Specifically, the model we used (Stewart and Ibarra 1991) underestimates respiration at lower ranges and overestimates it at higher ranges with a total mean-squared error of 0.18 (Trudel et al. 2004). However, this bioenergetic model can still be used to compare estimates on a relative basis and to contrast the outcome of various scenarios if the biases are consistent (Trudel et al. 2004). We compare two model outputs, changing the temperature input only, thus fulfilling this requirement. In addition, growth and consumption obtained from model-output and field studies of Lake Ontario chinook agree (Rand and Stewart 1998*a*), and midsummer stress predicted by our bioenergetic analysis is corroborated by observed condition factor and by otolith and scale stress marks (Fig. 7).

Rand and Stewart (1998*b*) suggested that the limit to salmonine production in this ecosystem is being approached. GCE has been trending downward in Lake Ontario, owing to

Fig. 7. (*a*) Monthly trend in body condition determined as the mean weight of a 600 mm long chinook after adjusting for differences in length and year using analysis of covariance at 95% confidence intervals. Fork length and wet weight of chinook were measured during angler surveys in 1988–1992 (n = 2468). (*b*) Image of a chinook otolith (specimen SAM12; this study) showing summer and winter check marks. Summer check marks, induced by stress, are opaque regions in the otolith that are less distinct than opaque regions associated with winter growth checks. It should be noted that this section is used for micromilling and not aging.



a reduction in prey quality. Rand et al. (1994) and Rand and Stewart (1998*b*) concluded that the chinook population might not have been sustainable at 1990 stocking rates because of declines in alewife population and quality. These conclusions were based on a bioenergetic analysis using assumptions about the thermal orientation of chinook that we determined to be inaccurate. We find adult chinook to be consuming more and growing less in midsummer than was previously modeled.

Intra-otolith $\delta^{13}C$ value and metabolic rate

Biological carbonates appear to derive carbon from two major sources: DIC from environmental water and blood carbon derived from the diet (e.g., McConnaughey et al. 1997). These two major pools of carbon are therefore reflected in the $\delta^{13}C$ value of the otolith (e.g., Høie et al. 2003). Tohse and Mugiya (2002) demonstrated, via radiocarbon labeling, both an ambient-water and a dietary carbon contribution in fish otoliths, the ratio of which was linked to metabolic activity. Although DIC is often the dominant source of otolith carbon (e.g., McConnaughey et al. 1997), intra-otolith variation in the $\delta^{13}C$ value might reflect changes in contributions between the two sources; this changing ratio is predominantly a result of a changing metabolic rate in the individual fish (Wurster and Patterson 2003; Høie et al. 2004*b*). This observation should hold true especially for fish, such as chinook, that do not change their diet greatly during pelagic residence (e.g., Brandt 1986; Rand and Stewart 1998*a*; Lantry 2001).

Chinook otolith $\delta^{13}C$ values display seasonal variability, with higher values during spring/fall and lower values in midsummer. This pattern is highlighted by a relatively strong covariation with $\delta^{18}O$ values, and is consistent with the metabolic-contribution hypothesis. Higher temperatures (lower $\delta^{18}O$ values) lead to a higher metabolic rate and a greater contribution of respiratory carbon to the otolith (and therefore lower $\delta^{13}C$ values relative to DIC). In contrast to intra-otolith $\delta^{18}O$ values, $\delta^{13}C$ values of individual otoliths are quite variable. The highest $\delta^{13}C$ values are approximately –4‰ to –5‰ VPDB, whereas lower values are approximately –8‰ to –10‰, with one specimen as low as –12‰. We estimate a summer metabolic contribution to otolith carbon as high as 50%–60% assuming a dietary $\delta^{13}C$ value of –25‰ VPDB (Kiriluk et al. 1995) and a $\delta^{13}C_{(DIC)}$ value of 0‰ VPDB (Hodell et al. 1998; Leggett et al. 1999; Hélie et al. 2002). Despite the individual variability in intra-otolith $\delta^{13}C$ values, we find least-squares regressions between seasonal pelagic-residence temperatures and $\delta^{13}C$ values not significantly different among archived (α = 0.05, $F_{[5,297]}$ = 1.59; ignoring SAM84) and Salmon River (α = 0.05, $F_{[9,184]}$ = 2.14) specimens and groups (α = 0.05, $F_{[1,529]}$ = 2.72). This suggests that although individual chinook may vary in activity, they respond similarly to temperature changes given a similar environment.

The environmental $\delta^{13}C_{(DIC)}$ value appears to have the largest modifying influence on intra-otolith $\delta^{13}C$ values because it represents the largest proportion of otolith carbon. Tributary $\delta^{13}C_{(DIC)}$ values are much lower than Lake Ontario values (e.g., Leggett et al. 1999; Hélie et al. 2002) and this is recorded by otolith $\delta^{13}C$ values, even during the spawning run, when dietary $\delta^{13}C$ values are derived from reserves stored during pelagic residence. In many cases, variation in intra-otolith $\delta^{13}C$ and $\delta^{18}O$ values can be used to infer when chinook migrate between Lake Ontario and tributaries (Fig. 6), although this should be corroborated using growth models. Therefore, seasonal changes in Lake Ontario $\delta^{13}C_{(DIC)}$ values and variation in habitat depth (e.g., Legget et al. 1999) may influence $\delta^{13}C$ values of chinook otoliths.

The diet of chinook in Lake Ontario varies little during pelagic residence (Brandt 1986; Rand and Stewart 1998*b*; Lantry 2001), and during the summer, $\delta^{13}C_{(DIC)}$ values in the epilimnion increase because of preferential incorporation of ^{12}C by phytoplankton, whereas values in the hypolimnion remain invariant (e.g., Leggett et al. 1999). However, $\delta^{13}C_{(otolith)}$ values decrease during the summer, suggesting an increasing influence of dietary carbon, with lower $\delta^{13}C$ values, over more positive $\delta^{13}C_{(DIC)}$ values. We therefore conclude that

Table 3. Estimates of metabolic contribution to otolith carbon made using a simple mass balance model.

	$\delta^{13}C$ (‰)		$\delta^{13}C_{(DIC)}$ (‰)		*M*	
	Otolith	Diet	Epilimnion	Hypolimnion	Epilimnion	Hypolimnion
Salmon River group						
Summer	–7.9	–25.2	–0.6	–2.5	0.41	0.36
Fall/spring	–5.3	–25.2	*	–2.5	*	0.24
Archived group						
Summer	–8.7	–25.2	–0.6	–2.5	0.44	0.39
Fall/spring	–6	–25.2	*	–2.5	*	0.27

Note: Metabolic contribution to otolith carbon is calculated using a model described by Wurster and Patterson (2003): $\delta^{13}C_{(otolith)} = M\cdot\delta^{13}C_{(diet)} + (1 - M)\cdot\delta^{13}C_{(DIC)} + 2.7$, where *M* is the proportional metabolic contribution. The $\delta^{13}C$ value of the dissolved inorganic carbon (DIC) is estimated for the epilimnion and hypolimnion and fall/spring (same as the hypolimnion) from Leggett et al. (1999). The $\delta^{13}C$ values for alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) reported in Kiriluk et al. (1995) were used in conjunction with dietary estimates to determine average $\delta^{13}C$ values for the chinook (*Oncorhynchus tshawytscha*) diet (*, no estimate).

intra-otolith $\delta^{13}C$ values are primarily influenced by a changing metabolic rate, as further evidenced by a strong and similar covariation with estimated temperature and corroborated by a covariation with the modeled specific respiration rate. A direct temperature effect of biogenic carbonates on $\delta^{13}C$ values is equivocal (e.g., Thorrold et al. 1997; Schwarcz et al. 1998) and, if it exists, is small (approximately –1.3‰ VPDB for a temperature increase of 10 °C (Grossman and Ku 1986).

We estimated various metabolic contributions assuming different depth habitats or varying $\delta^{13}C_{(DIC)}$ values (Table 3). It is important to note that $\delta^{13}C$ values vary greatly among individuals; on average, however, summer $\delta^{13}C$ values for the archived group are almost 0.8‰ more negative than those for the Salmon River group. This corresponds to an additional 3% metabolic contribution to the otolith carbon of the archived group. An alternative explanation is that chinook inhabited the hypolimnion more often in the late 1980s and early 1990s than in the mid-1990s (Table 3). This, however, contrasts with our contention that chinook are feeding in the epilimnion, inferred from $\delta^{18}O$ values.

This study clearly demonstrates the need for detailed laboratory studies to determine the relationship between metabolic rate, diet, and intra-otolith $\delta^{13}C$ values. However, we hope that we have demonstrated that $\delta^{13}C$ can be used to determine metabolic rate "in the field", and perhaps can be used as an additional proxy with which to infer vertical distributions of fish within a water column. Alternatively, if metabolic rate can be accurately modeled and the environmental $\delta^{13}C_{(DIC)}$ value is known, it may be possible to estimate diet changes in longer lived fish.

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