Isotopic composition of otoliths as a chemical tracer in population identification of sockeye salmon (*Oncorhynchus nerka*)

Y.W. Gao and R.J. Beamish

Abstract: The feasibility of stable oxygen and carbon isotope ratio ($\delta^{18}O$ and $\delta^{13}C$) analyses in sagittal otoliths of sockeye salmon (*Oncorhynchus nerka*) was tested by analyzing the seasonal and annual otolith zones of 44 samples collected from different localities in the northeast Pacific coast. The $\delta^{18}O$ and $\delta^{13}C$ values of these otoliths ranged from −14.23 to +1.62‰ and from −15.18 to −3.17‰, respectively. The $\delta^{18}O$ variations can be divided into two stages from freshwater (−14.2 to −2.5‰) to marine (−2.5 to +1.6‰) that were consistent with the life history of sockeye salmon from juvenile to adult stages. The transition occurred after age 1, during which the timing of seaward migration of smolts was different. The marine component of the isotope variation in sockeye salmon otoliths (ages > 2) was uniform but showed a consistent and strong shift towards oceanic changes around 1996. Thus, $\delta^{18}O$ and $\delta^{13}C$ values of otoliths can be potentially used as a chemical tracer in population identification, and their marine portions can be used in the study of ocean environmental changes.

Résumé : La possibilité d'effectuer des analyses des rapports des isotopes stables de l'oxygène et du carbone ($\delta^{18}O$ et $\delta^{13}C$) dans les otolithes sagittaux du saumon rouge (*Oncorhynchus nerka*) a été vérifiée par l'étude des zones saisonnières et annuelles des otolithes de 44 échantillons prélevés en différents endroits de la côte nord-est du Pacifique. Les $\delta^{18}O$ et $\delta^{13}C$ de ces otolithes variaient respectivement de −14,23 à +1,62 ‰ et de −15,18 à −3,17 ‰. Les variations du $\delta^{18}O$ peuvent être divisées en deux étapes, de l'eau douce (−14,2 à −2,5 ‰) à l'eau de mer (−2,5 à +1,6 ‰), qui correspondent au cycle vital du saumon rouge, de l'état de juvénile à celui d'adulte. La transition se produisait après l'âge 1, période pendant laquelle le moment de l'avalaison des saumoneaux était différent. La composante marine de la variation isotopique des otolithes des saumons rouges (âge > 2) était uniforme, mais présentait un décalage constant et important en fonction des changements océaniques vers 1996. Par conséquent, les $\delta^{18}O$ et $\delta^{13}C$ pourraient servir de traceurs chimiques pour l'identification des populations et leur composantes marines pourraient servir à l'étude des changements de l'environnement océanique.

[Traduit par la Rédaction]

Introduction

Otoliths are laminated calcium carbonate structures located in the inner ears of teleost fish and have long been used in aging (Beamish and McFarlane 1987). The theory and practice of using otoliths in stable isotope analysis are rooted in Urey's (1947) hypothesis and the experiments that calcium carbonates are precipitated in oxygen isotopic equilibrium with the surrounding waters in which the organism (including fish) lived and thus retained the isotopic records of the life history of the animal (e.g., Epstein et al. 1953; Friedman and O'Neil 1977; Grossman and Ku 1986). Yearly, seasonal, and even daily increments in otoliths (Pannella 1971) are produced throughout the life of a fish and are geochemically inert after precipitation. Thus, stable oxygen isotope ratios ($^{18}O/^{16}O$) extracted from otoliths can provide unique information about habitat alteration, water temperature, migration, and decadal-scale ecosystem changes experienced by the individual fish (e.g., Devereux 1967; Mulcahy et al. 1979; Nelson et al. 1989; Kalish 1991. In contrast, stable carbon isotope ratios ($^{13}C/^{12}C$) in otoliths are deposited in isotopic disequilibrium with the ambient seawater and can record changes in maturation of the fish and the dietary shifts (Schwarcz et al. 1998).

Sockeye salmon (*Oncorhynchus nerka*) are commercially the most valuable of the five species of Pacific salmon in North America (Forrester 1987). The recent decline in abundance of this species has raised concerns in both the scientific community and the public. In this paper, we report the results of stable isotope ratio analysis from the proxy of otoliths. Previous stable isotope studies on sockeye salmon have concentrated on the trophic hierarchy of salmonids and used flesh as proxy materials in general (Welch and Parsons 1993; Perry et al. 1996; Kline et al. 1998). Compared with otoliths, the flesh of a fish is convenient to sample, but it is impossible to get a proper time series for retrospective studies. Kalish (1991) reported oxygen and carbon isotopic composition in otoliths of Australian salmon (*Arripis trutta*) from captive and wild fish, but his data also lack the connection with a time series. As the life of sockeye salmon is so dependent, from year to year, on food sources and oceanic

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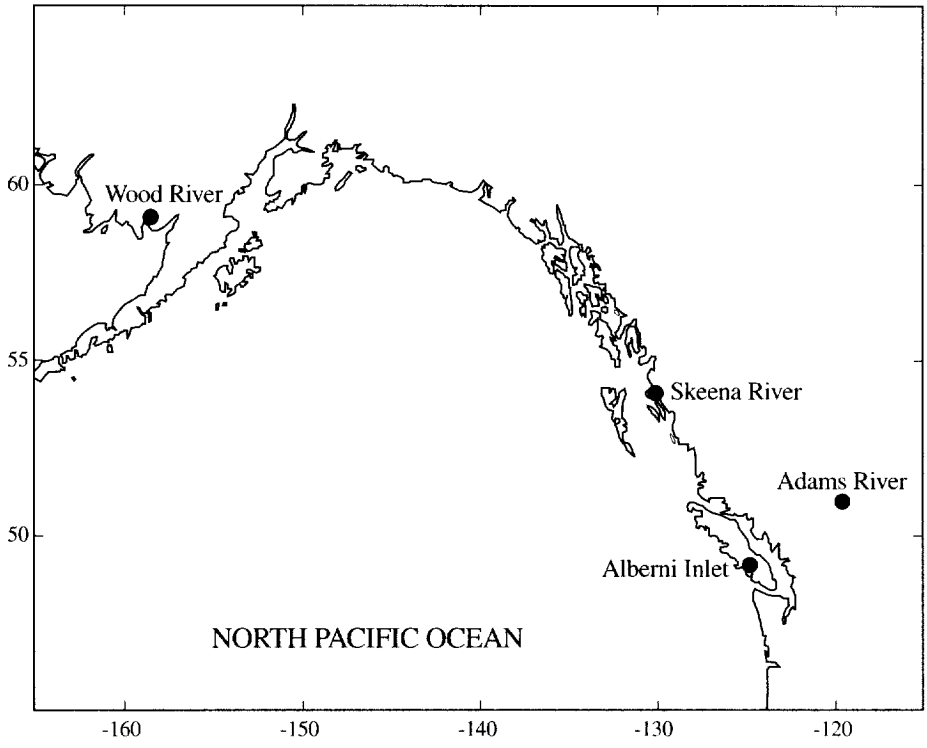
Fig. 1. Location map showing the sampling sites in the northeast Pacific.



conditions, it is necessary to analyze the isotope data within a suitable time series, whether at seasonal or annual scales. In particular, there have been no attempts to analyze stable isotopes in archived otoliths that could provide information on the growth conditions and survival of sockeye salmon in the past. Fortunately, the recent development of microsampling (at annual and intraannual/seasonal scales) coupled with mass spectrometric techniques capable of analysis of microgram quantities of carbonate has resulted in a powerful new tool in otolith geochemistry (Patterson et al. 1993; Gao 1999). The first purpose of the study was to examine the lifetime isotopic composition of individual otoliths to evaluate whether the characteristics of isotope variations are consistent with the life history and behavior of sockeye salmon. The second goal was to examine the use of isotope data as chemical tracers in population identification of sockeye salmon and the potential of using the marine portion of otoliths for ocean environmental and ecological studies.

Materials and methods

Sockeye salmon otoliths (15–20 from each locality) were collected throughout the northeast Pacific coast. These sagittal otolith pairs were taken in the summer of 1998 from July 10 to August 1 from the Wood River in Bristol Bay of Alaska, Skeena River, British Columbia, and Alberni Inlet on Vancouver Island (Fig. 1). Sockeye salmon scales and background information, such as fork length, weight, and sex, were also taken during the sample collection. In addition, 57 sockeye salmon otoliths from the Adams River, British Columbia, were gathered in the fall of 1996. Although only 5–10 Adams River sockeye salmon were reported here, the detailed isotopic analyses from translucent and opaque otolith zones (winter and summer) provided an example for the feasibility and future application of the technique.

Otolith samples of sockeye salmon were first cleaned in a supersonic water bath for about 15 min, rinsed with ethanol, and then dried naturally. The samples were first placed in an aluminum mold and then embedded in pigmented resin. The embedding medium that we used consists of a common fiberglass resin, black pigment, and a TR mold release. After hardening, the block was removed from the mold and sectioned into rectangles for polishing. Each otolith section was polished using an ECOMET 3 variable-speed grinder–polisher with self-adhesive paper (240–2400 grit). At the final stage, an AP-Cloth was used for surface polishing with 0.3 μm Alumina powders. Care was taken to polish only until annual growth zones became visible. Using the Dremel microsampling method (Gao 1999), cores of about 50 μg of aragonite were removed from the otolith surface. These samples were generally obtained from the annual otolith zones (annuli), except for the first 1 or 2 years in which single translucent and opaque (winter and summer) otolith zones were taken. To avoid any confusion with the age designation, sockeye salmon ages are reported as years old or total ages throughout this paper (Burgner 1991). The aragonite powder samples were analyzed on a VG Optima mass spectrometer at the School of Geography and Geology, McMaster University, using an Autocarb carbonate preparation device. All the measurements are reported in the standard δ notation (per mill), $\delta^{18}O = \{[(^{18}O/^{16}O)_X/(^{18}O/^{16}O)_S] - 1\} \times 1000$, where X is sample and S is standard (Vienna Peedee belemnite). The precision of analyses is better than ±0.06‰ for both $\delta^{18}O$ and $\delta^{13}C$.

Results

The $\delta^{18}O$ and $\delta^{13}C$ values of sockeye salmon otoliths ranged from −14.23 to +1.62‰ and from −15.18 to −3.17‰, respectively. There were slight differences in the isotope values between different geographic areas (Table 1). Based on the early life study and aging, all the samples analyzed were divided into two major groups: freshwater and marine. The range in isotope values and the mean of each group are

Table 1. Summary of stable isotope analysis of sockeye salmon otoliths in this study.

Settings	Localities	*N*	$\delta^{13}C$ (‰) Range	Mean	SD	$\delta^{18}O$ (‰) Range	Mean	SD
Freshwater (ages 0–1)	Wood River	10	−15.18 to −7.11	−12.76	2.22	−11.33 to −2.78	−8.36	2.30
	Skeena River	10	−14.41 to −7.91	−11.21	1.91	−13.54 to −3.74	−9.64	2.63
	Alberni Inlet	10	−14.99 to −7.08	−12.49	1.96	−9.55 to −2.37	−6.88	1.85
	Adams River	10	−13.29 to −9.92	−11.68	1.05	−14.23 to −9.30	−12.05	1.60
Marine (ages 2–5)	Wood River	7	−5.82 to −3.33	−4.21	0.58	−0.88 to +1.58	+1.06	0.60
	Skeena River	10	−5.75 to −3.17	−4.54	0.72	−0.48 to +1.62	+0.83	0.69
	Alberni Inlet	10	−6.57 to −3.44	−4.74	0.64	−1.49 to +1.61	+0.66	0.68
	Adams River	7	−5.01 to −4.23	−4.55	0.22	−0.16 to +1.12	+0.55	0.36

Fig. 2. $\delta^{18}O$ variations of individual otolith samples from the Adams River. The life history of sockeye salmon can be isotopically divided into two stages from freshwater to marine, and the transition occurred after age 1.

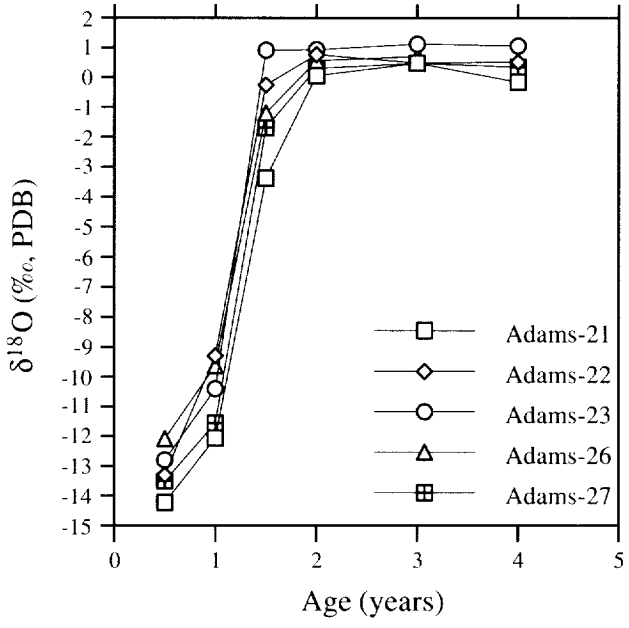
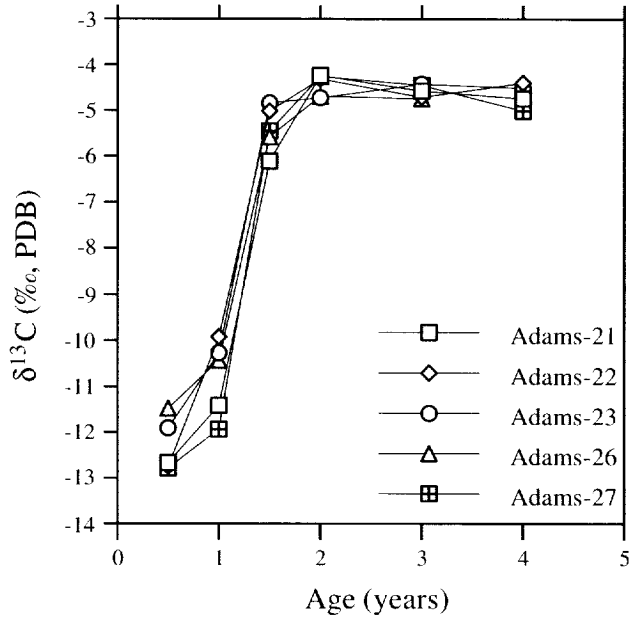


Fig. 3. $\delta^{13}C$ variations of individual otoliths from the Adams River showing a consistent trend in $\delta^{18}O$ in the lives of sockeye salmon.



slightly different (ANOVA, $F_{3,75} = 2.73$, $p = 0.050$). For example, the mean $\delta^{13}C$ value of Wood River sockeye salmon in freshwater was slightly lower than that of Skeena River sockeye salmon (−12.76 versus −11.21‰), whereas the mean $\delta^{18}O$ value of the marine group was higher (+1.06 versus +0.83‰). Overall, the variation in isotope values of sockeye salmon in freshwater environments was much larger than that in marine environments (freshwater SD from 1.60 to 2.63 and marine SD from 0.36 to 0.69) (Table 1).

The $\delta^{18}O$ values of individual Adams River sockeye salmon ranged from −14.23 to +1.12‰, very homogeneous from the first season to age 4 (Fig. 2). Because otolith growth is limited during the spawning run of adult sockeye salmon, we were unable to obtain discrete carbonate that represents that life history stage. However, based on $\delta^{18}O$ values, the life history of sockeye salmon can be divided into two stages: freshwater (−14.23 to −2.37‰) and marine (−1.49 to +1.62‰) (Table 1), the latter being relatively uniform. The transition started after age 1 in an estuarine environment (e.g., −2.5 to 0.5‰), during which the individual fish entering the sea were slightly different (between ages 1 and 2 in Fig. 2). The $\delta^{13}C$ variation of individual Adams River sockeye salmon was consistent with that of $\delta^{18}O$, ranging from −13.29 to −9.92‰ in freshwater and from −5.01 to −4.23‰ in marine settings (Fig. 3). A similar pattern and range of isotope variations (averaged from 5 to 10 fish) were shown for other localities (Fig. 4).

For the first season of sockeye salmon otoliths (winter in freshwater), the relationships of $\delta^{18}O$ and $\delta^{13}C$ in the neighboring areas, between Adams River and Alberni Inlet and between Skeena River and Wood River, are easily distinguished (Fig. 5). Because $\delta^{18}O$ variations are related to the physical properties of seawater, whereas $\delta^{13}C$ variations are related to trophic conditions, this separation appears to suggest that the isotopic signals can be used as a habitat index to distinguish the natal sources of different sockeye salmon populations.

Although $\delta^{13}C$ values of British Columbia coastal samples are slightly lower (Fig. 6), the marine portion of isotope variations in sockeye salmon otoliths showed a pronounced overlap among different populations from the Gulf of Alaska

Fig. 4. Average isotope range and variation of sockeye salmon otoliths from different areas in the present study (sample size in parentheses). (*a*) Mean $\delta^{18}O$ values; (*b*) mean $\delta^{13}C$ values.

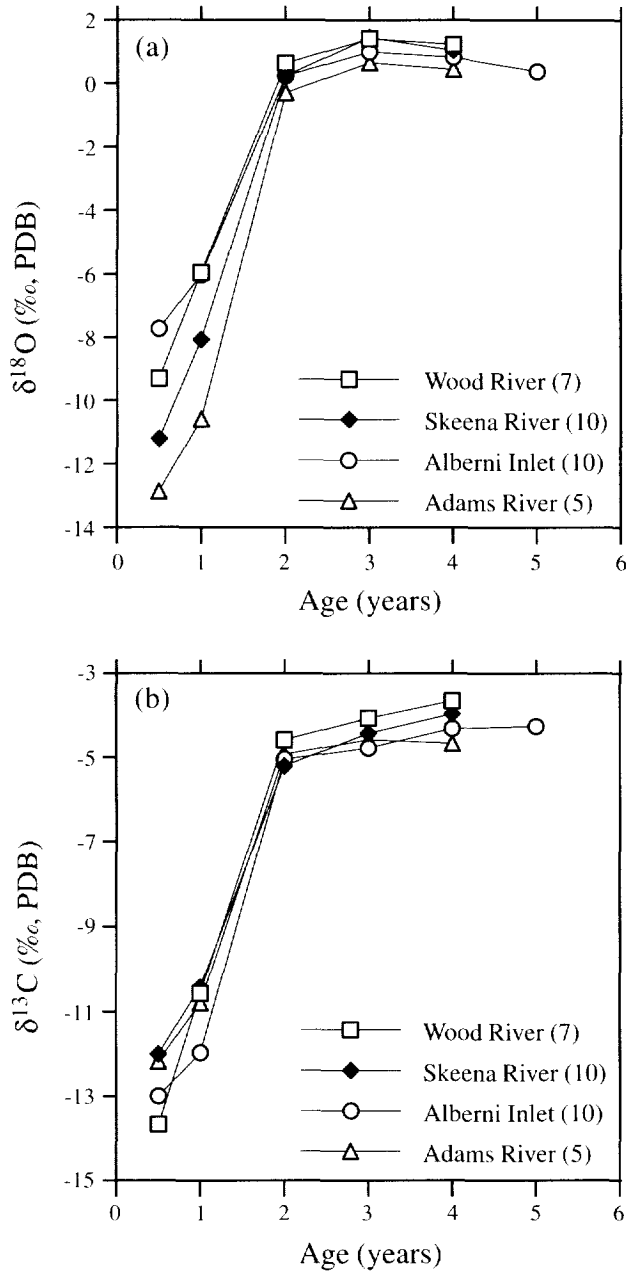
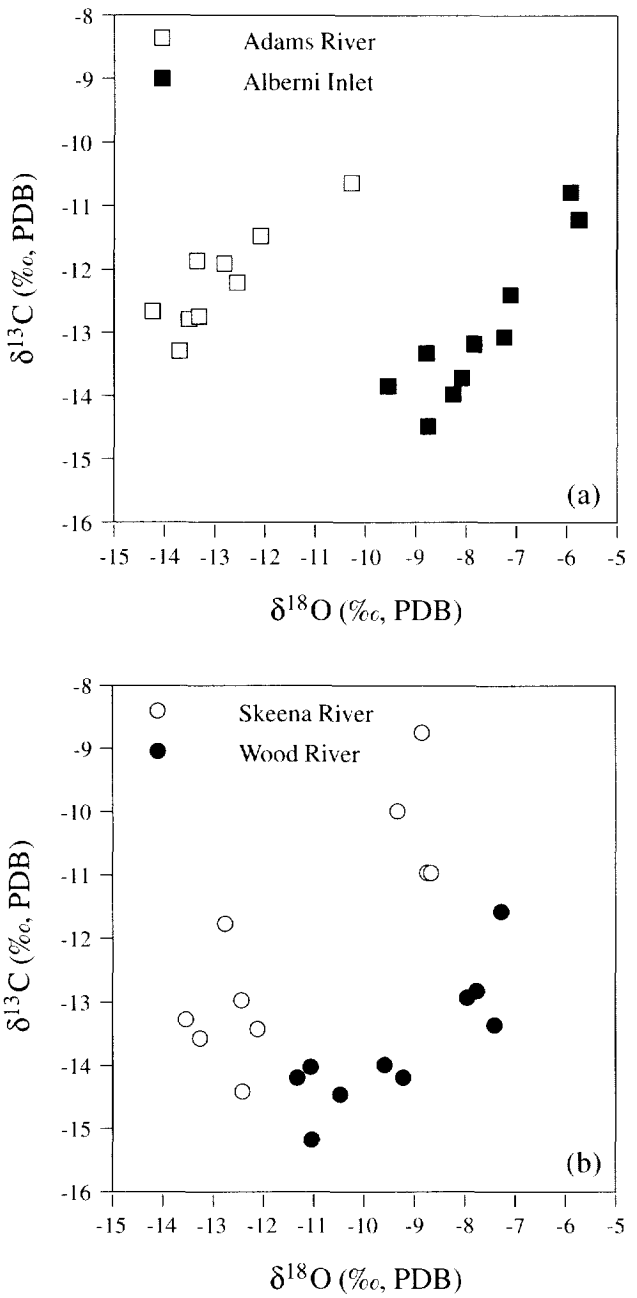


Fig. 5. Relationship between $\delta^{18}O$ and $\delta^{13}C$ of sockeye salmon otoliths from the first season. (*a*) Adams River and Alberni Inlet; (*b*) Skeena River and Wood River. See text for details.

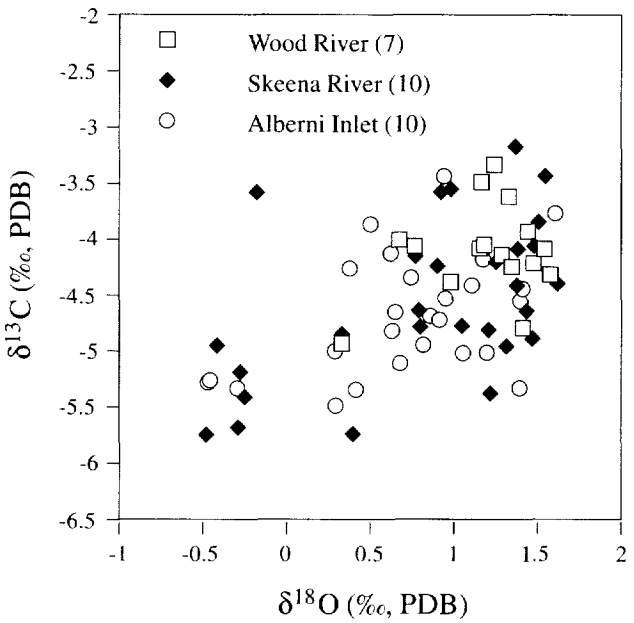


to Vancouver Island (ANOVA, $F_{2,73} = 1.88$, $p = 0.160$). The overlap was probably due to similar timing of smolts moving into the sea around age 2, or mixing of sockeye salmon from different stocks during their oceanic pastures. The average isotope values (both $\delta^{13}C$ and $\delta^{18}O$) for different sockeye salmon stocks were consistent from ages 2 to 4, corresponding to the time series of calendar years 1995–1997 (Fig. 7). Over that period the mean $\delta^{13}C$ values of all sockeye salmon otoliths along the coast were steadily increasing, whereas the mean $\delta^{18}O$ values shifted around 1996. The shift of 0.6–0.8‰ in $\delta^{18}O$, if any, would represent a significant change in oceanic conditions of the North Pacific.

Discussion

As an anadromous fish, sockeye salmon spend most of their lives (2–5 years) in coastal and high-seas environments and, after maturity, return to their parent coastal streams to spawn (Foerster 1968; Burgner 1991). The isotopic composition of sockeye salmon otoliths did reveal anadromous stages from freshwater to marine settings in both $\delta^{18}O$ and $\delta^{13}C$ values (Figs. 2 and 3). It is known that $\delta^{18}O$ values in standard seawater are around 0‰ and in freshwater are generally lower than –10‰ (Craig 1961). Thus the $\delta^{18}O$ data from sockeye salmon otoliths are consistent with previous

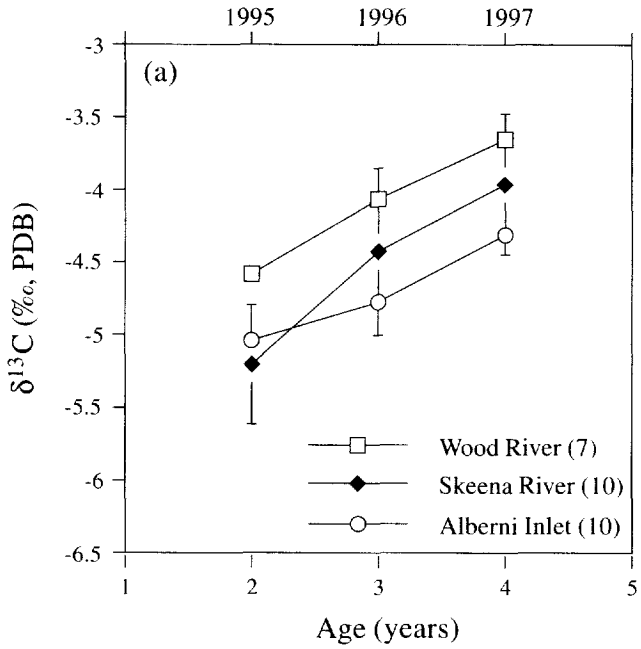
Fig. 6. Overlap of $\delta^{18}O$ and $\delta^{13}C$ from the marine portion of otoliths from different sockeye salmon populations.

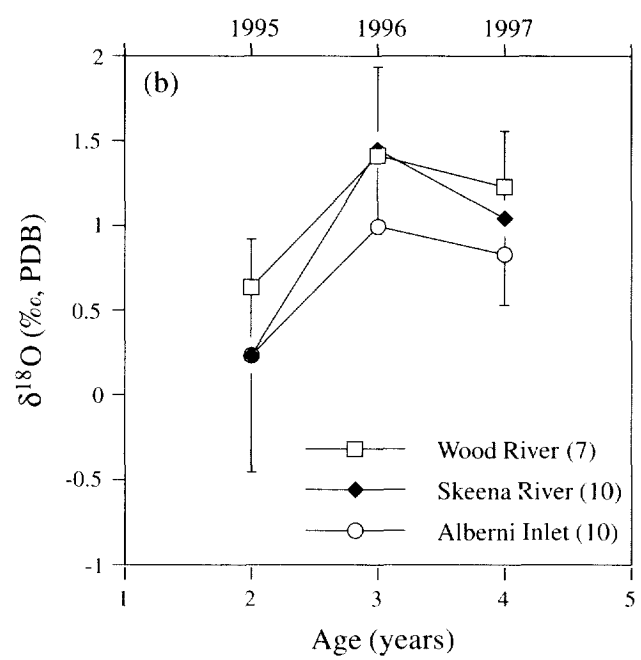


studies of stable isotope geochemistry and fisheries biology. The $\delta^{13}C$ values are also consistent with the two stages of sockeye salmon life history, although their isotopic meanings in otoliths are not primarily related to water conditions (Schwarcz et al. 1998). The $\delta^{13}C$ values from –13.5 to –7.0‰ and from –7.0 to –3.5‰ (Fig. 4*b*) probably represent the isotope variations of planktonic crustaceans in the freshwater environment and pelagic plankton organisms in the marine environment (Welch and Parsons 1993).

The identification of sockeye salmon populations or stocks has been documented by tagging and some physical methods (Foerster 1968). From tagging, the locations of release and recapture of sockeye salmon in the ocean are recorded, and the subsequent movement of the fish can be followed. In addition to the cost, however, this "human-made" marker has the disadvantage of low recovery rates (<10‰ in general). The physical methods, such as scale patterns of sockeye salmon and morphological features of otoliths (Bugaev 1987), are dependent primarily on the examiner's experience and it is sometimes difficult to obtain quantitative measurements. Genetic markers, such as protein electrophoresis (Rutherford et al. 1992) and the new development of microsatellite DNA (Beacham and Wood 1999), have also been used in stock identification of sockeye salmon. Comments on the role of genetic markers and points for attention have been made by Ferguson and Danzmann (1998). Here, we suggest that stable isotope ratio analysis in otoliths could be used for population identification of sockeye salmon. The isotopic analysis generates a natural "chemical" marker, which can determine not only the origin of the fish (Fig. 5), but also the tracks of migration of individuals (Fig. 2). From the first seasonal isotope values between populations, we see that the Alberni Inlet sockeye salmon are more enriched in ^{18}O but depleted in ^{13}C than the Adams River sockeye salmon (Fig. 5*a*). In contrast, the Skeena River sockeye salmon salmon are more enriched in

Fig. 7. Average isotope variations of the marine portion of otoliths from different sockeye salmon populations (sample size in parentheses). (*a*) $\delta^{13}C$ variation: a stable increase from ages 2 to 4; (*b*) $\delta^{18}O$ variation: a shift around age 3 that corresponds to calendar year 1996.





^{13}C than the Wood River sockeye salmon and slightly depleted in ^{18}O (Fig. 5*b*). These isotopic differences may result from different $\delta^{18}O$ values in the natal rivers or lakes, or from the food sources of different residences or from both. If this is true, it will indicate that the freshwater discharge in the Adams River system has stronger influences than that on Vancouver Island (from $\delta^{18}O$) and that the trophic level of planktonic crustaceans is also slightly higher than the latter (from $\delta^{13}C$). Similar conclusions can be made for Skeena

River and Wood River sockeye salmon. We did not know from the present study whether the isotopic technique would be effective in discriminating among stocks within a watershed such as the Fraser River basin (Dr. J. Woodey, Pacific Salmon Commission, Vancouver, B.C., personal communication). Nevertheless, the key premise is whether there are distinct isotopic differences in the natal sources of individual populations and how the isotopic signals from those differences can be distinguished. As compared with the tagging method, one of the greatest advantages is that the isotopic marker can trace the movement or migration of individual sockeye salmon between release and recovery and reconstruct the dynamic history of the stock.

It should be noted that for the techniques of stock identification, a recent development in trace elemental concentrations in otoliths has been extensively documented as "fingerprinting" (Campana et al. 1994). Multivariate analyses of the elemental fingerprints show success and potential in discrimination of cod stocks. Because of the theoretical uncertainty and technical difficulties in elemental analyses (Campana et al. 1997), stable isotope variations may be more useful than trace element methods as environmental tracers.

During sockeye salmon early life, the downstream and (or) seaward movement of smolts (Burgner 1991) occurred after age 1, with $\delta^{18}O$ values from –8.5 to –3.5‰. If we roughly defined –2.5‰ in $\delta^{18}O$ as the value of estuarine environments (Fig. 2), for instance, samples 23 and 22 were already living in the ocean, while sample 21 was still in the mouth of the Adams River system. The seaward migration of smolts and the rate of migrants thus could be potentially estimated from the isotope values of otoliths, although the migration pattern and speed were uncertain. In the Strait of Georgia, British Columbia, the distribution of sockeye salmon smolts is reported to be driven by the variability of winds, while tides and river discharges are of secondary importance (Peterman et al. 1994). The differences in temperature (warmer in nursery lakes and cooler in the estuary) and food sources between freshwater and marine settings might also play an important role in sockeye salmon early life (Figs. 2 and 3). Thus, the time differences of seaward migration for individual smolts were probably stimulated by both internal (e.g., age, growth, and heredity of the smolts; Wood et al. 1987) and external factors (e.g., temperature, salinity, and nutrients in the water; Burgner 1991). If the above isotopic interpretation and discussion are valid, it would be a very useful tool in determining the rate and proportion of seaward migrants.

It is quite surprising that during the marine stage of life history, both the $\delta^{18}O$ and $\delta^{13}C$ values of sockeye salmon otoliths are relatively uniform (Fig. 4). Previous studies concluded that sockeye salmon were found in a vast grazing area across the whole North Pacific between 46 and 60°N, where the summer surface temperature ranged from 5 to 16°C and salinity less than 32.2‰ (Foerster 1968; Burgner 1991). Because sockeye salmon are basically shallow-water swimmers (normally in the upper 20–30 m stratum), the overlap of isotope values of otoliths from different localities (Fig. 6) confirms that these sockeye salmon intermingle during their ocean lives and disperse as they return to their home streams after maturity. The isotopic interpretation is also consistent with evidence from tagging and biological studies (Foerster 1968). Furthermore, the average isotope variations of marine portions (ages 2–4) from different populations are also identical (Fig. 7). Since the distribution and abundance of sockeye salmon in the North Pacific varied from year to year and appeared to respond to climate conditions (Bisbal and McConnaha 1998), it is possible and potentially important to analyze the marine portion of sockeye salmon otoliths for long-term ecosystem changes or regime shifts as defined in Francis and Hare (1994) and Beamish et al. (1999). The gradual increase of $\delta^{13}C$ from 1995 to 1997 might suggest that there was a slow shift in pelagic plankton biomass (Fig. 7*a*). In contrast, the 0.6–0.8‰ shift in $\delta^{18}O$ around 1996 would be a sudden and significant change for the physical oceanic conditions (Fig. 7*b*). This phenomenon, if comparable, would correspond to a seawater temperature decrease of about 3–4°C (cf. Kalish 1991). To date, we have no direct evidence of a large-scale temperature change in 1996. However, the isotopic signal is an indication of how the thermal history of the ocean surface can be monitored in the otoliths of sockeye salmon and would be of interest in reconstruction of long-term ocean environmental changes.

In summary, we have demonstrated that the isotopic composition of otoliths is a promising chemical tracer in the study of sockeye salmon. Stable isotope ratio analysis (both $\delta^{18}O$ and $\delta^{13}C$) can be potentially used for (*i*) identification of the natal origin and distribution of sockeye salmon stocks in the northeast Pacific coast, (*ii*) determining the timing and rate of downstream and seaward migration of smolts, and (*iii*) studying the marine environmental and ecological changes as they pertain to climate-related regime shifts.

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References

Beacham, T.D., and Wood, C.C. 1999. Application of microsatellite DNA variation to estimation of stock composition and escapement of Nass River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **56**: 297–310.

Beamish, R.J., and McFarlane, G.A. 1987. Current trends in age determination methodology. *In* Age and growth of fish. *Edited by* R.C. Summerfelt and G.E. Hall. Iowa State University Press, Ames, Iowa. pp. 15–42.

Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V., and Kurashov, V. 1999. The regime concept and

natural trends in the production of Pacific salmon. Can. J. Fish. Aquat. Sci. **56**: 516–526.

Bisbal, G.A., and McConnaha, W.E. 1998. Consideration of ocean conditions in the management of salmon. Can. J. Fish. Aquat. Sci. **55**: 2178–2186.

Bugaev, V.F. 1987. Scale patterns and biology of juvenile sockeye salmon (*Oncorhynchus nerka*) in the Kamchatka River. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 36–43.

Burgner, R.L. 1991. Life history of sockeye salmon. *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C. pp. 3–117.

Campana, S.E., Fowler, A.J., and Jones, C.M. 1994. Otolith elemental fingerprinting for stock identification of Atlantic cod (*Gadus morhua*) using laser ablation ICPMS. Can. J. Fish. Aquat. Sci. **51**: 1942–1950.

Campana, S.E., Thorrold, S.R., Jones, C.M., Günther, D., Tubrett, M., Longerich, H., Jackson, S., Halden, N.M., Kalish, J.M., Piccoli, P., Pontual, H., Troadec, H., Panfili, J., Secor, D.H., Severin, K.P., Sie, S.H., Thresher, R., Teesdale, W.J., and Campbell, J.L. 1997. Comparison of accuracy, precision, and sensitivity in elemental assays of fish otoliths using the electron microprobe, proton-induced X-ray emission, and laser ablation inductively coupled plasma mass spectrometry. Can. J. Fish. Aquat. Sci. **54**: 2068–2079.

Craig, H. 1961. Standard for reporting concentrations of deuterium and oxygen-18 in natural waters. Science (Washington, D.C.), **133**: 1833–1834.

Devereux, I. 1967. Temperature measurements from oxygen isotope ratios of fish otoliths. Science (Washington, D.C.), **155**: 1684–1685.

Epstein, S., Buchsbaum, R., Lowenstam, H.A., and Urey, H.C. 1953. Revised carbonate-water isotopic temperature scale. Geol. Soc. Am. Bull. **64**: 1315–1326.

Ferguson, M.M., and Danzmann, R.G. 1998. Role of genetic markers in fisheries and aquaculture: useful tools or stamp collecting? Can. J. Fish. Aquat. Sci. **55**: 1553–1563.

Foerster, R.E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Board Can. No. 162.

Forrester, C.R. 1987. Distribution and abundance of sockeye salmon (*Oncorhynchus nerka*). *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 2–10.

Francis, R.C., and Hare, S.R. 1994. Decadal-scale regime shifts in the large marine ecosystems of the Northeast Pacific: a case for historical science. Fish. Oceanogr. **3**: 279–291.

Friedman, I., and O'Neil, J.R. 1977. Compilation of stable isotope fractionation factors of geochemical interest. *In* Data of geochemistry. *Edited by* M. Fleischer. U.S. Geol. Surv. Prof. Pap. 440-KK.

Gao, Y.W. 1999. Microsampling of fish otoliths: a comparison between DM 2800 and Dremel in stable isotope analysis. Environ. Biol. Fishes, **55**: 443–448.

Grossman, E.L., and Ku, T.-L. 1986. Oxygen and carbon isotope fractionation in biogenic aragonite: temperature effects. Chem. Geol. **59**: 59–74.

Kalish, J.M. 1991. Oxygen and carbon stable isotopes in the otoliths of wild and laboratory-reared Australian salmon (*Arripis trutta*). Mar. Biol. **110**: 37–47.

Kline, T.C., Wilson, W.J., and Goering, J.J. 1998. Natural isotope indicators of fish migration at Prudhoe Bay, Alaska. Can. J. Fish. Aquat. Sci. **55**: 1494–1502.

Mulcahy, S.A., Killingley, J.S., Phleger, C.F., and Berger, W.H. 1979. Isotopic composition of otoliths from a bentho-pelagic fish, *Coryphaenoides acrolepis*, Macrouridae: Gadiformes. Oceanol. Acta, **2**: 423–427.

Nelson, C.S., Northcote, T.G., and Hendy, C.H. 1989. Potential use of oxygen and carbon isotopic composition of otoliths to identify migratory and non-migratory stocks of the New Zealand common smelt: a pilot study. N.Z. J. Mar. Freshwater Res. **23**: 337–344.

Pannella, G. 1971. Fish otoliths: daily growth layers and periodical patterns. Science (Washington, D.C.), **173**: 1124–1126.

Patterson, W.P., Smith, G.R., and Lohmann, K.C. 1993. Continental paleothermometry and seasonality using the isotopic composition of aragonitic otoliths of freshwater fishes. *In* Climate change in continental isotopic records. *Edited by* P. Swart, K.C. Lohmann, J. McKenzie, and S. Savin. Geophys. Monogr. **78**: 191–202.

Perry, R.I., Hargreaves, N.B., Waddell, B.J., and Mackas, D.L. 1996. Spatial variations in feeding and condition of juvenile pink and chum salmon off Vancouver Island, British Columbia. Fish. Oceanogr. **5**: 73–88.

Peterman, R.M., Marinone, S.G., Thomson, K.A., Jardine, I.D., Crittenden, R.N., Leblond, P.H., and Walters, C.J. 1994. Simulation of juvenile sockeye salmon (*Oncorhynchus nerka*) migrations in the Strait of Georgia, British Columbia. Fish. Oceanogr. **3**: 221–235.

Rutherford, D.T., Wood, C.C., Hyatt, K.D., Margolis, L., McDonald, T.E., Riddell, B.E., and Withler, R.E. 1992. Biological characteristics of coastal populations of sockeye salmon (*Oncorhynchus nerka*) in British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. No. 1849.

Schwarcz, H.P., Gao, Y.W., Campana, S., Browne, D., Knyf, M., and Brand, U. 1998. Stable carbon isotope variations in otoliths of cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **55**: 1798–1806.

Urey, H.C. 1947. The thermodynamic properties of isotopic substances. J. Chem. Soc. **1947**: 562–581.

Welch, D.W., and Parsons, T.R. 1993. $\delta^{13}C$–$\delta^{15}N$ values as indicators of trophic position and competitive overlap for Pacific salmon (*Oncorhynchus* spp.). Fish. Oceanogr. **2**: 11–23.

Wood, C.C., Riddell, B.E., and Rutherford, D.T. 1987. Alternative juvenile life histories of sockeye salmon (*Oncorhynchus nerka*) and their contribution to production in the Stikine River, northern British Columbia. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 12–24.