Contrasts in the hypo-osmoregulatory abilities of a freshwater and an anadromous population of inconnu

K. L. HOWLAND*, W. M. TONN AND G. GOSS

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

(Received 21 June 2000, Accepted 30 June 2001)

Juvenile freshwater and anadromous inconnu Stenodus leucichthys regulated plasma ions following a direct transfer from fresh to brackish water (10–15‰), but suffered osmoregulatory collapse with 100% mortality in 48 h when directly transferred to 25‰ salinity. Acclimation to brackish water for 2 weeks improved hypo-osmoregulatory capacity in both populations, with acclimated fish showing smaller increases in blood plasma ion concentrations, higher Na⁺-K⁺ ATPase activity, and lower mortality than non-acclimated fish following transfer to 25‰ sea water. Anadromous inconnu maintained pre-treatment plasma ion levels during acclimation, whereas these levels increased during acclimation in freshwater inconnu. Juvenile anadromous inconnu are therefore able to adapt physiologically to sea water of at least 25‰, if brackish-water acclimation is available, but freshwater inconnu have diminished saltwater tolerance, relative to the anadromous form.

Key words: salinity; osmoregulation; Na⁺-K⁺ ATPase; inconnu; whitefish.

INTRODUCTION

Anadromy, the movement between freshwater spawning and marine feeding areas, is a characteristic of many salmonid species (Stearly, 1992; Moyle & Cech, 1997). Consequently, substantial interest has developed around the osmoregulatory capacities and physiological mechanisms that allow salmonids to move between these distinct environments. Most research on this topic has focused on the Pacific and Atlantic salmon Oncorhynchus spp. and Salmo salar L. (McCormick et al., 1985; Zaugg & Beckman, 1990; Birt et al., 1991; Morgan & Iwama, 1998), as well as Arctic charr Salvelinus alpinus (L.) (Finstad et al., 1989; Nilssen et al., 1997; Eliassen et al., 1998). In contrast, little is known about the salinity tolerance of whitefishes (de March, 1989; Madsen et al., 1996), many of which also have anadromous populations in the northern parts of their ranges, and even less is known regarding their physiological responses to salinity change.

Inconnu Stenodus leucichthys (Güldenstadt) is an arctic whitefish found in large rivers and lakes throughout much of Siberia and the western Arctic of North America (McPhail & Lindsey, 1970), where they contribute to both subsistence and commercial fisheries (McCart, 1986; Bodaly et al., 1989). Distinct anadromous and freshwater populations have been reported in Siberia...
(Berg, 1948; Nikol’skii, 1954) and Alaska (Alt, 1977, 1988), and the occurrence of both forms in the Mackenzie River system of northwestern Canada have recently been documented (pers. obs.). The freshwater form occurs in Great Slave Lake and its southern tributaries, whereas anadromous inconnu are distributed throughout most of the lower Mackenzie River system north of Norman Wells (Howland et al., 2000); no mixing appears to occur between the two forms. Based on the glacial history of this region (Lindsey & McPhail, 1986), inconnu colonized the Mackenzie River system ≤10 000 years bp and the freshwater and anadromous forms have probably developed since that time.

Otolith microchemistry reveals that anadromous inconnu in the Mackenzie River system migrate seaward annually after reaching 1–2 years of age (Howland, 1997), however, size of first time migrants has, as far as is known, never been documented. These annual migrations appear to involve feeding in brackish coastal waters of the Beaufort Sea during the summer months, and returning to deeper areas of the Mackenzie Delta or estuary to overwinter (Howland et al., 2000). After reaching sexual maturity (7–10 years, unpubl. data), anadromous inconnu migrate long distances upstream into freshwater tributaries (e.g. Peel and Arctic Red Rivers), where they spawn in the autumn (J. N. Stein et al., unpubl. data; Howland et al., 2000). Inconnu are repeat spawners and are believed to spawn every 3–4 years (Scott & Crossman, 1973).

Little is known about the extent of anadromous migrations, e.g. whether inconnu venture into full-strength sea water offshore or to deeper areas along the coast during summer feeding, and whether they undergo seasonal preparatory physiological changes similar to Arctic charr and Atlantic salmon. Survey data suggest that anadromous inconnu from the Mackenzie River system rarely enter coastal waters of salinities>20‰ (Bond, 1982; Lawrence et al., 1984; Bond & Erickson, 1989; Chiperzak et al., 1991). However, strontium concentrations in otoliths suggest that inconnu occupy waters with salinities similar to those used by anadromous Arctic charr (Howland, 1997), which are known to undergo seasonal physiological changes and are capable of adapting to full-strength sea water (32–35‰) during summer (Finstad et al., 1989; Eliassen, 1998).

Likewise, the hypo-osmoregulatory capabilities of freshwater inconnu have not been studied, and it is not known if the two forms have diverged in their osmoregulatory abilities. Although some studies have found greater seawater adaptability in anadromous forms of salmonids (Staurnes et al., 1992a; Barbour & Garside, 1993; Birt & Green, 1993; Eliassen et al., 1998), others find no difference (McCormick et al., 1985; Staurnes et al., 1992b; Schmitz, 1995; Pirhonen & Forsman, 1998). The hypo-osmoregulatory abilities were examined of juvenile freshwater and anadromous inconnu from Mackenzie River system that were reared under common laboratory conditions to address the following questions: (1) What salinity levels are inconnu able to tolerate and thus what is their potential distribution in coastal waters? (2) Can inconnu undergo aclimatory physiological changes to occupy salt water, similar to other salmonids? (3) Given the relatively short time span they have been separated from each other, how do the hypo-osmoregulatory capabilities of freshwater and anadromous inconnu differ?
EXPERIMENTAL ANIMALS AND REARING CONDITIONS

Experimental inconnu originated from two areas of the Mackenzie River system. The Arctic Red River is a tributary to the lower Mackenzie River and contains spawning anadromous inconnu, whereas spawning freshwater inconnu inhabit the Slave River, a southern tributary to Great Slave Lake. Eggs from spawning females of both populations were collected and fertilized in the field in September–October 1996. Fertilization of Arctic Red River eggs occurred c. 1 month earlier due to differences in spawning times. Within 12 h of fertilization, eggs were flown to Edmonton, where they were incubated and hatched in the aquatic facility of the University of Alberta during January–February 1997. Juveniles from both populations were reared under similar conditions, at a photoperiod of 16L : 8D, in multiple 20 l plastic containers with flow-through, dechlorinated water held at an average temperature of 7°C (range 4°C–12°C due to fluctuations of incoming city water and limitations of the aquatic facility). Inconnu were fed ad libitum with live brine shrimp nauplii, trout starter mash (Moore-Clarke), and later, frozen adult brine shrimp. Salinity tolerance experiments were conducted when fish reached c. 1 year of age.

SALINITY TOLERANCE EXPERIMENTS

Salinity tolerance of freshwater and anadromous populations were compared in two experiments designed to represent potential situations in the wild: (1) an acute transfer from fresh water into various salinities (0–25‰), such as might be experienced by fish during coastal storm events, tidal events, or during feeding forays; (2) a step transfer from fresh water to brackish water (15‰) for 2 weeks and then into higher strength sea water (25‰), which might be experienced during the annual spring migrations of this species from the freshwater deltas and tributaries, into brackish coastal areas and then into higher strength sea water.

For both the acute and step-transfer experiments, dechlorinated water that was aerated, filtered and recirculated with a pump was used. Fish were transferred to experimental containers (20 l pails for the acute transfer experiments, and 80 l tubs for the step-transfer experiments) and allowed to adjust to their new surroundings in fresh water for 2 days. Concentrated artificial brine (Hagen 50 Fathoms Sea Salt) was then added to the fresh water to obtain the desired salinities. Salinities were measured daily using a hygrometer and held to within ±1‰. Fish were fed ad libitum throughout the course of the experiments. Excess food and faeces were removed daily by siphon and lost water volume was replaced as required.

Acute transfer
This experiment was run from late January to March, 1998; the trials of the two populations were staggered by 1 month (anadromous, 26 January–3 February; fresh water, 27 February–7 March) to minimize age and size differences resulting from different spawning and/or hatch times. Experimental fish were 79·4 ± 4·7 mm and 3·2 ± 0·6 g, and 76·3 ± 4·4 mm and 2·7 ± 0·5 g (mean ± s.e. fork length, L_f, and wet mass) for inconnu from the Arctic Red and Slave rivers, respectively. Experiments were carried out in a 5°C (± 0·1°C) growth chamber, at a constant photoperiod of 16L : 8D. Twelve fish were sampled at time 0, prior to the saltwater transfer to serve as a reference control. Then, anadromous and freshwater inconnu were transferred directly to four different salinities: 0 (control), 10, 15 and 25‰ sea water (n=31 fish for each salinity and population). Six fish were subsequently sampled from each treatment at 12, 24, 48 and 192 h post-transfer.

Step transfer
This experiment was run from mid-June to late August, 1998, again staggering the trials by c. 1 month to minimize age and size differences between anadromous and freshwater inconnu. Fish (86·5 ± 7·1 mm and 3·9 ± 1·0 g, and 87·4 ± 6·1 mm and 4·0 ± 0·8 g, for Arctic Red and Slave river, respectively) were held in 10°C (± 1·0°C) water on a
24 h photoperiod. The fish had been held at this photoperiod since early May, following a gradual increase from 16L:8D, simulating natural light conditions they would experience in the north during spring. Inconnu from each population were either acclimated to 15‰ (brackish) for 2 weeks and then transferred to 25‰ (n=28 anadromous, n=36 fresh water) or were directly transferred from fresh water to 25‰ (n=22 anadromous, n=30 fresh water). Six fish were sampled prior to the brackish-water acclimation to serve as a reference control. Another six fish from each population were sampled from the brackish-water treatment at the end of the acclimation period. Subsequently 6 fish from each treatment were sampled at 12, 24 and 192 h post-transfer.

SAMPLING AND DETERMINATION OF PLASMA ION CONCENTRATIONS AND NA\(^+\)-K\(^+\) ATPASE ACTIVITY

At each sampling individual fish were stunned with a blow to the head and \(L_F\) and mass were measured. The tail was then severed and blood collected from the caudal vein using a heparinized haematocrit tube. Blood plasma was separated by centrifugation and stored at \(-20^\circ\)C. One gill basket was removed and immersed in a solution of 250 mm sucrose, 10 mm EDTA, 50 mm imidazole (pH 7.3) and frozen at \(-80^\circ\)C for subsequent determination of sodium-potassium (Na\(^+\)-K\(^+\)) ATPase activity.

Changes in blood sodium (Na\(^+\)) and chloride (Cl\(^-\)) concentration, and Na\(^+\)-K\(^+\) ATPase activity were used as indicators of salinity tolerance. Mortality levels and feeding behaviour were also incidentally recorded. Plasma [Na\(^+\)] was measured using atomic absorption spectrophotometry. Plasma [Cl\(^-\)] was determined using a ferric nitrate and mercuric thiocyanate colorimetric assay (Zall et al., 1956). Sodium-potassium ATPase activity was measured for the later step-transfer experiment using a slightly modified version of a microassay developed by McCormick (1993); 2.5 µl of homogenate was used and the assay was run at 24°C.

STATISTICAL ANALYSES

All reported values are means (± s.e.) from sample sizes of \(n=6\) unless otherwise indicated. The General Linear Models (GLM) procedure for factorial data (SPSS 8.0) was used to test for effects of treatment, population and time on plasma ion and gill Na\(^+\)-K\(^+\) ATPase activity levels of fish following transfer to 25‰ sea water. For the acute-transfer experiment, two partial GLM analyses (1, without 25 ppt treatment; 2, without 48 h and 192 h treatments) were run to accommodate for complete missing data in some cells. Comparisons between pre- and post-transfer levels within each treatment were made using one-way analyses of variance (ANOVA\(s\)), followed by the Dunnett’s test. The assumptions of normality and homogeneity of sample variances were assessed using the Kolmogorov–Smirnov test (with Lilliefor’s correction) and \(F\)-tests, respectively. In cases where these assumptions were not met, data were either log-transformed or non-parametric statistical tests were used (Kruskal–Wallis ANOVA on ranks). Mortality levels of inconnu from fresh water and anadromous populations were compared with Fisher’s Exact Test. Differences were considered significant at \(P=0.05\).

RESULTS

ACUTE TRANSFER

Blood plasma ions

Inconnu from both freshwater and anadromous populations responded similarly to a direct transfer from fresh water into salinities ranging from 0 to 25‰ sea water (Fig. 1), and no consistent effect of population was seen (partial GLMs, [Na\(^+\)] \(1−P<0.0001\) 2 – \(P=0.16\), [Cl\(^-\)] \(1−P=0.30\) 2 – \(P<0.0001\)). Significant effects of salinity (relative to control group) were observed for both freshwater and anadromous inconnu when transferred to brackish and 25‰ (GLMs with \(post-hoc\) Tukey’s, \(P<0.0001\) for all pairwise comparisons). Both
populations showed an initial increase in plasma $[\text{Na}^+]$ and $[\text{Cl}^-]$ between 12 and 48 h post-transfer to all salinities $>0\,\%$ (GLMs, $P<0.0001$). Plasma ion concentrations stabilized or returned to pre-transfer levels by 8 days in 10 and 15\%. At 25\% plasma ion concentrations increased steadily with time and all fish died between 24 and 48 h post-transfer. Inconnu from both populations appeared to exhibit normal feeding behaviour in the freshwater and brackish water treatments, but stopped feeding by 12 h post-transfer to 25\% sea water.

**STEP-TRANSFER**

**Blood plasma ions and mortality**

In the second, step-transfer experiment, the GLM procedure revealed a significant effect of treatment (acclimated v. non-acclimated, $[\text{Na}^+] \ P<0.0001$, $[\text{Cl}^-] \ P=0.004$), some effect of time ($[\text{Na}^+] \ P=0.02$, $[\text{Cl}^-] \ P=0.05$), and no effect of population ($[\text{Na}^+] \ P=0.20$, $[\text{Cl}^-] \ P=0.33$) on post-transfer blood plasma ion levels. Individuals from both populations that acclimated to brackish water showed less overall increase in blood plasma ion concentrations (GLMs, $[\text{Na}^+] \ P<0.05$, $[\text{Cl}^-] \ P<0.0001$), had lower mortality (acclimated five of 21 fish died, non-acclimated 14 of 22 fish died; Fisher’s Exact Test, $P=0.014$), and exhibited normal feeding behaviour, compared to non-acclimated individuals following transfer to 25\% sea water.
In the non-acclimated groups, both anadromous and freshwater inconnu showed a steady increase in plasma $[\text{Na}^+]$ and $[\text{Cl}^−]$ until 24 h post-transfer (Fig. 2), as in the earlier acute transfer experiment, but survived longer. Fish did not begin to die until 72 h post-transfer and some individuals were still alive and behaving normally after 8 days. Mortality was similar at 57% (four of seven died) and 67% (10 of 15 died) between 72 h and 8 days for anadromous and freshwater inconnu, respectively (Fisher’s Exact Test, $P=0.67$). Plasma ion concentrations of survivors stabilized by 8 days, although remaining greater than pre-treatment levels (Kruskal–Wallis ANOVA on ranks with post-hoc Dunnett’s test).

After 2 weeks in brackish water, anadromous inconnu maintained plasma $[\text{Na}^+]$ and $[\text{Cl}^−]$ (Kruskal–Wallis ANOVA on ranks with post-hoc Dunnett’s test, $P>0.05$), whereas concentrations increased in freshwater inconnu (Kruskal–Wallis ANOVA on ranks with post-hoc Dunnett’s test, $P<0.05$; Fig. 2). Following the subsequent transfer to 25‰ sea water, both groups reached similar plasma $[\text{Na}^+]$ and $[\text{Cl}^−]$ (GLMs, $P>0.05$), which stabilized by 8 days. Despite reaching similar plasma ion concentrations, the anadromous group suffered no mortality following transfer to 25‰ (seven fish), whereas 35% (five of 14) of the fish in the freshwater group died between 72 h and 8 days post-transfer. The

![Fig. 2. Changes in plasma chloride (a), (b) and sodium (c), (d) concentrations (mean ± 1 s.e.) of anadromous (a), (c), and freshwater (b), (d) inconnu following transfer to 25‰ sea water, either with (acclimated △) or without (non-acclimated ▲) a 2 week acclimation period at 15‰. △. Pre-treatment freshwater levels; *, significant difference ($P<0.05$) from the pre-treatment freshwater level (Kruskal–Wallis ANOVA on ranks with post-hoc Dunnett’s test). Numbers in parentheses represent sample sizes if other than $n=6$.](image)
small sample size in the anadromous group, however, prevented this difference from being significant (Fisher’s Exact Test, \( P=0.12 \)).

**Na\(^+\)-K\(^+\) ATPase activity**

Although freshwater and anadromous inconnu had similar ATPase activity prior to treatment, activity increased during the 2 week acclimation to brackish (15‰) water among the freshwater (Kruskal–Wallis ANOVA on ranks with post-hoc Dunnett’s test, \( P<0.05 \)), but not anadromous inconnu (Kruskal–Wallis ANOVA on ranks with post-hoc Dunnett’s test, \( P>0.05 \); Fig. 3). The difference in ATPase levels between acclimated freshwater and anadromous inconnu carried over following their transfer to 25‰, resulting in a significant population effect also at this stage (GLMs \( P<0.0001 \)). Although their absolute ATPase levels differed at the post-transfer stage, acclimated inconnu from both populations showed a similar pattern of increased Na\(^+\)-K\(^+\) ATPase activity in the first 12–24 h (GLMs time \( P<0.0001 \)). Levels then remained higher than non-acclimated individuals through to 8 days (GLMs, treatment \( P<0.0001 \); Fig. 3). Non-acclimated survivors also increased Na\(^+\)-K\(^+\) ATPase activity above pre-treatment levels by day 8 (Kruskal–Wallis ANOVA on ranks with post-hoc Dunnett’s test, \( P<0.05 \)), although they remained lower than in acclimated fish (Fig. 3).

**DISCUSSION**

Juvenile inconnu of freshwater and anadromous origin responded similarly to an acute transfer from freshwater into various salinities. At the age of 1 year (c. 3 g), both populations could survive a direct transfer to brackish water of 10–15‰, but not to higher strength (25‰) sea water, for up to 8 days. The steady increase in plasma ions, abnormal feeding behaviour, and rapid death of fish transferred to 25‰ indicated that at this age, neither population was capable of osmoregulating at this salinity, and all fish probably died of osmoregulatory collapse.
Differences in adaptability to higher strength sea water, however, were manifested at age 1.5 years following acclimation to brackish water. During the 2 week acclimation, anadromous inconnu maintained plasma ion concentrations near pre-treatment levels, something freshwater inconnu were unable to do. Although fish of both forms reached similar ion concentrations following transfer to 25‰, all anadromous fish survived whereas several freshwater individuals showed signs of stress in the form of abnormal swimming behaviour or increased pigmentation and died following transfer. Thus, under more realistic conditions of brackish-water acclimation, anadromous inconnu withstood higher strength salt water better than their freshwater counterparts. Because both forms were equally capable of regulating ions following transfer to higher strength sea water, mortality in the freshwater form may have been due to their inability to control water loss (Hoar, 1976; Handeland et al., 1998).

Although freshwater inconnu had diminished hypo-osmoregulatory capabilities following acclimation, they increased gill Na⁺-K⁺ ATPase activity in response to both the acclimation conditions and to the subsequent transfer to 25‰. Anadromous inconnu showed only the latter increase, and therefore, had lower levels of post-transfer activity compared with the freshwater group. The higher levels of ATPase activity in the freshwater form were probably a response to a greater transport demand due to higher blood ion levels. Perhaps freshwater inconnu are not as well equipped to excrete ions through other mechanisms (e.g. gill structure, Evans, 1984; gut or kidney function, Hoar, 1976) and must compensate by increasing gill Na⁺K⁺-ATPase activity at a lower salinity.

In addition to life history or population differences, a variety of other factors, including fish size, photoperiod and pre-acclimation may influence the ability of fish to tolerate and or adapt to sea water. For example, older, larger inconnu used in the later step transfer experiments (1.5 years, c. 4 g) were better able to tolerate a direct transfer to 25‰ sea water than the smaller, younger fish from the first experiment, resulting in stabilized plasma ion concentrations and lower mortality among non-acclimated individuals from the later experiment. It is likely that the larger size of fish used in the later experiment, compared to those used earlier, contributed to their improved survival (Conte & Wagner, 1965; McCormick & Naiman, 1984; McCormick & Saunders, 1987; Hoar, 1988).

Seasonal changes in photoperiod, particularly increasing day length associated with spring, are known to increase salinity tolerance by inducing preparatory physiological changes in species, such as Arctic charr, that spend their summers at sea (Finstad et al., 1989; Arnesen et al., 1992), and in Pacific and Atlantic salmon that undergo parr-smolt transformation in spring (Wagner, 1974; McCormick et al., 1987; Berge et al., 1995). Such changes, e.g. elevated cortisol levels, increased chloride cell density, and accompanying gill activity, lead to improved hypo-osmoregulatory capabilities (Langdon & Thorpe, 1985; McCormick & Saunders, 1987; McCormick, 1995). It is possible that the longer photoperiod used in the later step transfer experiment also contributed to improved salinity tolerance. The 24 h light to which these fish were gradually adjusted is comparable to what wild inconnu would experience across their range during spring and summer, when they move into coastal areas to feed. The experimental design, however, did not allow the relative influences of size and photoperiod on the development of salinity tolerance in inconnu to be separated.
Nevertheless, the step transfer experiment clearly demonstrated that pre-acclimation to brackish water greatly improves the hypo-osmoregulatory abilities of both freshwater and anadromous inconnu. Increases in plasma ion concentrations and mortality were both lower in acclimated than non-acclimated individuals. This improved hypo-osmoregulatory ability was associated, in acclimated fish, with initially elevated Na\(^+\)-K\(^+\) ATPase activity, which increased steadily over time following transfer to 25‰ sea water. Increased enzyme activity was eventually seen in surviving non-acclimated fish, but not until 8 days post-transfer. This time lag probably explains the poor salinity tolerance of non-acclimated individuals, since an increase in gill Na\(^+\)-K\(^+\) ATPase activity is considered essential for euryhaline fishes to maintain normal electrolyte and water balance in sea water (McCormick et al., 1987).

There is some controversy surrounding the types and sequence of cues that may induce increases in Na\(^+\)-K\(^+\) ATPase activity. One-time ocean migrants, such as Pacific and Atlantic salmon, pre-adapt to a saltwater existence while still in freshwater (Wagner, 1974; McCormick et al., 1987; Berge et al., 1995) but McCormick (1994) and McCormick & Saunders (1987) suggested that fishes that migrate annually between salt water and freshwater (e.g. Arctic charr and whitefish species) rely primarily on salinity for the induction of appropriate physiological changes. The present results, and those of Schmitz (1995), support this hypothesis, but Arnesen et al. (1992) and Eliassen et al. (1998) found that anadromous Arctic charr underwent seasonal increases in chloride cell numbers and gill Na\(^+\)-K\(^+\) ATPase activity even when held in freshwater only; however, exposure to sea water could induce further increases in enzyme activity. Although both of the sea water exposures of the two present experiments are plausible in nature, inconnu are more likely to encounter full strength sea water following exposure to brackish water, rather than going directly into full strength sea water. If so, then salinity change may be sufficiently reliable as a trigger for the induction of hypo-osmoregulatory mechanisms.

The present study demonstrates that inconnu, like other salmonids, undergo physiological changes in response to salinity by increasing gill Na\(^+\)-K\(^+\) ATPase activity, and perhaps chloride cell densities, since the two are known to be correlated (Langdon & Thorpe, 1985; Eliasson et al., 1998). Although both anadromous and freshwater inconnu possess the ability to hypo-osmoregulate, the former appear better adapted to a euryhaline lifestyle than the latter. Selective pressure probably maintains salinity tolerance in anadromous populations. Anadromous fishes that are less able to switch between marine and freshwater environments are probably less successful than those capable of migrating periodically into the more productive marine habitat. Although freshwater inconnu in the Slave River are probably derived from anadromous populations that initially became established in the lower Mackenzie (Lindsey & McPhail, 1986), selective pressure for salinity tolerance in freshwater inconnu is now reduced, resulting in a diminution of this characteristic. Indeed, the varied findings of other comparative studies may be explained, in part, by differences in the length of time various freshwater populations have been separated from their founding anadromous populations. Alternatively, there may be a strong genetic linkage between saltwater adaptability and the behavioural component of migration, which is retained in some freshwater populations, but not others (Schmitz, 1995).
Based on their salinity tolerance under experimental conditions, anadromous inconnu may be able to use more coastal habitat and venture farther from shore and the Mackenzie estuary than past surveys indicate. This is consistent with otolith microchemistry that indicates inconnu occupy saline coastal waters by the age of 1 year (Howland, 1997). Given the large body of literature demonstrating size-dependent salinity tolerance in other salmonid species, it is reasonable to expect that larger inconnu may tolerate even higher salinities than those examined in the current study.

For their invaluable help with the field collection and rearing of the inconnu used in our experiments we thank N. Berg, D. Chiperzak, M. Gendron, A. Little, J. Loaiza, F. MacDonald, G. Niditchie, E. Pilarski, K. Reid, P. Taylor, B. Wakeford and K. Wescott. We thank D. Kieller for help in the laboratory and S. McCormick for providing detailed advice about the sodium-potassium microassay. This research was supported by funds from the DIAND Northern Studies Training Program (KLH), NSERC (GG and WMT), and an Izaak Walton Killam Memorial Scholarship research allowance (KLH). KLH was supported by an ACUNS Northern Studies Trust Fund Scholarship, Jennifer Robinson Memorial Scholarship, NSERC PGSB Scholarship, Province of Alberta Graduate Fellowships, and Walter H. Johns Graduate Fellowships. Logistical support for the field collection was provided by DFO (Winnipeg, Hay River, and Inuvik), Polar Continental Shelf Project, the Inuvik Science Institute of the Northwest Territories, and NWT Department of Renewable Resources (Fort Smith).

References


