



## Comparison of life history traits between anadromous and lacustrine stocks of broad whitefish (*Coregonus nasus*): An intra-specific test of Roff's hypothesis

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with 4 figures and 1 table

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**Abstract:** ROFF (1992) hypothesized that more migratory fishes would have later maturity, higher fecundity and faster growth than less migratory forms. We compared the demographic structure of anadromous and lacustrine populations of broad whitefish (*Coregonus nasus*) to determine if vital rates would conform to expectation. Size-at-age (otolith annulus measurements), reproductive effort (fecundity and egg size), and observed age-at-maturity were compared between two anadromous populations, the Peel River and Arctic Red River, and a lacustrine population in Travaillant Lake. Populations were minimally exploited and selected from the same latitude to avoid extraneous effects. Fish from the anadromous populations were not the same size-at-age until age 15 and beyond. Fish from Travaillant Lake were larger than the fish from the Peel River at all ages, but similar to those from Arctic Red River from age two to nine years. The anadromous populations were not significantly different in estimates of fecundity, but both were significantly more fecund than fish from Travaillant Lake. Observed age-at-maturity for fish in the Peel and Arctic Red Rivers were age 7 and 6 years, respectively, compared to 6 years for Travaillant Lake. We conclude that for broad whitefish, ROFF's predictions may only be applicable to the reproductive trait of fecundity. Unlike other anadromous species, freshwater existence was not associated with younger age-at-maturity or lower growth rate. We provide some explanations why the characteristics we observed did not correspond to Roff's predictions.

**Keywords:** broad whitefish, *Coregonus nasus*, Mackenzie Valley, Peel River, Arctic Red River, Travaillant Lake, anadromous, life history, growth, fecundity, age-at-maturity.

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### Introduction

Life history traits such as size-at-age, age-at-maturity, and reproductive effort are shaped by natural selection and often involve phenotypic, genetic, and behavioural trade-offs (STEARNS 1992). Variations in these characteristics occur widely both among and within species (ROFF

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1992). One such variation in these traits is the degree of migration undertaken prior to reproduction. In fishes, sympatric populations of several Arctic species with both anadromous (highly migratory) and lacustrine or potamodromous (non- or lesser migratory) counterparts have been documented (TALLMAN & REIST 1997, LOEWEN et al. 2009). Anadromous fish migrate between the sea and freshwater at some point in their lives, while lacustrine and potamodromous fish spend their entire life cycle within or near a particular lake and in some cases, associated tributaries (REIST & CHANG-KUE 1997, TALLMAN et al. 2002). These alternative migratory forms can have dramatically different life histories (MAZZONI & IGLESIAS-RIOS 2007, WHITING et al. 2008). For example, TALLMAN et al. (1996) noted that migratory populations of Arctic charr lived longer, matured later, had higher fecundity, and were larger at age than their non-migratory counterparts. Similarly, SNYDER & DINGLE (1989) found delayed reproduction, larger size, and higher fecundity in laboratory experiments of migratory three-spine sticklebacks relative to resident (non-migratory) counterparts. These observations are consistent with the hypothesis of ROFF (1992): among similar genotypes, taxa that are more migratory will grow faster, delay maturity, and increase fecundity compared to those that are less migratory.

Migratory populations must sustain a large physiological cost of migration relative to their non-migratory counterparts (ROFF 1992). However, larger fish expend less energy per unit mass relative to smaller fish to travel the same distance and therefore suffer less relative tissue depletion (GLEBE & LEGGETT 1981, ROFF 1992). Consequently, the energetic cost of migration is inversely proportional to body size and a larger size is expected in migrants, relative to non-migrants (ROFF 1988). Obtaining a larger size to minimize the cost of migration, as well as the energetic cost of migration itself, leads to direct or indirect energetic trade-offs in other life history traits (ROFF 1991). Life history theory suggests that highly migratory individuals should direct more energy into somatic growth by delaying sexual maturation (ROFF 1992). Further, since length is positively correlated with fecundity in fish (HOCUTT & STAUFFER 1980, WOOTON 1990), it is expected that a highly migratory form will be more fecund than a less migratory counterpart (ROFF 1988).

Various studies suggest the existence of highly migratory anadromous forms and less migratory, mainly lake-dwelling potamodromous (hereafter referred to as "lacustrine"), forms of broad whitefish in the lower Mackenzie River system, Northwest Territories, Canada. The broad whitefish in the Peel River, Arctic Red River, and Mackenzie River have been clearly shown to have an anadromous life history, migrating between spawning areas in the upper reaches of these tributaries and feeding areas in the Mackenzie estuary and along the Beaufort Sea coast (STEIN et al. 1973, REIST & BOND 1988, CHANG-KUE & JESSOP 1997, VANGERWEN-TOYNE et al. 2002, THOMPSON & MILLAR 2007). In contrast, several lines of evidence including physical features, traditional knowledge, and empirical evidence suggest that the broad whitefish population in Travaillant Lake is less migratory and more lacustrine in nature (TALLMAN & REIST 1997, REIST 1997, CHUDOBIAK 1995, TALLMAN et al. 2002, DRYDEN et al. 1973, CRAIG 1989, HARRIS & HOWLAND 2005, STRANGE & MACDONELL 1985, VANGERWEN-TOYNE 2002, HATFIELD et al. 1972, MILLAR 2005).

There is further evidence that provides support for the existence of alternative migratory strategies among broad whitefish populations in the lower Mackenzie River system, including, morphology, genetics and otolith microchemistry. Traditional and local knowledge of subsistence harvesters in the Gwich'in Settlement Area identify two forms of broad whitefish

that differ morphologically: a lake form found only in Travaillant Lake which is relatively smaller and darker in color and a river form which is relatively larger and lighter in color (FREEMAN 1997, GWICH'IN RENEWABLE RESOURCE BOARD 1997). TALLMAN et al. (2002) identified morphological differences between broad whitefish caught in Travaillant Lake and those from the anadromous population spawning in the Arctic Red River. Genetic evidence and otolith strontium levels suggest differences between the Travaillant stock and stocks from the Peel, Arctic Red and Mackenzie Rivers (BABALUK & REIST 1996, REIST 1997).

In this study, we set out to compare life history traits between one non-migratory lacustrine and two migratory anadromous populations of broad whitefish to test if Roff's hypothesis would hold for an Arctic species. We predicted that the anadromous broad whitefish by virtue of their extensive migrations would have higher growth rate, delayed maturity and greater fecundity than the lacustrine form. The two anadromous populations share a common long-distance migratory pattern, and were therefore expected to have similar life history traits.

## Methods and materials

### Study area

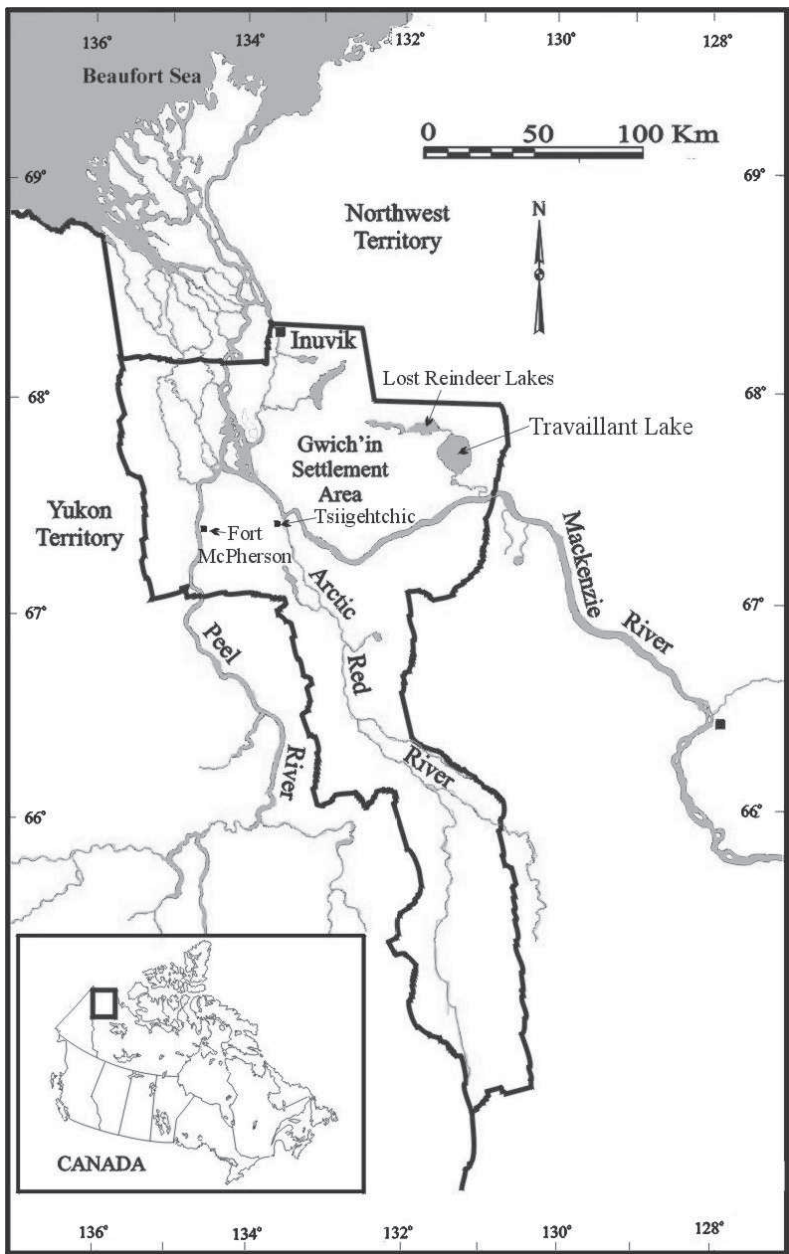
We estimated length-at-age, observed age-at-maturity, and reproductive investment of anadromous broad whitefish populations in the Peel River and Arctic Red River, and lacustrine broad whitefish from Travaillant Lake. The Peel River and Arctic Red River are large tributaries of the Mackenzie River in the lower Mackenzie Delta (Fig. 1). The Peel River enters the Mackenzie River downstream of the town of Fort McPherson, while the Arctic Red River joins the Mackenzie River at the town of Tsiigehtchic. The Peel River and Arctic Red River have total lengths of 440 km and 357 km respectively, with total drainage areas of 110,149 km<sup>2</sup> and 31,707 km<sup>2</sup>, respectively (HATFIELD et al. 1972, DRYDEN et al. 1973). Both rivers contain coarse and fine gravel substrate upstream, which provides ideal spawning habitat for broad whitefish (HATFIELD et al. 1972, DRYDEN et al. 1973).

Travaillant Lake occurs within the Travaillant River system; which originates at the Lost Reindeer Lakes and empties into the Mackenzie River (Fig. 1). The river has a length of 126 km and a total drainage area of 308 km<sup>2</sup> (DRYDEN et al. 1973). The substrate is coarse and fine gravel with a low silt load; good spawning habitat for broad whitefish (HATFIELD et al. 1972, DRYDEN et al. 1973). The depth of this river ranges from 0.1 m to 5.0 m (HATFIELD et al. 1972, CHUDOBIAK 1995).

Travaillant Lake is approximately 40 km north of the Mackenzie-Travaillant River confluence (Fig. 1). It has an area of 115 km<sup>2</sup> (HESSLEIN et al. 1991) that contains both deep and shallow sections suitable for broad whitefish rearing and feeding (CRAIG 1989). The west shore contains a littoral zone, but the east shore is made up of gravel shoals in deep water. Broad whitefish spawning has been documented on both the eastern shoal and in the sandy southern region (CHUDOBIAK 1995).

### Data collection

Broad whitefish were collected from the Peel River in the fall of 1998 and 1999 as part of the Peel River fish-monitoring program. This program was co-managed between the Gwich'in Renewable Resource Board (GRRB), Fisheries and Oceans Canada (DFO), and the Tetlit Renewable Resource Council (RRC). Broad whitefish from the Arctic Red River and Travaillant Lake were collected in the summer and fall of 1993, as part of a study by DFO (CHUDOBIAK 1995). However, for this paper, the data from the Arctic Red River and Travaillant Lake were restricted to September through mid-November, to maintain consistency with the data for broad whitefish from the Peel River.



**Fig. 1.** Map of the lower Mackenzie Delta, NWT, Canada, illustrating the Peel River, Arctic Red River and Travillant Lake.

In all studies, fish were caught with 12.7 cm (5 inch) stretched-mesh gillnets, as well as experimental gillnets with panels of 3.8 cm (1.5 inch) to 10.1 cm (4 inch) stretched-mesh size. Gillnets were set perpendicular to shore in eddies and left in the water continuously (24-hour set on average), except during ice freeze-up. After ice freeze-up, the nets were set under the ice. All fish were processed by measuring fork length (mm), round weight (kg), sex, maturity stage, gonad weight (g) and the collection of sagittal otoliths. Female gonads from broad whitefish were also collected and frozen.

The sex of individual broad whitefish was assigned based on the presence or absence of eggs. This method works even for spent females as residual eggs are retained after spawning. Qualitative assessments of maturity for fish travelling upstream were assigned based on definitions by BOND & ERICKSON (1985). All fish were aged using two sagittal otoliths via the 'break and burn' procedure of CHILTON & BEAMISH (1982). A sub-sample of 200 sagittal otoliths from the Arctic Red River and Travaillant Lake (CHUDOBIAK 1995) were re-aged to ensure consistency in age estimates between studies.

The gonads of female fish were collected and frozen in the field. Once in the lab, they were thawed in 10% formalin for two days. The gonads were then rinsed under tap water and the eggs manually separated from the connective tissue. Eggs were dried until the total egg weight was consistent ( $\pm 5$  g). Sub-samples of eggs were counted and weighed to the nearest 0.001 g. Fecundity was calculated as the average weight of the sub-sample / weight of all eggs \* size of sub-sample.

To avoid potential errors associated with traditional back-calculation methods, we opted to analyze otolith radius as a proxy of fish size (HARE & COWEN 1995). To do so, a digital image of a broken and burnt otolith was taken using a Kodak® DC120 Zoom Digital camera, attached with a Kodak® MDS120 Universal Adapter to a Zeiss® dissecting microscope at a magnification of 50X. Scion Image® was used to measure the distance from the otolith nucleus to each annulus along a 45° angle of the slow-growing portion of the otolith. Scion Image® was calibrated to 0.001 mm with a micrometer slide. In the size-at-age analyses, 'size' refers to the distance from the otolith nucleus to each annulus and 'age' refers to the number of annuli from the otolith nucleus.

## Statistical analysis

It was difficult to estimate the exact center of the otolith nucleus. Therefore, the distance from the nucleus to the first annulus was variable and could not be used as a landmark for measurements. As an alternative, we measured all annuli relative to first annulus.

To ensure that otolith growth was proportional to fish growth, we regressed otolith size onto fork length for each population and calculated the Pearson Correlation Coefficient ( $r$ ). To ensure that the relationship between otolith size and fish fork length was equal in all populations, we tested equality of slopes (SNEDECOR & COCHRAN 1980). Within each population, we compared the growth of male and female fish by testing for differences in mean size via two tailed  $t$ -tests. Finally, to compare growth between populations, we tested for differences in size-at-age via analysis of variance (ANOVA) and the *post hoc* Bonferroni test ( $\alpha = 0.05$ ). Broad whitefish size-at-age was tested independently for ages 2–17 years.

Anadromous broad whitefish use the Peel River and Arctic Red River solely for spawning. As a result, immature anadromous fish were not captured in our study. To ensure consistency, we removed the known juvenile individuals from Travaillant Lake in our analysis and then calculated minimum age-at-maturity as the youngest age of mature individuals captured. To provide an average age-at-maturity and reduce the chance of a single early maturing individual from skewing the result, we omitted the youngest 5% of individuals observed in the population.

For fecundity and egg size estimates, we sampled from fish during the estimated spawning time only to ensure we were considering female reproductive traits from the current season. We estimated fecundity using a modification of the method described by CHUDOBIAK (1995) and TALLMAN et al. (2002). Rather than using a single sub-sample of 1000 eggs (CHUBODIAK 1995), we used the average from three sub-samples of 200 eggs. Mean sub-sample weights were then combined and divided by three to estimate the mean number of eggs per fish. To ensure the slight difference in procedure produced equivalent results, we estimated fecundity for 10 broad whitefish (whole gonads stored in preservative)

using both methods and tested for a difference in mean fecundity due to methodology via a two-tailed paired *t*-test. We tested for differences in fecundity among populations via ANCOVA.

Fecundity itself is only a true representation of yearly reproductive effort if there is no difference in the size of eggs being compared. Therefore, we calculated the ratio of gonad weight (g) to fecundity to estimate the average egg size (g/egg) for each individual. However, because there may be a correlation between egg size and fish size (HOCUTT & STAUFFER 1980), we first regressed egg size onto fork length for each population and calculated the Pearson Correlation Coefficient (*r*). We then used analysis of variance (ANOVA) to test for differences in the mean size of eggs between populations.

We chose an *a priori* set level of 80% for the test of power in the results relevant to female reproductive traits such as fecundity and egg size.

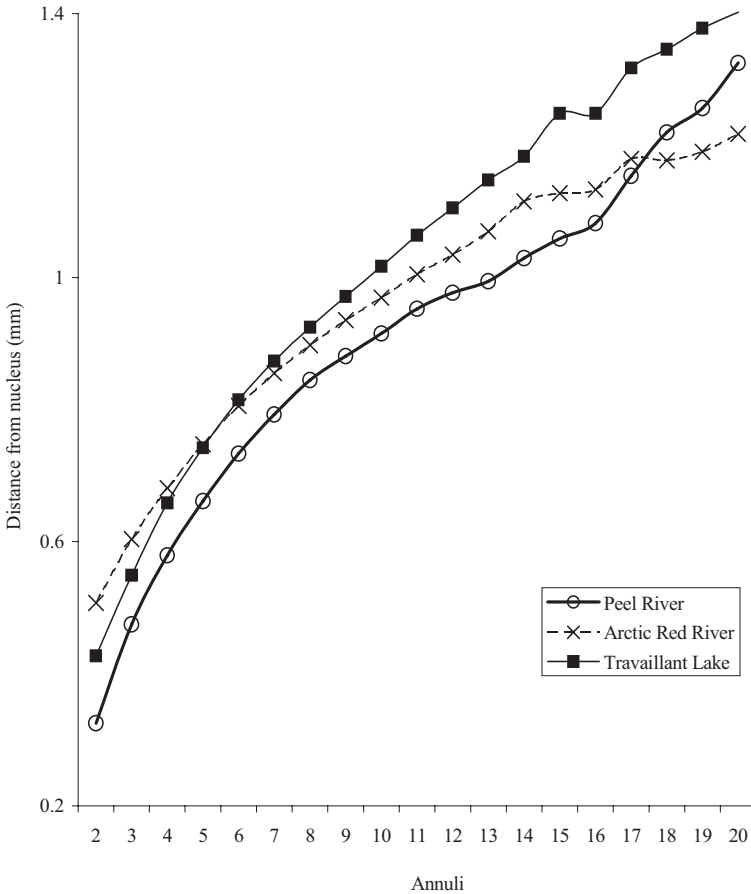
## Results

### Size-at-age

Otolith size was significantly correlated to fork length for all populations (Peel:  $r = 0.52$ ,  $P < 0.001$ ; Arctic Red:  $r = 0.544$ ,  $P < 0.001$ ; Travaillant:  $r = 0.42$ ,  $P < 0.001$ ); however, the Pearson Correlation Coefficient (*r*) values were not as high as might be expected. This is likely an artifact from limitations of the data. In this study, only mature/larger fish were sampled and thus the analyses lacked representation from the smaller size classes. Sample truncation in this manner has been shown to result in a decrease in the statistical relationship between body size and otolith size (MEEKAN et al. 1998).

Table 1

Annuli	Bonferonni test (p-value)		
	Peel – Arctic Red	Peel – Travaillant	Arctic Red – Travaillant
2	0.001*	0.001*	0.001*
3	0.001*	0.001*	0.001*
4	0.001*	0.001*	0.188
5	0.001*	0.001*	1.00
6	0.001*	0.001*	1.00
7	0.001*	0.001*	0.587
8	0.001*	0.001*	0.195
9	0.001*	0.001*	0.063
10	0.005*	0.001*	0.014*
11	0.014*	0.001*	0.003*
12	0.013*	0.001*	0.001*
13	0.007*	0.001*	0.001*
14	0.019*	0.001*	0.012*
15	0.232	0.001*	0.001*
16	0.94	0.001*	0.004*
17	1.00	0.001*	0.013*



**Fig. 2.** Mean size-at-age (distance from otolith nucleus to annuli) for broad whitefish from the Peel River (o), Arctic Red River (x), and Travaillant Lake (■). Trend lines are shown for the Peel River (thick solid line), Arctic Red River (dashed line) and Travaillant Lake (thin solid line).

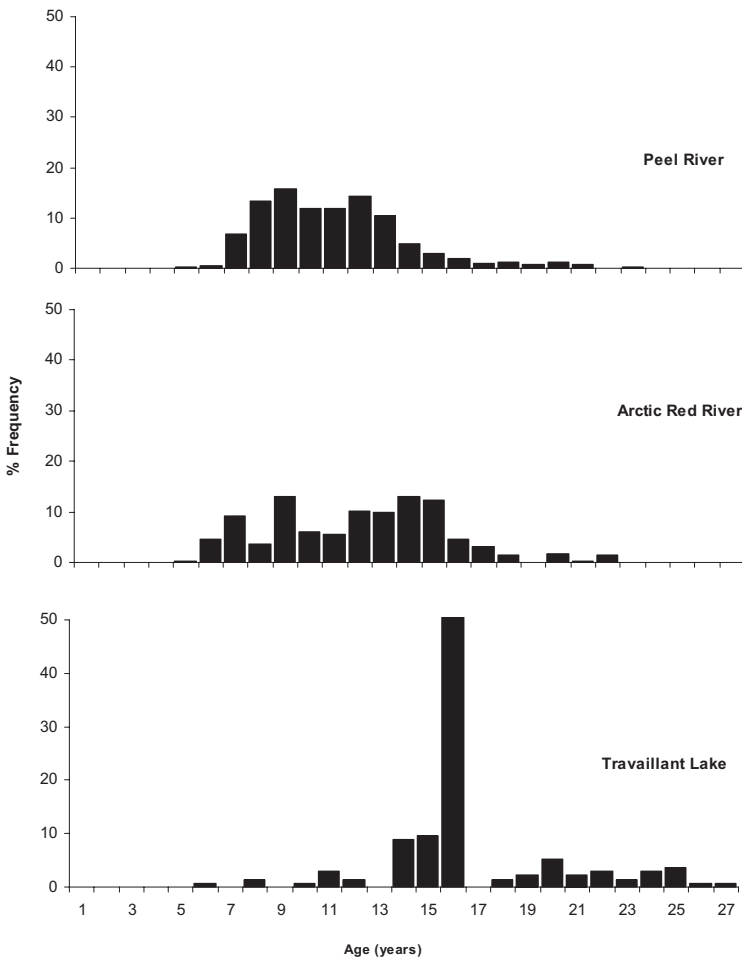
The slopes of the regressions for otolith size on fork length were not significantly different between populations (ANCOVA,  $F_{2,171} = 1.979$ ,  $P = 0.142$ ). No significant difference was found between the size of male and female fish in any population (Peel:  $t_{66} = 1.00$ ,  $P = 0.31$ , power = 95.2% for an effect size of 0.015 mm; Arctic Red:  $t_{43} = 0.89$ ,  $P = 0.37$ , power = 98.2% for an effect size of 0.015 mm; and Travaillant:  $t_{60} = 0.92$ ,  $P = 0.35$ , power = 81.2% for an effect size of 0.015 mm). Therefore, male and female data within each population were pooled.

A significant difference in size (distance from otolith nucleus) between populations was found at all ages (ANOVA, all  $P < 0.05$ ). At all ages, the sizes for fish from the Peel River were significantly smaller than those from Travaillant Lake (Table 1 and Fig. 2). Sizes for fish from the Peel River were also significantly smaller than those from Arctic Red River, but only until age 15, after which no significant difference was found. Sizes for fish from Arctic

Red River were significantly larger than those for Travaillant Lake at ages two and three, not significantly different from ages four to nine years, and then significantly smaller at age 10 and beyond.

### Age-at-maturity

All broad whitefish caught in the Peel River ( $n = 694$ ) and Arctic Red River ( $n = 286$ ) during the sampling period were sexually mature. The youngest mature fish caught in both rivers were five years (Fig. 3). The average age at sexual maturity based on the first 5% of the distribution was age seven for Peel River fish and age six for Arctic Red River fish. In the



**Fig. 3.** Age-frequency distribution for mature broad whitefish from the Peel River, Arctic Red River and Travaillant Lake.



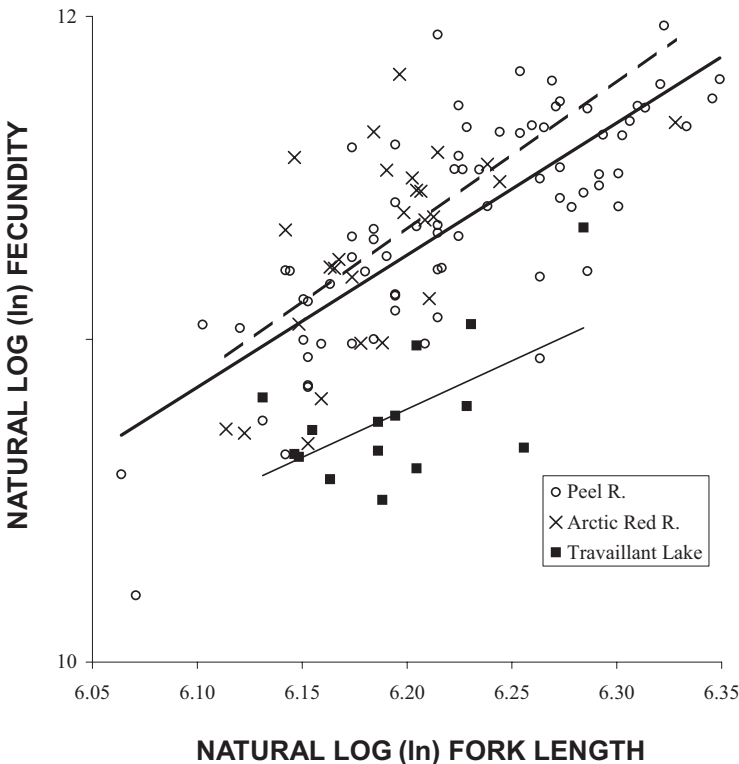
Travaillant system ( $n=134$ ), the youngest sexually mature fish and average age-at-maturity based on the first 5% of the mature distribution occurred at age six (Fig. 3), but the data for this population is sparse and not well representative of the population as a whole, making interpretation difficult.

## Fecundity

No significant difference was found in the estimates of fecundity by different sampling methodologies ( $t_9 = 2.20$ ,  $P = 0.788$ , power = 80.0% for an effect size of approximately 4000 eggs).

The size of eggs was not significantly correlated to fork length in any populations (Peel:  $r = 0.052$ ,  $P = 0.328$ ; Arctic Red:  $r = 0.004$ ,  $P = 0.495$ ; Travaillant:  $r = 0.094$ ,  $P = 0.365$ ) and no significant difference was found in the size of eggs between populations (ANOVA,  $F_{2,132} = 1.35$ ,  $P = 0.263$ , power = 80.0% with an effect size of approximately 0.0008 g).

There was however, a significant correlation between fecundity and fork length in all populations (Peel:  $r = 0.67$ ,  $P < 0.001$ , Arctic Red:  $r = 0.63$ ,  $P < 0.001$ , Travaillant:  $r = 0.46$ ,  $P = 0.03$ , Fig. 4). No significant difference in fecundity was found between broad whitefish from



**Fig. 4.** Regression of natural log (ln) fecundity on ln fork length for broad whitefish from the Peel River (o), Arctic Red River (x) and Travaillant Lake (■). Regressions are presented for broad whitefish from the Peel River (thick solid line), Arctic Red River (dashed line) and Travaillant Lake (thin solid line).

the Peel River and Arctic Red River (ANCOVA,  $F_{1,113} = 3.79$ ,  $P = 0.078$ , power = 80.0% for an effect size of approximately 4000 eggs). However, both were significantly more fecund than fish from Travaillant Lake (Peel – Travaillant: ANCOVA,  $F_{1,102} = 14.76$ ,  $P < 0.001$  and Arctic Red – Travaillant: ANCOVA,  $F_{1,40} = 44.92$ ,  $P < 0.001$ ).

## Discussion

Broad whitefish caught in Travaillant Lake appear to be different than the anadromous populations in the Peel River and Arctic Red River. While the sizes for Peel River fish were always smaller than those for Travaillant Lake, younger fish from the Arctic Red River and Travaillant Lake had similar sizes, but the trend in size-at-age diverged at later ages with fish from Travaillant Lake having a larger estimated size than the anadromous populations. Although age-at-maturity was similar among populations, the anadromous Peel River fish appeared to have a slightly older average age at maturity. Broad whitefish from Travaillant Lake had a significantly lower fecundity than both the anadromous stocks

Although our results for fecundity support Roff's predictions regarding the relationship between reproductive effort and migration, the overall results for growth (size-at-age) are the reverse of what was expected; migratory stocks were smaller at age than the more sedentary stock, especially after sexual maturity. We propose two explanations for this. 1) Broad whitefish occupy a different trophic level compared to most other salmonids that have been compared in the literature. Generally, whitefish can process food items from lower in the food web in freshwater systems (e.g., zoo-benthos) and still reach a large size compared to other salmonids, such as salmon or charrs (e.g., HUTCHINGS & MORRIS 1985, TALLMAN et al. 1996). Thus, the growth payoff of migrating to the marine environment may not be great or may even be reversed from what would be expected. On the other hand, the more varied nutrient types available in the marine environment may greatly enhance reproductive output in the anadromous form. 2) Travaillant Lake broad whitefish could be similar to the anadromous populations based on the conclusions of HESSLEIN et al. (1991) that these fish are a migrant population that incorporated  $\delta^{34}\text{S}$  from outside the Travaillant system. We, however, suggest that this is unlikely given that if these fish had extensive migrations out of Travaillant Lake, their life history traits would be expected to match those of the known anadromous populations.

In examining the growth pattern among the stocks in more detail, a number of other possible explanations may be relevant. At ages four to nine years, (presumably immature or maturing) the estimated sizes of broad whitefish from the Arctic Red River and Travaillant Lake were not significantly different. However, age three- to nine-year-old Peel River fish were significantly smaller than those from Travaillant Lake and Arctic Red River. CHANG-KUE & JESSOP (1997) proposed that broad whitefish spawning in the Peel River remain on the western side of the Mackenzie delta, while fish spawning in the Arctic Red River remain on the eastern side of the delta. If so, the results of this study may suggest that feeding areas in the western Mackenzie delta are less productive than those in the east, resulting in a smaller size-at-age in the Peel River population.

At older ages (presumably after sexual maturity), the estimated sizes of the anadromous broad whitefish in the Peel River and Arctic Red River converged and were not significantly

different and much smaller than those from Travaillant Lake. This may reflect the life history of these populations, as the mature portion of life is presumably more energetically demanding (due to gonadal development and migration). After maturity, energy must be apportioned to reproductive effort, growth and maintenance. Further, mature anadromous fish migrate long distances against the current to spawning areas (BABALUK & REIST 1996, CHANG-KUE & JESSOP 1997). The spawning migration appears to be energetically costly: during the upstream migration, the fish are initially fat with firm tissue, but are skinny with soft tissue as they return downstream (FRED KOE, local fisherman, Fort McPherson, NWT, pers. comm.). If, in the anadromous stocks, energy is heavily invested in increased fecundity plus a costly migration there may not be much additional energy for growth, resulting in a reduced rate of growth post-maturation. Therefore, the energetic demands of migration to spawning areas may dominate the expression of life history traits and result in the two anadromous populations becoming more similar at older ages.

One consideration that can be eliminated in the size-at-age analysis is the possible biases due to methodology. The analysis of size-at-age for this study was based on measurements from sagittal otoliths; therefore, effects of Lee's Phenomenon (RICKER 1969, RICKER 1975) are possible. However, instead of using a formula (based on a fitted trend line) to back-calculate fork length, the distance from the nucleus to each annulus was directly measured. By measuring otoliths individually, the natural variation in the population was included. Gear selectivity also influences effects of Lee's Phenomenon, but all studies included in the analysis for this study used the same equipment. For the two anadromous populations, all broad whitefish were caught in mesh sizes of 10.1 cm or greater, therefore any variation in size of fish is likely due to natural causes and not gear selectivity. Also, in all populations, fish age seven and beyond were used for the annulus measurements and the same estimation techniques were used. Therefore, bias introduced by Lee's Phenomenon should be approximately equal in all populations and result in minimal repercussions for these analyses.

There were no differences in the observed age-at-maturity of anadromous broad whitefish from the Peel River and Arctic Red River (ages seven and six years, respectively) and the lacustrine population in Travaillant Lake (age six years). The estimates for the anadromous broad whitefish are similar to those previously reported by others for stocks in the Mackenzie Delta (age seven to nine years) (BOND 1982; BOND & ERICKSON 1985, 1987). Further, our findings are consistent with TALLMAN *et al.* (2002) who were unable to find evidence that age-at-maturity differed between putative anadromous and resident populations of broad whitefish in the lower Mackenzie River. However, in other studies, populations that undertake longer migrations have been shown to delay sexual maturity with respect to non-migratory or lesser migratory counterparts (TALLMAN *et al.* 1996, GROSS 1987, HUTCHINGS & MORRIS 1985).

The lack of variation in age-at-maturity among stocks we studied may indicate that these stocks are selected to the point of an evolutionary constraint (ROFF 1992). That is, a minimum age must be reached before an individual can mature. The existence of a threshold minimum also implies that there is a constraint on the age-at-maturity (STEARNS 1992). If this is the case for broad whitefish in the lower Mackenzie River system, then these stocks may not differ in age-at-maturity because they are selected (constrained) to the evolutionary minimum by forces other than differences in migration. An alternative explanation, that fishing has driven age-at-maturity to a common low level, is unlikely as these stocks are all considered to be lightly exploited.

The estimated size-specific fecundities for the anadromous populations were not different from one another, yet both were more fecund than the lacustrine broad whitefish from Travaillant Lake. This finding is consistent with other studies where it has been found that populations which migrate extensively have a higher average fecundity than populations that do not migrate as far (SNYDER & DINGLE 1989, 1990; TALLMAN et al. 1996). What is intriguing is that the increased fecundity was developed neither from delaying maturity nor from greater average size-at-age. It appears to have evolved independently from adjustments to other life history traits. It would be interesting to determine if such flexibility in fecundity was also characteristic of other whitefishes.

Broad whitefish is an important species in the Mackenzie Delta because many aboriginal communities rely on these fish for consumption, local sale and cultural tradition (TREBLE 1996). However, management of this species is difficult because different life history types may exist (TALLMAN 1997) and anadromous populations traverse multiple Aboriginal Settlement Areas. Understanding the life history strategies of harvested populations such as these is important for proper management, and management strategies are likely to differ between migratory and non-migratory forms. For instance, sustainable harvest levels are influenced by the mean level of replacement in the population and highly migratory populations are typically more fecund (and may therefore have higher recruitment) than lesser migratory populations of the same species (HUTCHINGS & MORRIS 1985, GROSS 1987). However, migratory populations tend to be more vulnerable to over-fishing, both spatially and temporally. Large groups of fish travel through specific areas at specific times of year, making their location at particular times highly predictable and therefore easy to capture, such as during upstream and downstream migration (REIST & BOND 1988, REIST 1997). Further, fish undergoing extensive migrations may be more vulnerable to multiple environmental stresses (BODALY et al. 1989).

This study has provided information on the variation in growth, age-at-maturity, and reproductive investment for anadromous broad whitefish populations in the Peel River and the Arctic Red River and a lacustrine population in Travaillant Lake. This information can be used by resource managers in the Mackenzie Delta to enhance the understanding of broad whitefish population dynamics, to compare to future data to detect potential changes in the populations, and to generally aid in management decisions for these populations. While this study suggests that broad whitefish in Travaillant Lake are distinct from the anadromous populations in the lower Mackenzie River system, more research, including tagging or radio-tracking studies, would be useful to clarify the activities of these fish.

Aside from the meaning of the results for fisheries management there is another important message for ecologists: it has been assumed in energetic models that life history traits must co-evolve as a unit. The core models for fisheries assessment, such as described in RICKER (1975), assume that growth, reproduction and mortality are intertwined. However, our results suggest that growth, age-at-maturity and fecundity can be uncoupled in evolution.

We compared life history traits between known anadromous broad whitefish populations in the Peel River and Arctic Red River and lacustrine broad whitefish from Travaillant Lake to test the hypothesis that the life history traits of the two anadromous populations would be similar because they both undergo extensive migration, while those of the lacustrine population would differ due to a reduced level of migratory behavior. We predicted that anadromous populations would have older age-at-maturity, larger size at age, and higher fecundity than

the less migratory population from Travaillant Lake. Although some predictions were supported by our findings, others were not.

Many aspects of the ecology of broad whitefish need to be better understood to clarify our results. More detailed studies of the migration patterns, the energetic demands of migration and critical habitats for rearing and over-wintering among the stocks need to be undertaken. As well, an examination of the genetic relatedness of these stocks is important. We hope that fisheries ecologists will undertake such studies that may help in better explaining our findings.

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