

Migration and life history alternatives in a high latitude species, the broad whitefish, *Coregonus nasus* Pallas

Tallman, R.F., Abrahams M.V., Chudobiak D.H. Migration and life history alternatives in a high latitude species, the broad whitefish, *Coregonus nasus* Pallas.

Ecology of Freshwater Fish 2002: 11: 101–111. © Blackwell Munksgaard, 2002

Abstract – We examined the expected changes in the life history trajectory of an Arctic species, broad whitefish, in the lower Mackenzie River between an anadromous population with spawning migrations of 350–450 km and a potamodromous population with spawning migrations of 5–12 km. Based on life history theory we predicted that the anadromous population would have faster growth, later age-at-maturity, and greater reproductive investment than the potamodromous population. Early in its life the anadromous population had faster growth than the potamodromous but later growth was slower. Age-at-maturity was greater in the anadromous population than the potamodromous. Reproductive investment was higher in the anadromous population. We conclude that the broad whitefish did not conclusively follow the pattern of variation observed between migratory and relatively sedentary populations in temperate zones. Fecundity was greater in the migratory population but not conclusively linked to age-at-maturity or growth-rate differences.

**R. F. Tallman¹, M. V. Abrahams²
and D. H. Chudobiak²**

¹Department of Fisheries and Oceans, Central and Arctic Region, 501 University Crescent, Winnipeg, Manitoba, R3T 2N6, Canada, ²Department of Zoology, University of Manitoba, Winnipeg, Manitoba, R3T 2N2, Canada

Key words: Arctic; broad whitefish; Coregonid; life history; migration

Ross F. Tallman, Department of Fisheries and Oceans, Central and Arctic Region, 501 University Crescent, Winnipeg, Manitoba, R3T 2N6, Canada; Tel: +1 204 983 3362, telefax: +1 204 984 2403; e-mail: tallmanr@dfp-mpo.gc.ca

Accepted for publication November 29, 2001

Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

In environments with highly patchy resources in time and space, such as the Arctic and Antarctic, many species are migratory (Power 1997). The evolution of migration can be interpreted in terms of a balance between benefits and costs (Stearns 1992). Migration confers advantage for better spawning habitat, better feeding opportunities, and/or finding refuge from inclement conditions (Myers 1949; Northcote 1978). However, a migratory lifestyle has costs, such as energy expenditure to migrate and additional mortality, especially in juveniles (Gross 1987). Most important, the energetic cost of migration must be expended by the individual before the reward is gained. Life history traits or behaviours that reduce the cost of migration will be advantageous in a migratory species (Gross 1987).

Roff (1988, 1992) suggests that the relative energetic cost of migration decreases with increasing fish size (length). Larger conspecifics have greater swimming endurance (Weihs and Webb 1983; Videler 1993). For example, in the American shad (*Alosa sapidissima*), smaller fish suffer from a greater somatic tissue depletion and higher post-migration mortality than larger fish (Glebe and Leggett 1981). Because there is usually a direct trade-off between growth and reproductive effort, larger size at maturity must be achieved by delaying the onset of first sexual maturation (Roff 1992). All surplus energy is then channelled into growth. Even for indeterminate growers such as fish, this principle applies, as the greatest growth occurs before sexual maturity (Popov 1975). Consequently, migratory populations will delay sexual maturity by having a longer juvenile growth period and consequently be larger at first repro-

duction than non-migratory populations. As well, to offset the loss in fitness due to delaying maturity, the longer period of juvenile mortality, and the higher rate of mortality associated with migration, migratory fish should have higher age-specific fecundity (Roff 1992). In contrast, non-migratory fish do not have their reproductive success so closely tied to maximizing adult size. As a result, earlier age-at-maturity and smaller size are selected (Williams 1966; Synder and Dingle 1990; Stearns 1992). Inter and intraspecific comparisons in temperate zone species have shown that migratory fishes are characterized by larger size-at-age, delayed maturity and higher fecundity compared to non-migratory fish (between species: Hutchings and Morris 1985; Roff 1988, 1992; within species: Gresswell & Varley 1988; Taylor 1992; Blair et al. 1993; Gresswell et al. 1994).

Many Arctic species have both non-migratory and migratory populations apparently similar to those observed in temperate fish (McPhail and

Lindsey 1970). For example, anadromous, potamodromous, and riverine populations of broad whitefish, *Coregonus nasus*, and inconnu, *Stenodus leucichthys*, have been recorded in Siberia and in the Yukon and Mackenzie rivers of North America (Berg 1965; Reist and Bond 1988). However, even though many Arctic fish are characterized by 2 or more migratory ecotypes empirical evidence is lacking that their vital rates conform to the pattern above. Except for Arctic charr (Tallman et al. 1996), there have been no studies of the patterns of vital rates in migratory ecotypes of Arctic species (Fig. 1).

In the Mackenzie River system, anadromous populations of broad whitefish have been confirmed in the Arctic Red, Peel, and Mackenzie rivers (Chang-Kue and Jessop 1997; Tallman and Reist 1997). Potamodromous populations occur in various large permanent lakes separated from the Mackenzie River, such as Campbell, Travailant, and Andre lakes (Chudobiak 1995). We examine the life history characteristics of an

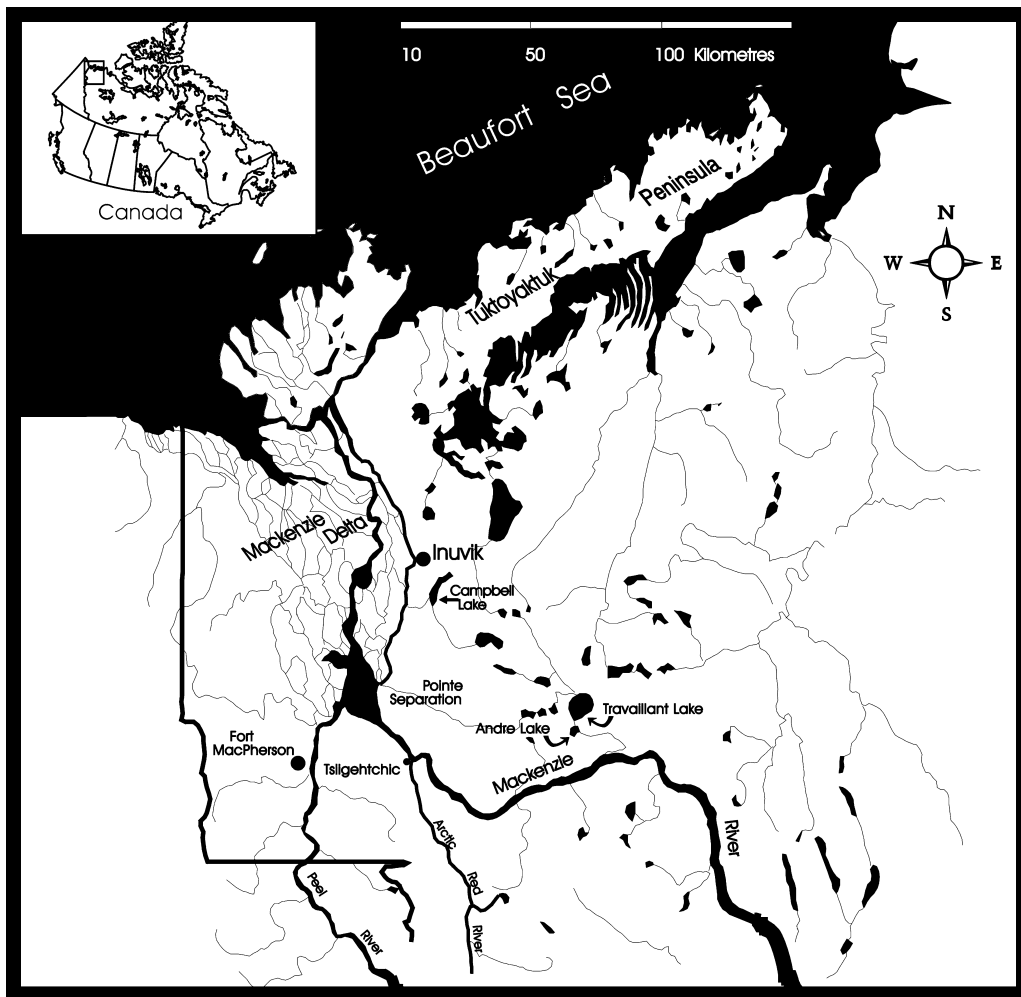


Fig. 1. The lower Mackenzie River, Arctic Red River, Travailant Lake and major communities and physical features.

anadromous population of broad whitefish from Arctic Red River and compare them to those of a potamodromous population from Travaillant Lake. We predict that the Arctic Red River population should mature later, have greater size-at-age, and higher fecundity than the Travaillant Lake population. Chudobiak et al. (2002) demonstrated that these populations are morphologically distinct from each other. According to Chudobiak (1995) the Travaillant population is able to complete spawning, rearing, and over-wintering within the Travaillant system while the anadromous population spawns in the Arctic Red River but uses the Mackenzie River delta for over-wintering and lakes on the Tuktoyaktuk Peninsula for rearing.

Materials and methods

Study Area and Populations

The Arctic Red River is a major tributary of the lower Mackenzie River (Fig. 1). It originates in the Mackenzie Mountains, where it is a clear, swiftly flowing mountain river, but becomes turbid and more convoluted as it passes through the lowlands. It enters the Mackenzie River near the town of Tsiigehtchic, where it is slow moving and turbid. Average discharge during 1992 and 1993 was $151.5 \text{ m}^3 \text{ s}^{-1}$, and surface water temperatures ranged from 0.5°C in winter to a maximum of approximately 20°C in late July (Environment Canada 1993–1994).

Broad whitefish spawn in the Arctic Red River at Weldon Creek, about 160 miles upriver from the mouth ('Gwich'in Dene traditional knowledge; Tallman, unpublished data). The minimum total distance that Arctic Red River anadromous broad whitefish migrate from their over-wintering grounds to spawning beds is 350–450 km. First-time spawners, arriving from rearing grounds on the Tuktoyaktuk Peninsula, migrate considerably farther (Chang-Kue and Jessop 1997).

Travaillant Lake is a deep, almost perfectly round lake about 10 km in diameter (Chudobiak 1995 and Fig. 1). The lake water is clear but stained with tannins from the surrounding spruce forest.

Broad whitefish from Travaillant Lake spawn in two locations, in the outlet of Travaillant Lake above Andre Lake to the south and in a major inlet to Travaillant Lake, directly to the north (Gabe Andre, Tsiigehtchic Gwich'in elder pers. comm. and Chudobiak 1995). The Travaillant Lake whitefish therefore migrate between 5 and 12 km to their spawning grounds.

Sampling

Sampling was conducted from the beginning of June up to and including the first week of December in 1993. To increase the sample size for fecundity estimates a small number of additional females were obtained from Travaillant Lake in 1996.

Floating gillnets used to sample were 25, 30 and 60 m long, 6 m deep and of five mesh-size patterns: 140 mm stretch mesh (25 m long); 102, 89 and 76 mm (three panels \times 10 m long); 63.5, 51 and 38 mm (three panels \times 10 m); 102, 89, 76, 63.5, 51 and 38 mm (6 panels \times 10 m); 114 mm (25 m). Samples were taken from the littoral zones of Travaillant and Andre lakes and from river eddies of the Arctic Red and Travaillant rivers. Sets were kept overnight and between 8 and 24 h duration. Gillnets were set perpendicular to the shoreline. When two gillnets were used, they were set in a parallel direction to each other. The second net was set one gillnet length further into the river and at least 100 m upstream relative to the first net to reduce interference between the two nets.

The following biological data and samples were collected from individual fish for determination of life history characteristics: fork length (± 1 mm), total weight (± 1 g), gonad weight (± 1 g), aging structures (scales, pectoral fin rays, and otoliths), sex and stage of maturity (Bond and Erickson 1985).

Ovaries of all mature females were preserved in 5% formalin for fecundity estimates. Ages of broad whitefish were determined from two readings of otoliths, prepared using the break-and-burn method (Chilton and Beamish 1982). An ageing comparison suggests that otoliths can be read more accurately and require the less preparation time than fin rays or scales (J. Babaluk, and R. Wastle, Freshwater Institute, pers. comm.).

To improve the data for the younger age groups we used the Biological Intercept Model method proposed by Campana (1990) to perform back-calculations on otoliths of the anadromous population. The Biological Intercept Model was suggested by Campana (1990) as a method to circumvent the effect observed where slower growing fish have proportionately larger otoliths. In this way, we were able to add 277 more samples of fork length between the ages of 1 and 7. For details and further assessment of the methodology refer to Secor and Dean (1992).

Broad whitefish may not spawn annually, and therefore, there is no simple criterion for identifying age-at-maturity. We calculated the age-at-maturity as the age at which the ratio of mature

to nonmature individuals equalled 50% (Morin et al. 1982). However, because the Arctic Red River is used for spawning only, the juveniles were poorly represented in our samples of the anadromous population. By combining data from a similar study in 1992 with the 1993 data we were able to calculate age-at-maturity.

Fecundity was determined for 18 broad whitefish from the Arctic Red River and 25 broad whitefish from Travaillant Lake. The samples were evenly distributed to cover more than 95% of the variation in adult length in each population. Eggs were separated from the ovarian connective material using Gilson's Solution followed by rinsing the ovaries under tap water and then manually removing the tissue. Cleaned eggs were placed on trays and air dried for a minimum of 2 weeks (Healey 1978). For each fish, a subsample of 1000 eggs was weighed to the nearest 0.001 g. Fecundity was calculated by dividing the total weight of the eggs by the weight of the subsample, then multiplying by 1000. Gonad weight was taken to the nearest 0.01 g.

Statistical Analysis

Size-at-age plots for both populations indicated that broad whitefish did not grow much after sexual maturity. The residual plots from a preliminary analysis of size-at-age for each population by simple linear regression indicated that a quadratic model would be more appropriate. As well, rearing experiments showed that broad whitefish were only a few (< 3 mm) millimetres at hatching. Thus, we used a quadratic model without an intercept. To determine whether the two populations differed in their growth patterns we used dummy variable regression (Neter et al. 1983) to compare the quadratic functions for each. The model was:

$$Y_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i1}^2 + \beta_3 X_i + \beta_4 x_{i1} X_i + \beta_5 x_{i1}^2 X_i^2 + \varepsilon_i$$

where X_i is the age of fish i in years, \bar{X} the arithmetic mean of X_i , $x_i = X_i - \bar{X}$; Y_i the expected fork length of fish i in mm, $X_i = 1$, if potamodromous population or 0 otherwise, $\beta_0 = 0$, β_1 the linear effect of age coefficient for the anadromous population, β_2 the quadratic effect of age coefficient for the anadromous population, $\beta_3 = 0$, β_4 the additional effect of the potamodromous population on the linear effect of age, β_5 = the additional effect of the potamodromous population on the quadratic effect of age coefficient, ε_i = the unknown true error in the regression

model. This is essentially analysis of covariance (ANCOVA) in quadratic form. We expressed the independent variable as a deviation from the mean as a way of reducing the effect of multicollinearity (Neter et al. 1983).

We used the methodology of DeMaster (1978) to obtain age-at-maturity for statistical comparisons between stocks. The average age of sexual maturity was then calculated as:

$$\bar{X} = \sum_{x=0}^w (x)P(x)$$

where x is the age, \bar{X} the average age of sexual maturity, $P(x)$ the estimated probability of first ovulating at age x , and w is the maximum age in the sample. The variance for \bar{X} is

$$v(\bar{X}) = \sum_{x=0}^w \frac{f(x)(1-f(x))}{n_x - 1} + \frac{w^2 f(w)(1-f(w))}{n(w) - 1}$$

The main assumption associated with this estimate is that all of the $f(x)$'s are independent of each other. This assumption was met because individuals were collected and not returned to the population (DeMaster 1978).

The 95% confidence interval can be approximated by

$$95\% \text{ CI} = \pm 1.96(v(\bar{X}))^{1/2}$$

where x is the age, and \bar{X} is the average age in years (Demaster 1978).

The choice to use parametric linear models to describe and compare size-at-age among populations was based on a desire to compare these groups using statistics with known probabilities of type 2 error. A problem with this approach is that it is difficult to attribute a biological significance to the quadratic-age parameter. An alternative might be to use the Von-Bertalanffy equation (see below) which has more statistical problems due to correlated parameters but is more easily understood by biologists.

The Von-Bertalanffy growth factor (VBGF) is expressed as follows:

$$L_t = L_\infty (1 - \exp(-K(t - t_0)));$$

where t is the age, L_t the length at age, L_∞ the asymptotic length, K the body growth coefficient, and t_0 is the theoretical age at which L is zero (Ricker 1975).

Standard nonlinear optimization techniques of curve fitting were used to estimate the coefficients and their associated standard error (Cerrato 1990).

The nonlinear formulation of the VBGF means that a general linear model could not be used for

ANCOVA. Instead, an analysis of the residual sum of squares (ARSS) was employed to compare VBGF among the two populations (Rao 1986, Chen et al. 1992).

Procedures for the ARSS were: (1) residual sum of squares (RSS) and associated degree of freedom (d.f.) of the VBGF were calculated for each sample (2) the resultant RSS and d.f. of each sample were added to yield summed RSS and d.f. (3) data of all samples were pooled to calculate the RSS and d.f. of a total VBGF, and (4) the *F*-statistic was calculated as:

$$F = \frac{(RSS_p - RSS_s)/(d.f._{RSS_p} - d.f._{RSS_s})}{RSS_s/d.f._{RSS_s}}$$

$$= \frac{(RSS_p - RSS_s)/3(K-1)}{RSS_s/(N - 3K)}$$

where: RSS_p , RSS of each VBGF fitted by pooled growth data; RSS_s , sum of RSS of each VBGF fitted to growth data for each sample; N , total sample size, K , number of samples in the comparison. To test whether there was a difference between the samples, the calculated *F*-value was compared with an *F*, with d.f.s of $3(K-1)$ (numerator) and $N - 3K$ (denominator).

In addition, we calculated the Von Bertalanffy parameters using weight instead of length so that we could compare the populations using Pauly's (1979 in Moreau 1987) index of growth performance. Pauly (1979) proposed the growth rate at the inflection point of the weight growth curve could be used as a standard for comparison of growth performance of different fishes. In a weight growth curve, the slope of the inflection point is given by:

$$\left(\frac{dW}{dt}\right)_{\max} = \left(\frac{4}{9}\right) \times 10^P, \quad \text{where}$$

$$P = \log_{10} K + \log_{10} W_{\infty}$$

Moreau (1987) argued that the growth curves of different fishes cannot be directly compared because the curves themselves are produced by growth rates that are constantly changing with time and size. The value of *P* is directly related to $(dW/dt)_{\max}$ and therefore can be used to compare the growth performance of fishes with different values of asymptotic size.

Simple linear regression equations relating fecundity to length and to age and gonad weight to total weight were determined using the PROC GLM procedure in SAS. For each regression, a goodness-of-fit test (R^2) was calculated. For the comparison between the populations of the relationship between gonad weight and body weight

we used the gonad weights of 'ripe' females only (Bond and Erickson 1985) so as to avoid additional effects due to seasonal changes in gonad weight. We used ANCOVA to compare the fecundity at age and fecundity at length between the populations.

Results

Growth appeared to be similar among the populations with little increase in size after age 6 (Fig. 2). The quadratic equation fitted for fork length at age for the anadromous population was: Fork length = $87.5 \times \text{age} - 3.40 \times \text{age}^2$ compared to Fork length = $70.1 \times \text{age} - 2.13 \times \text{age}^2$ for the potamodromous population. Both equations were highly significant ($P < 0.001$). The residual plots suggested that the models were appropriate.

However, ANCOVA indicated that there was a significant effect of population (anadromous or potamodromous) in the relationship between fork length and age ($P = 0.001$). The length- and weight-based VBGFs were significantly different ($P < 0.0001$, anadromous: $L_{\infty} = 521.03$, $t_0 = -0.8655$, $K = 0.26$, $N = 603$; potamodromous: $L_{\infty} = 501.36$, $t_0 = 0.220$, $K = 0.36$, $N = 149$; $W_{\infty} = 1981.02$, $t_0 = 2.010$, $K = 0.52$, $N = 393$; potamodromous: $W_{\infty} = 1939.71$, $t_0 = 1.629$, $K = 0.27$, $N = 204$) and the direction indicated the maximum size (length or weight) was greater in the anadromous population. As well the index of growth performance was greater in the anadromous population (3.01, anadromous vs. 2.72, potamodromous). We conclude that there was a difference in growth pattern between anadromous and potamodromous broad whitefish.

The higher coefficient of age of the anadromous stock suggests that it grows more rapidly in the early ages than the potamodromous stock. Conversely, the high negative coefficient with the quadratic term suggests that in the later years

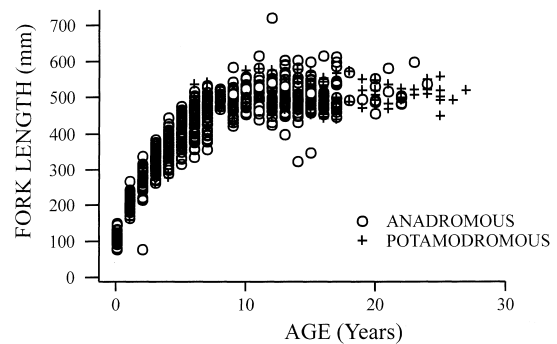


Fig. 2. Fork length (mm) plotted against age (years) for the anadromous ($N = 62$) and potamodromous ($N = 151$) population.

of life, growth slows down more rapidly in the anadromous population. Thus, the anadromous population appears to invest heavily in growth initially to attain a size that migrates efficiently. Subsequent to the onset of sexual maturity, energy attained by the anadromous type is heavily invested in reproduction at the expense of growth.

The length-based VBGFs are interesting because the estimated maximum size, L_{∞} , shows the anadromous population being about 4% larger than the potamodromous. The lower t_0 of the anadromous population along with the higher L_{∞} suggests that the growth is more rapid than in the potamodromous (Moreau 1987). Although the lines would not be considered significantly different the parameter values are consistent with the results from the analysis using linear models.

The index of growth performance shows that the anadromous stock was much higher than the potamodromous, especially considering that it is on a log scale. Broad whitefish fall in the same range as average-sized commercial marine species (Pauly 1979). The difference in P among these two populations is as great as the maximum observed within species (described by Pauly 1979).

Age-at-first-maturity for the anadromous population was 5.67 years while the age-at-maturity for potamodromous population was 5.00 years using Morin et al.'s (1982) method. Using DeMaster's (1978) method the 95% CIs were 5.74–5.75 for the anadromous and 5.02–5.98 for the potamodromous population. These values overlap and, given the low representation of juveniles at the anadromous stock site, are probably close to equal. However, the difference in the means was in the direction predicted.

The youngest mature broad whitefish previously reported ranged from age 7–10 years (Kogl 1972; DeGraaf and Machniak 1977; Bond 1982; Bond and Erickson 1985, 1993; Reist and Bond 1988). All of the above estimates are reports of the minimum age observed rather than the estimated age when 50% of the population becomes mature. Our estimates of age-at-maturity for the anadromous population are considerably lower than those reported for coastal surveys of broad whitefish. To some extent this may be explained in that our result is biased downward because early maturing fish will migrate from the coast to the spawning ground while juveniles (immature fish) in the same age group generally will not. This would mean that within the transitional age groups adults would be disproportionately represented in Arctic Red River collections. In any case there is no indication from the literature that is contrary to our finding that the ana-

dromous population has a higher age-at-maturity than the potamodromous.

Using the age-at-maturity estimate and the quadratic growth functions for each population we obtained values of 387 and 297 mm length-at-first-maturation for the anadromous and potamodromous stocks, respectively. Thus, the size-at-first maturity appears to be about 30% greater in the anadromous population.

Of 399 adult fish sampled during the months of June to September from the Arctic Red River and Mackenzie River downstream, 31 (8%) were 'resting' meaning they were not going to spawn in that year. Only 25 of 273 fish (9%) sampled from Travaillant, Andre and Campbell Lake populations were resting. The high incidence of repeat year spawning (over 90%) could be due to a low probability of post-spawning mortality. Several lines of evidence suggest that post-spawning mortality is relatively low. Chang-Kue and Jessop (1997) using radio-telemetry found that all broad whitefish that migrated to the spawning grounds remained mobile well after the expected date of spawning, generally completing a migration back to the over-wintering grounds. Treble and Tallman (1997) estimated the instantaneous mortality rate, Z , as 0.32 or an annual mortality from fishing and natural causes of 27% in the broad whitefish exploratory fishery. Their estimates of fishing mortality varied from about 8–20% and thus natural mortality from spawning, over-wintering, predation, parasites, disease and other factors would be 7–19% per year. Simulations by Thera (1998) also suggest that post-spawning mortality would be between 5 and 10%. Finally, the number of age groups in each population with fish 20–30 years of age not uncommon suggests that natural mortality factors are probably low. Thus, broad whitefish appear to spawn quite regularly and population and fecundity estimates comparisons can be made without adjustment for differences in spawning frequency.

Fecundity varied from 13 823 to 51 333 in the potamodromous stock and 18 375–69 007 in the anadromous stock. In each population fecundity apparently declined with age (Fig. 3). However, the simple linear regression of fecundity on age was not significant in either case (anadromous: $P = 0.08$, $R^2 = 0.18$; potamodromous: $P = 0.97$, $R^2 < 0.01$). Fecundity increased with fork length in the anadromous population ($P = 0.0001$, $R^2 = 0.58$) but not in the potamodromous population ($P = 0.102$, $R^2 = 0.11$) although there was some appearance of a trend (Fig. 4). The equations were: Fecundity (number of eggs) = $-297\,985 + 710$ Length (mm) for the anadromous population; Fecundity (number of eggs) = $-19\,843 + 98.7$

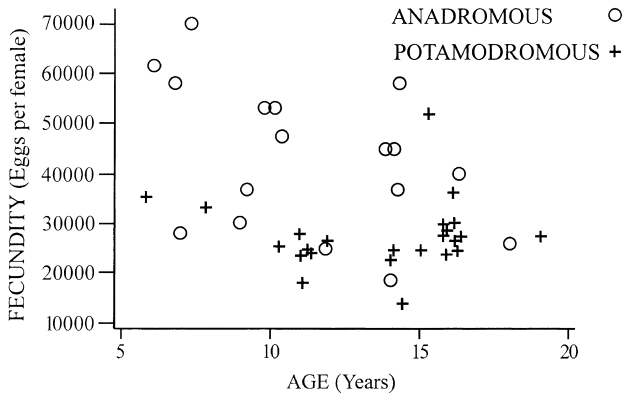


Fig. 3. Comparison of fecundity (eggs/female) at age (years) among the anadromous and potamodromous population.

Length (mm) for the potamodromous population

Residual plots indicated that the models were appropriate.

The anadromous stock showed higher fecundity at age and by length than the potamodromous population (Figs 3 and 4) (ANCOVA, $P < 0.001$ in both cases). When age and length effects were considered simultaneously the effect of population ($P < 0.001$) and length ($P = 0.02$) were significant but age was not ($P = 0.42$).

The fecundity observed for the anadromous stock (mean = 45 027 eggs, SD = 14 803) has a similar range to other published values. DeGraaf and Machniak (1977) recorded fecundity estimates ranging from 26 922 to 65 798 eggs per female with a mean of 39 721 eggs per female for lower Mackenzie River stocks. Prasalov (1989) recorded a range of about 26 000–81 000 eggs per female for anadromous stocks in the Ob River, Siberia. Thera (1998), using Prasalov's data, found a significant relationship between distance migrated and fecundity in anadromous broad whitefish. Thera's (1998) function predicted

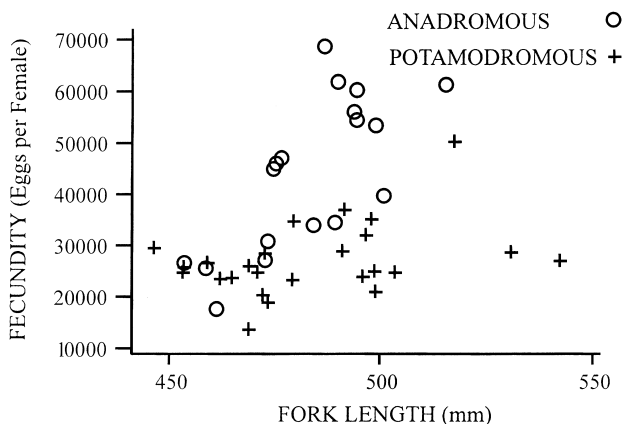


Fig. 4. Comparison of fecundity (eggs/female) at fork length (mm) among the anadromous and potamodromous population.

Variation in broad whitefish vital rates

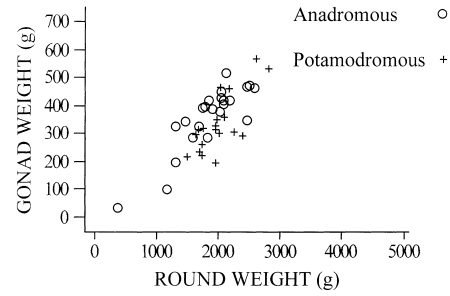


Fig. 5. Comparison of gonad weight (g) against round weight (g) between anadromous and potamodromous population.

that the mean fecundity of an anadromous stock migrating the same distance as the one sampled here should be 44 447 eggs per female.

Gonad weight was positively correlated with round weight in both populations (Fig. 5). The best fit equation for the relationship in the anadromous population was:

$$\text{gonad weight} = -4.1 + 0.198 \times \text{round weight}$$

The equation was highly significant and explained 75% of the variation in the data ($P < 0.001$; $R^2 = 0.75$). For the potamodromous population the best fit equation was:

$$\text{gonad weight} = -64 + 0.199 \times \text{round weight}$$

The equation was also highly significant but only explained about 50% of the variation in the data ($P = 0.001$; $R^2 = 0.48$). ANCOVA with round weight as covariate showed that the anadromous had a higher reproductive investment per body weight than the potamodromous ($P = 0.008$).

The age structure of the two populations differed in that the potamodromous population was dominated by age 16 individuals (Fig. 6). Overall,

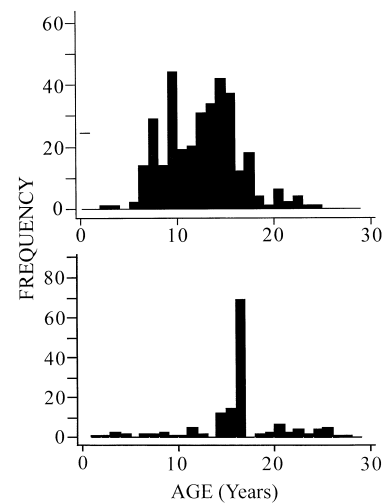


Fig. 6. Age frequency of anadromous (Arctic Red River) (upper panel) and potamodromous (Travaillant Lake) (lower panel) populations.

the potamodromous population had more juveniles in evidence but the maximum age was similar.

Anadromous broad whitefish had significantly higher fecundity and they invested a greater amount of energy into the gonad, as we predicted. As well, anadromous broad whitefish had a different growth pattern than potamodromous broad whitefish and the parameter values were in a direction expected from life history theory (see below). Although by standard measures the age at 50% maturity was greater in the anadromous population, we were unable to demonstrate conclusively that anadromous broad whitefish mature significantly later than the potamodromous broad whitefish. The longevity appeared to be similar between the populations.

Discussion

Life history theory predicts that migratory fishes should delay reproduction, be larger at first reproduction, and have higher fecundities than non-migrants (Roff 1988, 1992; Synder and Dingle 1990). We tested this hypothesis by comparing vital rates of anadromous and potamodromous broad whitefish from the lower Mackenzie River drainage. Fecundity of anadromous whitefish was substantially higher than in the potamodromous. There was a different pattern of growth between the anadromous and potamodromous populations that followed predictions from theory. As well, age-at-maturity pattern was in the expected direction. The lack of statistically conclusive differences in the age-at-maturity may reflect a considerable amount of stabilizing selection acting on the phenotypes of conspecifics. Divergence in life history traits is probably somewhat constrained within a 'broad whitefish universe' which would not allow unlimited divergence in fitness-related traits. In addition, separation has probably been relatively recent in geological terms since the entire area was under ice less than 10 000 years ago (Pielou 1992, Powell 1994).

Life history comparisons of anadromous and potamodromous fish have demonstrated a larger size at age of maturity, delayed maturity, and a higher fecundity in the migratory group (Gross 1987). The relationships of age and size at maturity and migration are clear even at an intuitive level – larger fish can migrate greater distances more efficiently. However, the connection between migration and increased fecundity is not as clear. It is well known in fish that absolute fecundity is positively correlated with fish length (Wootton 1990). If in this case, interpopulation differences in fecundity were a function only of

length, then one might expect that in comparing fish of the same size the anadromous population might have lower fecundity due to migration's energetic demands. Clearly, this is not the case; anadromous fish produced more eggs from gonads that were a greater proportion of the body weight suggesting that increased fecundity was selected for in the anadromous population, independent of size. In turn the large energy investment into reproduction could be responsible for the greater reduction in growth in later life in the anadromous population. The increased reproductive effort does not appear to substantially decrease lifespan although the maximum age of anadromous fish was lower than that of the potamodromous population.

Initially, we proposed that the energetic costs of adult migration would drive the life history to include later maturity and, cascading from this change, greater age-specific growth and fecundity. While the pattern of differences bears this out, differences in age-at-maturity and growth are not statistically significant. In contrast, fecundity differences are substantial. As an alternative to Roff's (1988) hypothesis of cascading effects on the life history due to the migratory costs on the adults, perhaps in this case the cost of migration is felt mainly in reduced juvenile survival. Fecundity has been substantially altered to offset this cost while age-at-maturity and growth are affected to a lesser degree. Such a conclusion would fit with Chudobiak et al. (2002) who found that there was little specific change among these two populations in the external morphology normally associated with long-distance swimming.

While the patterns of variation observed seem to fit comfortably into a framework of life history trade-offs there are some concerns with the results. First, this study has a major limitation in that it examines only two populations directly. Therefore the confounding effect of the environment on the findings cannot be discounted without replication of populations. Lobon-Cervia et al. (1997) demonstrated that fecundity variations within species could be the result of site-specific environmental factors. Slow-growing brown trout, *Salmo trutta*, from low-food energy sites spawned less and had fewer, larger eggs than those faster growing fish from high-food energy sites. These results suggest an alternative possibility that the early slow growth of the potamodromous population might result in a correlated response of lower fecundity. Recent laboratory rearing experiments where the effect of the environment was made constant showed that early growth is greater in the anadromous population (Tallman 2002) but one must be guarded when

making conclusions about other life history traits.

Secondly, the differences between the potamodromous and anadromous populations appear to be more subtle than found between similar pairs within temperate species such as sockeye salmon. In particular, there is not as large a difference in growth or age-at-maturity. Several factors may be responsible. First, the theory may not be valid for the Arctic. The Arctic has often been supposed to impose unique constraints on the life history of fishes (Johnson 1980). However, Arctic charr, another Arctic species, has large differences between potamodromous and anadromous populations along predicted lines (Tallman et al. 1996). Iteroparity vs. semelparity is also ruled out as charr and Atlantic salmon are iteroparous while sockeye salmon is semelparous. Two other possibilities are more attractive. First, the coregonids have a different ecological position from the more salmon-like fishes where this occurs. Perhaps minimum size and age-at-maturity constraints prevent the development of a dwarfed potamodromous population in whitefish without its becoming another species altogether. Secondly, divergence between the two types is at an earlier phase than other groups. This could account for a lesser degree of alteration. Thus, we would conclude that the principle investigated holds for high latitude species as well as temperate ones.

Resumen

1. Examinamos los cambios esperados en las trayectorias biológicas de una especie ártica, *Coregonus nasus* entre dos poblaciones de la región inferior del río Mackenzie: una población anadroma con migración reproductiva de 350–450 km y una población potamodroma con migración reducida de unos 5–12 km. Basados en la teoría biológica predecimos que la población anadroma tendría mayor crecimiento, mayor edad en la primera madurez y mayor inversión reproductiva.
2. En los estadios iniciales de la vida, la población anadroma tuvo mayor crecimiento que la potamodroma pero posteriormente fue menor. Tanto la edad en la primera madurez como la inversión reproductiva fueron mayores en la población anadroma. La fecundidad fue mayor en la población migratoria pero no estuvo relacionada ni con la edad en la primera madurez ni con diferencias en la tasas de crecimiento. Concluimos en que en la región templada, *C. Nasus* no sigue de forma conclusiva el patrón de variación observado entre las poblaciones migratorias y las relativamente sedentarias.

Acknowledgements

Much of this research was supported by grants from the Inuvialuit Fisheries Joint Management Committee. Other supporting agencies were the Polar Continental Shelf Project, the Northern Studies Training Program, and the Science Institute of the North-west Territories. The Water Surveys Branch of the Department of Environment provide accom-

modation at Tsiigehtchic. We thank the community of Tsiigehtchic, who kindly consented to the study on their lands. George Niditchie, James Blake, Danny Andre and Gabe Andre of Tsiigehtchic provided much knowledge regarding how to fish and assisted with the field work. Kimberley Howland, Trevor Thera, Fernand Saurette, Margaret Treble ran the field program when Ross Tallman or Darryl Chudobiak could not be present. Kimberley Howland set up much of the database and sampling protocol. Age determinations were verified by Rick Wastle and John Babaluk of the Department of Fisheries and Oceans. John Babaluk and Rick Wastle kindly provided the data for back-calculation. Melanie Van Gerwen key-punched the back-calculation information. Jim Reist and Mike Papst provided much encouragement and the working environment to carry out the study. Rob Stewart and Stew Innes provided helpful discussions on the analysis of life history traits. Rob Stewart and Bill Bond reviewed earlier versions of this manuscript. An anonymous reviewer provided valuable comments on the originally submitted version of this manuscript.

References

- Berg, L.S. 1965. Freshwater fishes of the USSR and adjacent countries. Israel Program for Scientific Translations. Jerusalem. pp. 374–379.
- Blair, G.R., Rogers, D.E. & Quinn, T.P. 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay. Alaska Transactions of the American Fish Society 122: 550–559.
- Bond, W.A. 1982. A study of the fishery resources of Tuktoyaktuk Harbour, southern Beaufort Sea coast, with special reference to life histories of anadromous coregonids. Can Fish Aquat Science (Technical Report) 1119, vii+90, p.
- Bond, W.A. & Erickson, R.N. 1985. Life histories of anadromous coregonid fishes of two freshwater lake systems on the Tuktoyaktuk Peninsula, Northwest Territories. Canadian Fish Aquat Science (Technical Report) 1336: 61p.
- Bond, W.A. & Erickson, R.N. 1993. Fisheries investigations in coastal waters of Liverpool Bay, Northwest Territories. Canadian Fish Aquat Science (Manuscr Report) 2204: vi+51p.
- Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths. Canadian Journal of Fish Aquat Science 47: 2219–2227.
- Cerrato, R.M. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Canadian Journal of Fish Aquat Science 47: 1416–1426.
- Chang-Kue, K.T.J. & Jessop, E. 1997. Determination of spawning and over-wintering areas of broad whitefish with radio telemetry in the lower Mackenzie River, 1982–1993. In: Tallman, R.F. & Reist, J.D., ed. Proceedings of the Workshop on the Biology, Traditional Knowledge and Scientific Management of Broad Whitefish in the Lower Mackenzie River. Canadian Journal of Fish Aquat Science (Technical Report). 2193: 117–146.
- Chen, Y., Jackson, D.A. & Harvey, H.H. 1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth rate. Canadian Journal of Fish Aquat Science 49: 1228–1235.
- Chilton, D.E. & Beamish, R.J. 1982. Ageing techniques for the North American ground fishery. Can. Spec. Publishers Fish. Aquat. Sci. 60: 1–15.
- Chudobiak, D.H. 1995. An Examination of Potamodromous and Estuarine Populations of Mackenzie Broad

- Whitefish (*Coregonus Nasus Pallas*): The role of migration and commercial exploitation on life history variation. MSc Thesis, University Manitoba, Winnipeg. 135p.
- Chudobiak, D.H., Abrahams, M.V. & Tallman, R.F. 2002. Variation in the morphology of two populations of Arctic broad whitefish. (*Coregonus nasus Pallas*), in the Mackenzie River. In: Todd, T.N. & Flerscher, G., eds. *Biology and Management of Coregonid Fishes—1999*. Arch. Hydrobiol. Spec. Issues Advance Limnol., in press.
- DeGraaf, D. & Machniak, K. 1977. Fisheries investigations along the Cross Delta pipeline route in the Mackenzie Delta. In: McCart P., ed. *Studies to Determine the Impact of Gas Pipeline Development on Aquatic Ecosystems Arctic Gas Biol (Report Series) 39 (4): 169p.*
- DeMaster, D.P. 1978. Calculation of the average age of sexual maturity in marine mammals. *Journal of Fish Research Board Canadian* 35: 912–915.
- Environment Canada. 1993–94. Surface water data, Yukon and Northwest Territories 1992–1993. Inland Waters Directorate, Water Survey of Canada, Ottawa.
- Glebe, B.D. & Leggett, W.C. 1981. Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. *Canadian Journal of Fish Aquat Science* 38: 806–820.
- Gresswell, R.E., Jiss, W.J. & Larson, G.L. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. *Canadian Journal of Fish Aquat Science* 51: 298–309.
- Gresswell, R.E. & Varley, J.D. 1988. Effects of a century of human influence on the cutthroat trout of Yellowstone Lake. *American Fisheries Society Symposium* 4: 45–52.
- Gross, M.R. 1987. Evolution of diadromy in fishes. *American Fisheries Society Symposium* 1: 14–25.
- Healey, M.C. 1978. Fecundity changes in exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*). *Journal of Fish Research Board Canadian* 35: 945–950.
- Hutchings, J.A. & Morris, D.W. 1985. The influence of phylogeny, size and behaviour on patterns of covariation in salmonid life histories. *Oikos* 45: 118–124.
- Johnson, L. 1980. The Arctic charr, *Salvelinus alpinus*. In: Balon, E.K., ed. *Charrs: Salmonid Fishes of the Genus Salvelinus*. The Hague: Dr W. Junk Publishers. pp. 15–98.
- Kogl, D.R. 1972. Monitoring and evaluation of Arctic waters with emphasis on the north Slope drainages: Colville River study. Alaska Department Fish Game, Federal Aid in Fish Restoration Project, Annual Report. 12: 23–61.
- Lobon-Cervia, J., Utrilla, C.G., Rincon, P.A. & Amezcua, F. 1997. Environmentally induced spatio-temporal variations in the fecundity of brown trout *Salmo trutta L.* trade-offs between egg size and number. *Freshwater Biology* 38: 227–288.
- McPhail, J.D. & Lindsey, C.C. 1970. *Freshwater Fishes of Northwestern Canada and Alaska*. Fisheries Research Board of Canada Bulletin. Volume 173. Ottawa. 381p.
- Moreau, J. 1987. Mathematical and biological expressions of growth in fishes: recent trends and further developments. In: Summerfelt, R.C. & Hall, G.E., ed. *The age and growth of fish*. Ames, IA: The Iowa State University Press. pp. 81–113.
- Morin, R., Dodson, J.J. & Power, G. 1982. Life history variations of anadromous cisco (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*) and round whitefish (*Prosopium cylindraceum*) populations of eastern James-Hudson Bay. *Canadian Journal of Fish Aquat Science* 39: 958–967.
- Myers, G.S. 1949. Usage of anadromous, catadromous and allied terms for migratory fishes. *Copeia* 1949: 89–97.
- Neter, J., Wasserman, W. & Kutner, M.H. 1983. *Applied linear regression models*. Homewood, IL: Irwin. 547p.
- Northcote, T.G. 1978. Migratory strategies and production in freshwater fishes. In: Gerking, S.D., ed. *Ecology of freshwater fish production*. Oxford: Blackwell: Sci. Publishers. pp. 326–329.
- Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of Von Bertalanffy's growth formula. *Berichte Aus Dem. Institute fur Meereskunde, Kiel University, Kiel, West Germany*. p. 63.
- Pielou, E.C. 1992. *After the ice age. The return of life to glaciated North America*. Chicago, IL: University of Chicago Press. 366pages.
- Popov, P.A. 1975. The growth and onset of sexual maturity of the broad whitefish, *Coregonus nasus*, and the Ob whitefish, *Coregonus lavaretus pidschian*, of the Tanama River. *Journal of Ichthyology* 17: 414–419.
- Powell, A.B. 1994. Life history traits of two allopatric clupeids. Atlantic menhaden and Gulf menhaden, and the effects of harvesting on these traits. *North American Journal of Fisheries Management* 14: 53–64.
- Power, G. 1997. A review of fish ecology in Arctic North America. *American Fisheries Society Symposium* 19: 13–39.
- Prasalov, P.P. 1989. On the biology of the broad whitefish, *Coregonus nasus*, from the lower Ob River Basin. *Voprosy Ikhtiologii* 3: 423–429.
- Rao, C.R. 1986. Some statistical methods for comparison of growth curves. *Biometrics* 14: 1–17.
- Reist, J.D. & Bond, W.A. 1988. Life history characteristics of migratory coregonids of the lower Mackenzie River, Northwest Territories. *Canada Finnish Fisheries Research* 9: 133–144.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191.
- Roff, D.A. 1988. The evolution of migration and some life history parameters in marine fishes. *Environmental Biological Fish* 22: 133–146.
- Roff, D.A. 1992. *The evolution of life histories: Theory and Analysis*. New York: Chapman & Hall. 535pages.
- Secor, D.H. & Dean, J.M. 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. *Canadian Journal of Fish Aquat Science* 49: 1439–1454.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford. 249p.
- Synder, R.J. & Dingle, H. 1990. Effects of freshwater and marine overwintering environments on life histories of threespine sticklebacks: evidence for adaptive variation between anadromous and resident freshwater populations. *Oecologia* 84: 386–390.
- Tallman, R.F. 2002. Genetic differences in growth between lacustrine and anadromous populations of broad whitefish, *Coregonus nasus*, of the lower Mackenzie River. In: Todd, T.N. & Fleischer, G., eds. *Biology and Management of Coregonid Fishes—1999*. Arch. Hydrobiol. Spec. Issues Advance Limnol., in press.
- Tallman, R.F. & Reist, J.D. 1997. Proceedings of the workshop on the biology, traditional knowledge and scientific management of broad whitefish in the lower Mackenzie River. *Canadian Journal of Fish Aquat Science (Technical Report)* 2193: xi+219p.
- Tallman, R.F., Saurette, F. & Thera, T. 1996. Migration and life history variation in Arctic charr, *Salvelinus alpinus*. *Ecoscience* 3: 33–41.

Variation in broad whitefish vital rates

- Taylor, E.B. 1992. Environmental correlates of life-history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *Journal of Fish Biology* 37: 1–17.
- Thera, T.M. 1998. A quantitative life-cycle model to identify research priorities and test management strategies for the Mackenzie River Broad Whitefish (*Coregonus Nasus Pallas*). MSc Dissertation. University of Manitoba, Wpg. Manitoba. 131pages.
- Treble, M. & Tallman, R.F. 1997. An assessment of the exploratory fishery and investigation of the population structure of broad whitefish from the Mackenzie River Delta, 1989–1993. *Canadian Journal of Fish Aquat Science (Technical Report)* p. 2180.
- Videler, J.J. 1993. *Fish swimming*. New York, NY: Chapman & Hall. 260pp.
- Weihs, D. & Webb, P.W. 1983. Optimization of locomotion. In: Webb, P.W. & Weihs, D., ed. *New York, NY: Fish Biomechanics* Prager Scientific. pp. 339–371.
- Williams, G.C. 1966. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton, NJ: Princeton University Press. 330p.
- Wootton, R.J. 1990. *Reproduction in ecology of Teleost fishes*. New York: Chapman & Hall Ltd. pp. 158–192.