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RELATIONSHIP BETWEEN ENERGY ACCUMULATION AND
MIGRATION COST AND ITS INFLUENCE ON LIFE-HISTORY
VARIATIONS OF ANADROMOUS CISCO (*COREGONUS ARTEDI*)³

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ABSTRACT

Life-history patterns of cisco (*Coregonus artedi*) from eastern James-Hudson Bay do not conform to evolutionary interpretations that predict reduced fecundity, increased age at maturity, and more iteroparity northwards. We test the hypothesis that the latitudinal gradient in reproductive traits of cisco may not be different from those expected theoretically if the cost of migration is included in the somatic cost of reproduction. Comparisons of the relative importance of the energy investment in gonads and migratory effort to the somatic cost of reproduction for the Little Whale River (Hudson Bay) and Eastmain River (James Bay) populations support this hypothesis. The somatic cost of reproduction was high and very similar for both populations despite a total energy budget 33% less in Little Whale River compared with the Eastmain River. Fish in the Little Whale River have a lower migratory cost due to the short distance migrated and the absence of rapids before spawning grounds. Lower migratory cost associated with lower energy accumulation permits cisco to maintain a similar somatic cost of reproduction in both rivers without reducing fecundity in the north. As a result, similar life-history patterns were observed in the two rivers. Thus, the cost of upstream migration interacts with resource input to determine life-history patterns.

Key words: *Coregonus artedi*, life history, reproduction, migrations, energy

1. INTRODUCTION

The physiological and behavioral demands of migration influence the evolution of life-history traits of anadromous fish (Shaffer, Elson 1975, Leggett, Carscadden 1978, Glebe, Leggett 1981a, b). The energy cost of migration may reduce the energy available to fecundity, growth and maintenance (Glebe, Leggett 1981b). In addition, the shorter growing season of the more northern fish may affect their life-history strategy by reducing fecundity, increasing the number of spawnings, and increasing the age of maturity (Morin et al. 1982; Leggett 1985). Our research program examines the energy budget of fish from different latitudes and with different migratory costs.

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Specifically, we study sympatric anadromous populations of cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) distributed over 1,200 km of the eastern coast of James-Hudson Bay (Fig. 1) to test the proposition that energy cost of migration determines the different reproductive strategies of these populations through its influence on reproductive cost.

The life history strategies of both species have been studied at various latitudes in James/Hudson Bay (Morin et al. 1980, 1982). Lake whitefish maintained their abundance throughout the region, reduced their fecundity in the north and exhibited variable growth. Life-history variations of cisco in the region do not conform to evolutionary interpretations that predict reduced fecundity, increased age at maturity, and more iteroparity northwards. Growth and abundance of cisco declined with latitude in James-Hudson Bay whereas fecundity remained constant. Dodson et al. (1985) hypothesized that the anomalous life-history variation of cisco may be due to a decreasing energy budget in the north whereby further tradeoffs in energy allocation among life-history traits, including migration, are not possible. Recently, (Kemp et al. 1989) revealed that cisco was the third most abundant salmonid captured in the Povungnituk River (Fig. 1) situated 200 km to the north of their proposed northern limit at Innuksuac (Morin et al. 1980). These results suggested that cisco is able to cope with a reduced growing season in the north of their range.

Freshwater migration represents a determinant factor in the reproductive effort and in the cost of reproduction of cisco and lake whitefish of the Eastmain River (Lambert, Dodson 1990a, b). The cost of cisco's freshwater migration in the Eastmain River (James Bay) was twice that of lake whitefish for the same migratory distance (Lambert, Dodson 1990a), and was related to the cisco's smaller size and higher active metabolic rate relative to lake whitefish (Bernatchez, Dodson 1985). Lambert and Dodson (1990 b) hypothesized that the latitudinal gradient in reproductive traits of cisco may not be different from those expected theoretically if the cost of migration is included in the

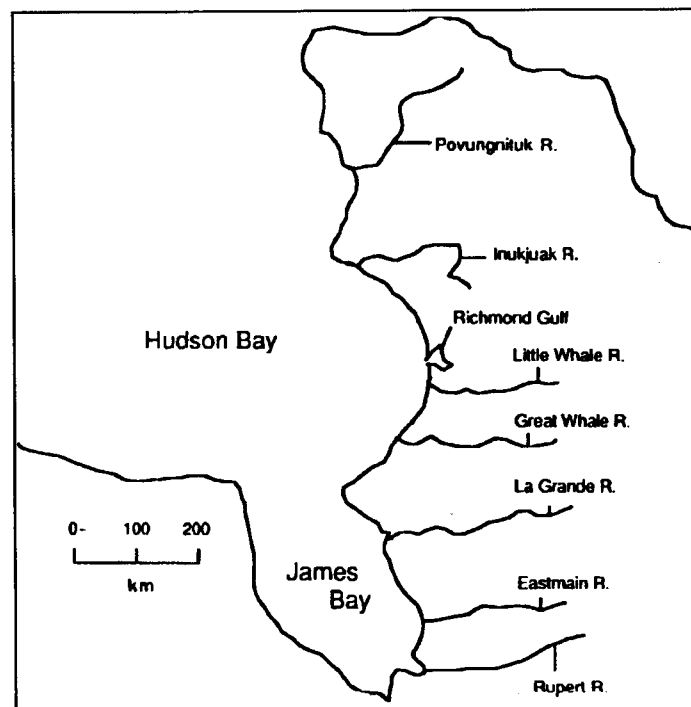


Fig. 1. Location map of the Little Whale River, Eastmain River and additional major rivers along the Eastern coast of James and Hudson bays

somatic cost of reproduction. We test this hypothesis in this study. More specifically the objectives were to: (1) quantify the partitioning of energy between growth, gonads and migration of female cisco in the Little Whale River (Hudson Bay); (2) document the growth, fecundity, age and length at maturity of cisco in the same river; and (3) compare these observations with the data of Lambert and Dodson (1990a) on cisco for the Eastmain River (James Bay) located 600 km to the south.

The Little Whale River was chosen as a study site because of its shorter growing season (Table I, Fig. 2). Previous studies reported that cisco grew slower in Hudson Bay rivers than did Eastmain cisco (Morin et al. 1980). Migration in the Little Whale River should also be easier than in the Eastmain River because of a shorter distance to the spawning ground (7 km vs 33 km in the Eastmain River) and the absence of intervening rapids (Table I, Fig. 2). Based on previous observations and our working

Table I. The major physical characteristics of the rivers studied. Growing season refers to the numbers of degree-days $>5.0^{\circ}\text{C}$ and are taken from *Environnement Canada* (1981). Mean breakup date is taken from Wilson (1971)

| River | Latitude | Growing season | Mean date of breakup | Migration distance (km) | Rapids (km) |
|--------------|----------|----------------|----------------------|-------------------------|-------------|
| Eastmain | 52°15' | 886 | May 10 | 33 | 7 |
| Little Whale | 56°00' | 548 | June 1 | 7 | 0 |

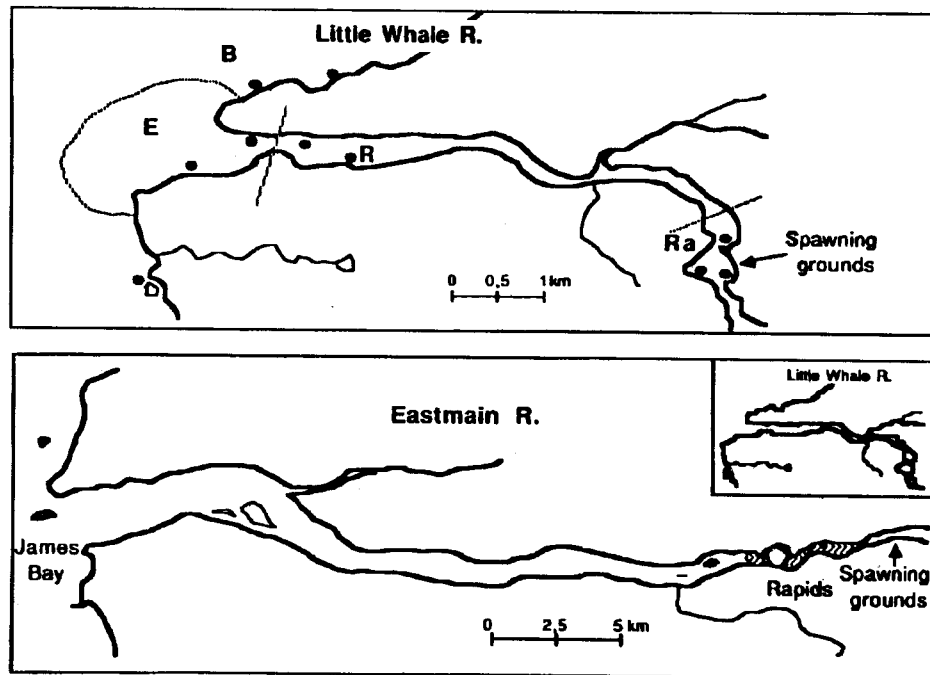


Fig. 2. Map of Little Whale River showing boundaries of sampling zones. Rapids: Ra; River: R; Estuary: E and Bay: B. Localization of gillnet sampling stations (•) and spawning grounds are also indicated. Map of Eastmain River illustrates rapids and spawning grounds (inset of Little Whale River is presented at the same scale)

hypothesis, we expected a decrease in the total energy budget of cisco in the Little Whale River as compared to the Eastmain, with a concurrent decrease in energy invested in migration.

2. MATERIALS AND METHODS

SAMPLING

The sampling program in Little Whale River was designed to catch reproductive and non-reproductive adult cisco at different stages of their annual cycle. Sampling dates and stations were selected to allow the measurement of seasonal changes in energy content associated with migration and reproduction. Fish were sampled with experimental gillnets along their general migratory route in 1985 and 1986 (Fig. 2): (a) at the river's mouth in June at spring break-up after overwintering period; (b) at the river's mouth in August prior to the upstream spawning migration; (c) at the spawning grounds in late September and early October (7 km upstream) prior to spawning.

After capture, fish were kept cold and were processed within 4 h. For each fish, fork length was measured to the nearest 0.1 cm and otoliths removed for age determination. Sex and maturity stages according to Nikolskii (Lagler 1978) were noted. Gonad, viscera, liver and carcass weight (whole eviscerated body, including head, skeleton and muscle) were recorded to the nearest 0.1 g. Tissue was individually frozen for analysis of energy content in the laboratory.

In the Little Whale River, length and age at maturity (at which 50% of the fish were maturing to spawn) were 26 cm and 5 years. Therefore, fish greater than 26 cm in length were considered as adult. Non-reproductive females were identified in the spring by the presence of unresorbed eggs, flaccid appearance of the ovaries and high moisture content of the gonads (up to 80%, according to Lambert and Dodson 1990a). Between August and October, maturity stages and the gonadosomatic index (weight of the gonads as a proportion of body weight) were used to identify reproductive and non-reproductive adult fish.

ENERGY MEASUREMENTS

Energy content was determined for the protein and fat portions of the gonads, liver, viscera and carcass of each fish. Protein, fat and moisture content for each tissue was measured according to techniques described by Lambert and Dodson (1990a). Energy content was determined by applying the energy equivalents $2.4 \times 10^4 \text{ J} \cdot \text{g}^{-1}$ for protein and $4.0 \times 10^4 \text{ J} \cdot \text{g}^{-1}$ for fat (Kleiber 1975).

Linear regressions between energy content and length (log transformed data) for reproductive and non-reproductive females were calculated for each sampling date. Comparisons between significant regressions were done by analysis of covariance (Sokal, Rohlf 1981). When the slope of the linear regression was not significantly different from 0, the mean value of tissue energy content and length were calculated. Comparisons between calculated mean values and predicted values of tissue content from linear regressions for the same length were done with T-test (Zar 1984). Absolute changes for each tissue were determined for a "standard" cisco corresponding to the mean length of reproductive adults (290 mm). The seasonal increase in length of the "standard" fish was used to calculate the absolute change in energy content during the season.

Interpopulation comparisons were made with original data for the Eastmain River population (Lambert, Dodson 1990a). Comparisons of energy content between the two populations were done by analysis of covariance on the appropriate linear regressions between energy content and length as described above.

ENERGY BUDGET AND COST OF REPRODUCTION

Cost of reproduction was calculated by comparing somatic and reproductive investments of reproductive females to that of non-reproductive females of the same length. Cisco do not spawn yearly once maturity is reached. Thus, reproductive and non-reproductive fish of similar lengths are common in these populations.

Cost calculations were based on the following parameters used by Lambert and Dodson (1990a) and modified after Tuomi et al. (1983):

(1) Somatic energy increase of non-reproductive females: estimated as the total energy accumulated by non-reproductive fish between June and October; (2) Somatic energy increase of reproductive females: estimated as the net energy accumulated by reproductive fish between June and October; (3) Gonad energy increase of reproductive females between June and October; (4) Absolute cost to somatic energy increase caused by reproduction: estimated as the difference between somatic energy accumulated by reproductive and non-reproductive fish; (5) Somatic cost of reproduction: measured by the extent to which reproduction reduced the somatic energy accumulated by reproductive fish below the level of non-reproductive fish [(4)/(1)]; (6) Proportion of the somatic cost of reproduction due to gonad energy increase [(3)/(1)].

Energy expenditure during spawning could not be estimated for female cisco in the Little Whale River. Therefore, comparisons of somatic energy changes between the two populations were made by eliminating data of energy expenditure during spawning for the Eastmain River population.

3. RESULTS AND DISCUSSION

ENERGY CONTENT

Total energy content of non-reproductive females in the Little Whale River and Eastmain River increased significantly between June and October, but differed between the two populations (Table II, Fig. 3). In the Little Whale River, non-reproductive females accumulated 859 kJ compared to 1,273 kJ in non-reproductive females of the Eastmain River. Therefore, energy gain was 33% lower in non-reproductive females of the Little Whale River relative to the Eastmain River which is consistent with the shorter growing season of the more northern Little Whale River.

Table II. Energy changes (kJ) between June and October and somatic cost of reproduction (%) for standard (290 mm) female cisco of Little Whale River and Eastmain River

| Parameter | Little Whale | Eastmain |
|---|--------------|----------|
| Gonad energy increase | 391 | 387 |
| Somatic energy increase | | |
| non-reproductive | 859 | 1,273 |
| reproductive | -25 | -99 |
| Reduction of energy gain (reproduction) | 884 | 1,372 |
| Somatic cost of reproduction | 103 | 108 |
| Distribution of somatic cost | | |
| (1) gonad investment | 45 | 29 |
| (2) migration | ? | 43 |
| (3) differential energy gain between reproductive and non-reproductive females | ? | 28 |
| sum of (2) and (3) | 55 | 71 |

Somatic energy content (total content – gonad content) of reproductive females did not differ (analysis of covariance, $P > 0.05$) between the two populations in spring and autumn (Fig. 3). Despite the seasonal growth in length no somatic energy increase was observed between June and October for reproductive females of both populations (Table II, Fig. 3). During the growing season, gonad energy investment of reproductive females was the same (analysis of covariance $P > 0.05$) in both populations (Fig. 3). We observed a reduction of somatic energy accumulated by reproductive females compared to non-reproductive females of 884 kJ in Little Whale River and 1,372 kJ in Eastmain River (Table II). The somatic energy gain of reproductive females was much lower than that of non-reproductive females in both rivers indicating that reproduction resulted in a somatic cost.

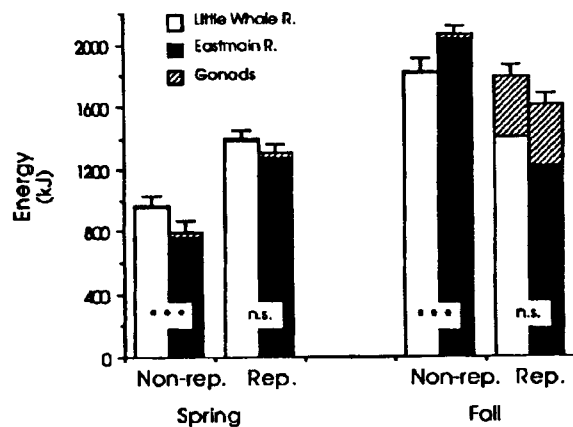


Fig. 3. Energy content of standard female cisco (290 mm) of Little Whale and Eastmain populations in spring and fall calculated from linear regression between energy content and length (log transformed data; T-bars indicate standard error of calculated value). *** – significant difference (ANCOVA, $P < 0.05$) between regressions; n.s.=no significant difference ($P < 0.05$)

Besides the difference in the growing season, the major difference between the two rivers is the difficulty of migration. Migration distance in Eastmain River is 33 km compared to 7 km in Little Whale River. The presence of 7 km of rapids with current speeds of 0.7 to $1.5 \text{ m} \cdot \text{s}^{-1}$ in the Eastmain River represents a major difficulty to migratory fish. Eastmain River conditions are hard for cisco due to their small size and their poor swimming capacity compared to most other salmonids (Bernatchez, Dodson 1985). These authors calculated that the mean current speed in the different sections of rapids is too elevated for cisco to traverse entirely without fatigue. Thus, cisco that migrate in Eastmain River probably spend time at levels of activity that would exceed the maximum sustainable metabolic rate in order to traverse zones of high velocities. However, in the Little Whale River, there are no rapids before the spawning grounds and average current speed at the river's mouth is $0.3 \text{ m} \cdot \text{s}^{-1}$ (Ingram 1979). Because of bad weather conditions, we were unable to catch enough cisco in August prior to the upstream spawning migration to estimate

energy losses associated with freshwater migration in Little Whale River. However, the swimming activity associated with migration in the Little Whale River should not represent an important energy constraint compared to the Eastmain River. Based on the swimming capacity of cisco (Bernatchez, Dodson 1985) a 350 g cisco in Little Whale River, moving at $0.6 \text{ m} \cdot \text{s}^{-1}$ over 7 km (migration distance), would only expend 17 kJ. This assumption of low migration cost in Little Whale River is also supported by the fact that the proportion of red muscle and the aerobic capacity of cisco are positively correlated with migration distance in James-Hudson Bay rivers (Couture 1989).

SOMATIC COST OF REPRODUCTION

The somatic cost of reproduction indicates that reproductive females of Little Whale River accumulated less somatic energy than non-reproductive females as was observed in the Eastmain population by Lambert and Dodson (1990a). The somatic cost of reproduction of female cisco was very similar for both populations (Table II). Somatic cost of reproduction includes gonad investment, migration cost, spawning activity costs, and reduction of the feeding period due to early freshwater migration. Energy losses during spawning were not included in our calculations, but we assumed that these costs were similar for both populations. The proportion of the somatic cost of reproduction due to gonad investments (29% in the Eastmain River compared to 45% in Little Whale River; Table II) indicates a large discrepancy between the two populations despite a very similar gonad investment (Table II). This result indicates clearly that fecundity alone may not be a good indicator of reproductive cost.

Somatic cost is also associated with energy loss during migration as well as with differences in energy accumulation between reproductive and non-reproductive females. In the Little Whale River this sum represented 55% of the somatic cost whereas it represented 71% of the somatic cost in the Eastmain River (Table II). Forty-three percent of the total somatic cost of reproduction for females in the Eastmain River was associated with the energy cost of migration and the difference in energy accumulation between reproductive and non-reproductive females represented 28% (400 kJ) of the total somatic cost of reproduction (Lambert, Dodson 1990a). The difference in energy accumulation was attributed to the early migration of reproductive individuals from the feeding grounds in August into freshwater while non-reproductive fish stay on the feeding grounds until September and October. Even so, migration cost alone in the Eastmain River is a major part of the somatic cost of reproduction.

In Little Whale River the proportion of the somatic cost of reproduction not due to gonad investment remained relatively high (55%) although migration distance and difficulty may be considered as a relatively minor constraint. However several consequences of migration must be considered, such as: (1) shorter marine feeding period; (2) fasting in freshwater; (3) physiological changes associated with osmoregulation and; (4) higher standard metabolism due to higher temperatures in freshwater. As active swimming to spawning grounds should not represent an important energy expense in this river, we conclude that other variables, mentioned above, are responsible for the remaining 55% of the somatic cost of reproduction.

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