Influence of Freshwater Migration on the Reproductive Patterns of Anadromous Populations of Cisco (*Coregonus artedii*) and Lake Whitefish (*C. clupeaformis*)[1]

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We tested the hypothesis that differences in the cost of freshwater migration are responsible for the different reproductive patterns exhibited by the Eastmain River (James Bay) populations of anadromous cisco and lake whitefish, as predicted by species-specific migration costs that result in interspecific differences in energy allocation to growth, survival, and reproduction. In the Eastmain River, cisco spawn at a younger age and a smaller size, have a shorter life span and show a higher fecundity and a higher mortality than lake whitefish. Assuming that the two populations are stable (being only lightly exploited), the two species spawn at an age that maximizes their lifetime fecundity. Either juvenile (between three and age at maturity) and/or adult mortality is of major importance in moulding the observed age at maturity but adult mortality may play a predominant role. Adult mortality is associated with migration, an obligatory cost representing a major proportion of the energy loss experienced by reproductive individuals. The difference in the energy cost of migration between the two species suggests that migration may play a predominant role in producing the different reproductive patterns of cisco and lake whitefish in the Eastmain River and that within the physiological and size constraints of each species, these patterns represent optimal adaptations maximizing fitness.

Nous avons testé l'hypothèse selon laquelle les différences dans le coût de la migration en eau douce étaient responsables des différences dans les patrons de reproduction observés chez les populations anadromes du cisco et du grand corégone de la rivière Eastmain (Baie James), comme prédit par les coûts de migration spécifiques à chaque espèce résultant en des différences inter-spécifiques dans la répartition de l'énergie entre la croissance, la reproduction et la survie. Dans la rivière Eastmain, le cisco se reproduit à un plus jeune âge et à une taille plus faible, a une durée de vie plus courte et montre une fécondité relative et une mortalité plus élevées. En supposant que les deux populations sont stables, les deux espèces se reproduisent à une âge où la fécondité totale pendant leur vie est maximisée. Les mortalités juvénile (≥3 ans) et adulte ont une influence importante sur l'âge à la maturité sexuelle mais la mortalité adulte pourrait jouer un rôle prédominant. La mortalité adulte est associée à la migration. Le coût obligatoire de la migration représente une proportion importante des dépenses énergétiques encourues par les poissons reproducteurs des deux espèces. La différence dans le coût énergétique de la migration entre les deux espèces suggère le rôle important de la migration dans la production de patrons de reproduction différents entre le cisco et le grand corégone de la rivière Eastmain et montrent qu'en fonction des différences physiologiques et de taille entre les deux espèces, les patrons de reproduction observés représentent des adaptations optimales.

The differential reproductive success of species living in a particular environment can produce a great diversity of reproductive patterns, each of them presumably maximizing the individual's lifetime reproductive success (Pianka 1976). Schaffer (1974) suggested that related species with similar ecologies may have very different life histories, the differences resulting from historical accidents which trapped each species in a different adaptive peak.

Anadromous forms of cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) provide a good opportunity to study the effect of the same environment on life history variables of similar species and to identify constraints which might explain differences in their life histories. Cisco and lake whitefish are found along the eastern coast of James and Hudson Bay. Both species represent a numerically important component of the fish communities of these regions (Morin et al. 1980; Lambert and Dodson 1982a,b; Kemp et al. 1989). These populations are assumed to be in stable equilibrium with their physical and biotic environment although subject to some exploitation by native subsistence fisheries (Morin et al. 1982) Natural selection should have molded the observed reproductive patterns so that each corresponds to a local optimum that maximizes the lifetime reproductive success of the individuals of each population. Cisco and lake whitefish are close phylogenetically and show in their natural range a large plasticity and considerable

overlap in their life history characteristics (Jensen 1981, 1985; Scott and Crossman 1974). In the rivers of James and Hudson Bay, the two species exhibit differences in some life history characteristics. In the La Grande river, lake whitefish attain a greater maximum age, a greater size and a later age at sexual maturity whereas cisco exhibit a greater rate of growth prior to reproduction and a greater fecundity (Morin et al. 1982).

The general ecology of the two species is quite similar. Both species spawn at the base of rapids in La Grande River (Morin et al. 1981) and in the Eastmain River (Dodson et al. 1985). Lake whitefish spawn between mid and late October when water temperatures are approximately 5°C whereas cisco spawn on the same grounds 2 to 3 wk later just before freeze-up. Larvae of both species hatch the following spring and are flushed at spring breakup from the rivers into James Bay (Ochman and Dodson 1982). They return as juveniles in September and October and they overwinter in freshwater. The next spring, they leave freshwater for their feeding migration to James Bay. Adult fish exhibit different patterns of migration according to sexual maturity. Although iteroparous, adults of both species do not spawn every year (Morin et al. 1982; Dodson et al. 1985; Lambert and Dodson 1990). The upstream migration of the reproductive adults begins in mid to late July. After spawning, reproductive adults leave the spawning grounds and join nonreproductive adults and juveniles for the overwintering period in freshwater.

Migration is an essential component of the life cycle of cisco and lake whitefish and must be accounted for in evaluating the adaptive significance of the reproductive patterns for the two species. The energy cost of freshwater migration has a significant effect on reproductive effort and somatic loss due to reproduction for both species (Lambert and Dodson 1990). However, there is a higher cost of migration for cisco in the Eastmain River which in turn results in a higher somatic cost for cisco. As the energy investment in gonads is comparable for both species, the difference in the somatic cost of migration is the major factor responsible for the difference in the cost of reproduction between the two species (Lambert and Dodson 1990).

These results may be related to the more general idea of differential allocation of energy resources where the optimal combination of life history traits may be achieved by allocating energy among growth, maintenance and reproduction in a way that maximizes the individual's contribution to future genotypes (Cody 1966; Holgate 1967; Gadgil and Bossert 1970; Charnov and Krebs 1973; and Mountford 1973). This hypothesis of a trade-off in energy allocation implies that an increase in reproductive effort inevitably results in both an increase in current reproductive output and an increase in somatic cost that will reduce the probability of surviving to the next breeding season (survival cost) and/or reduce future reproductive output (Williams 1966; Gadgil and Bossert 1970). Bell (1980) for example, suggested that the degree of anadromy in salmonids, through its influence on adult survival, may affect the pattern of covariation in life histories. Schaffer and Elson (1975) examined variations in life history data among local populations of Atlantic salmon and found that the pattern of variation was correlated with the difficulty of migration; the mean age of first spawning increased with the difficulty of upstream migration as estimated by the distance the fish ascended into freshwater. Glebe and Leggett (1981) also demonstrated the relation between energy expenditures for migration and reproduction with semelparity and iteroparity along a latitudinal cline for the American shad (*Alosa sapidissima*).

In this study, we hypothesized that the higher cost of migration and higher somatic cost of reproduction in cisco, relative to lake whitefish, should result in different survival and fecundity costs and consequently in different species-specific reproductive patterns. The higher somatic cost of reproduction in cisco should be associated with a higher adult mortality, shorter life and an earlier age at maturity in cisco relative to lake whitefish. To examine the influence of migration on the reproductive patterns of the two species, the following aspects of their reproductive patterns were studied; age at maturity, growth, survival, and reproductive life span. Lifetime fecundity was used as the measure of fitness to estimate the optimal age at maturity of the two species.

Materials and Methods

Catch Analysis

Field work took place in the Eastmain River and adjacent areas from 1979 to 1981 using experimental gill-nets (Lambert and Dodson 1990). Variations in catch per unit of effort of gill-net samples were used to document the seasonal migration patterns of cisco and lake whitefish (Lambert and Dodson 1982b). The sampling area was divided into three regions (river, river mouth, and bay) and three periods (May to mid-June, mid-June to mid-August, and mid-August to October) corresponding to the major distributional pattern of fish. CPUE was estimated in each region for each period of time, the unit of effort being 24 h of fishing with one experimental gill-net. Although fish of one species can be in different regions according to their maturity stage and their age, no major movements between the regions occurred within each period of time. Considering the area sampled as the distributional area of the two populations, it was assumed that the sampling in the three regions during one period represented a discrete sampling of the whole population. For these reasons, the average CPUE of the different regions were summed for each period. A mean annual CPUE for each species was calculated with the values of the three periods and used as the observed CPUE of each species.

Each specimen sampled was measured (fork length) and weighed, maturity stage (Nikolskii 1963) and sex determined and otoliths taken. Gonad weight was also taken and for females, eggs were fixed in Gilson's fluid. Fecundity was estimated gravimetrically by the dry weight method (Bagenal 1978).

Life History Variables

Age determinations were made from otoliths, as scales underestimate the age of older fish (Morin et al. 1982; Power 1978). The otoliths were embedded, sanded on their sagittal section and immersed in glycerine to improve the contrast between the zones (Panella 1980). Two independent readings were made for each fish. In case of disagreement between the first two readings, a third was made to determine age. When the three readings gave different ages, otoliths for that fish were rejected. The agreement between the two readings was good for both species; 90% and 80% for cisco and lake whitefish, respectively. Total otolith radius and otolith radius at each annulus was measured at the posterodorsal area of the otolith. These measures were used to back-calculate fork length of fish at each age. The relation between fork length and total otolith radius was established using the different regression models outlined by Jonsson and Stenseth (1976). The third degree polynomial

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was chosen as the mean square deviation between observed and estimated fish lengths was lowest. The relation between total otolith radius and fork length was estimated for both species with the 1979 to 1981 data as there was no difference graphically between the years. The equation of the third degree polynomial relating fork length to total otolith radius for cisco ($n = 894$) is

$$L = 9.68 - 9.45\,X + 130.69\,X^2 - 31.16\,X^3$$
$$r^2 = 0.989,$$

where L is fork length in millimetres and X total otolith radius in millimetres. For lake whitefish ($n = 903$) the corresponding equation is

$$L = -59.25 + 135.11\,X + 87.35\,X^2 - 25.48\,X^3$$
$$r^2 = 0.994.$$

The following correction was applied if total otolith radius of a fish of a given length was different than the average otolith radius for that length (Bagenal 1978):

$$S_n = \frac{S\,s_n}{s},$$

where S_n is the adjusted distance to the nth annulus; S is the average otolith radius for a fish of the observed length; s_n is the radius of the nth annulus; and s is the total otolith radius.

Mean fork length at each age for each sex was estimated with the back-calculated fork length at the last complete annulus to eliminate variance caused by the date of fish capture. Differences among means for each sex between years and for each year between sexes were tested using the t-test for paired comparisons (Sokal and Rohlf 1981). Back-calculated fork lengths at each age for fish of the same cohort sampled in different years were also analysed to detect any possible Lee's phenomenon which might indicate possible bias in growth curves due to size selective mortality or sampling bias (Ricker 1975). Between years comparisons were done by analysis of variance (Sokal and Rohlf 1981). Back-calculated fork lengths at the last complete annulus were fitted to a von Bertalanffy growth model to describe changes in length with age (Ricker 1975). The model was fitted using an iterative, nonlinear regression computer program (SAS 1985, NLIN procedure) described by Vaughan and Kanciruk (1982).

In northern fish populations, individuals do not spawn yearly and there is no simple criterion for identifying age at maturity. There is normally an increase in proportion of maturing fish with age which peaks at an age and level set by the frequency of spawning, the age at first maturity, and the pattern of mortality (Morin et al. 1982). Furthermore, no spawning marks which could indicate the past history of cisco and lake whitefish are observed. For these reasons, the youngest age-group in which at least 50% of the fish were maturing to spawn was adopted as the age at maturity.

Patterns of seasonal growth and CPUE were used to calculate catch curves. Fish were divided in length classes of 20 mm and a length frequency distribution established. Length frequency distributions were corrected to remove the effect of date of capture on length of fish using logistic curves describing seasonal increase in length. A frequency table relating length classes to proportion of fish of the same age in the different length classes was made and used to estimate the CPUE of fish of each age class. The annual survival rate was estimated from the catch curves relating the logarithms of CPUE and age with the data of 1979 to 1981 (Ricker 1975).

Fecundity of the two species was calculated by regressing fecundity on length (log transformed data) and compared by analysis of covariance (Sokal and Rohlf 1981).

Lifetime Reproductive Success

The maximum lifetime fecundity was selected as the measure of success of each species since these populations are believed to be in stable equilibrium with their physical and biotic environment (Morin et al. 1982). The expected lifetime fecundity was measured by

$$(1) \quad F = \sum_{t=x}^{y} l_t\, m_t,$$

where l_t is the age-specific survival rate, m_t the age-specific fecundity, x the age at sexual maturity and y the age at death. First, a complete schedule of survival and fecundity was made for each female population. The survival rate for juveniles older than three and adults were estimated with the CPUE at age and the catch curves. The survival rate per year between birth and age three was estimated with the relative egg production of the female populations for each year and the mean CPUE at age 3. The relative egg production of the female populations was estimated by:

$$(2) \quad Ep = \sum_{t=x}^{y} CPUE_t\, R_t\, m_t,$$

where $CPUE_t$ is the catch per unit of effort of fish of age t, R_t the proportion of spawners in age class t, m_t the number of female births at age t and the parameters x and y the minimum and maximum age of spawners observed, respectively. The number of female births at each age was evaluated by:

$$(3) \quad m_t = 10^{(a + b\,\log\,(L_\infty\,(1 - e^{-K(t+1-t_o)})))}/2,$$

where the von Bertalanffy equation gives the length of fish of age t at reproduction (in the equation age $t + 1$ since the equation gives the length at the beginning of the season and the fish are spawning in the fall at a length corresponding to an age of $t + 1$) and a and b are the coefficients of the regression of the logarithm of fecundity on the logarithm of length. The division by 2 gives the number of female births assuming a ratio of $1/1$ between males and females (observed male/female ratio for cisco $1.05/1$ and for whitefish $1.16/1$). The estimate of survival between birth and age 3 is calculated by dividing the CPUE of age 3 by the obtained value of egg production of the adult population.

The optimal age at maturity for individuals maximizing the expected lifetime fecundity was estimated by setting $l_0 = 1$ (number of fish at age 0) and using the calculated age-specific survival rates. Lifetime fecundity of individuals was estimated for different ages at first reproduction and a 2-yr interval between spawnings as the two species are unable to reproduce in successive years (Morin et al. 1982; Dodson et al. 1985; Lambert and Dodson 1990). Female birth rate was estimated with equation (3) given above.

Results

Life History Traits

Lake whitefish can live up to twice as long as cisco in the Eastmain River (Fig. 1). Most cisco are less than 8 yr old and
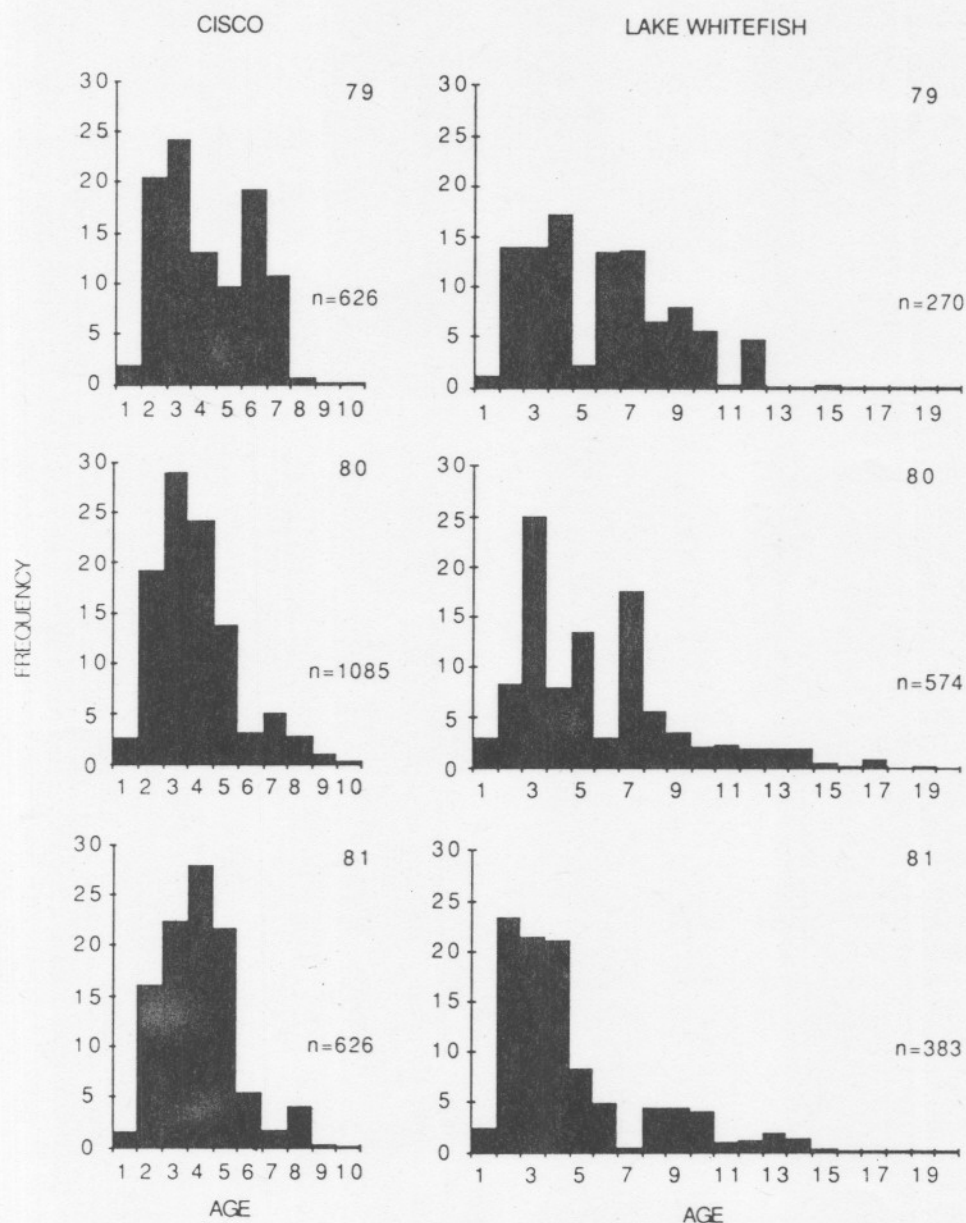
FIG. 1. Age-frequency distribution of cisco and lake whitefish in the Eastmain River from 1979 to 1981.

TABLE 1. Parameter estimates of the von Bertalanffy equation for cisco and lake whitefish of the Eastmain River with the grouped data of 1979 to 1981. L_t is length at year t; L_∞ is the asymptotic length; K is the growth rate; t_o is a constant inserted to improve the fit; and n is the number of fish analysed.

		L_∞	K	t_o	n
Lake whitefish	Male	422.5	0.238	0.016	452
	Female	439.2	0.222	0.001	451
Cisco	Male	328.5	0.331	0.206	430
	Female	344.7	0.324	0.293	464

most lake whitefish are less than 14 yr old. The age frequency distributions also show the low abundance of the 1974 year class (age 5 in 1979) for both species for the 3 yr analysed (Fig. 1).

Comparisons of mean fork lengths back-calculated to the last complete year of growth showed no consistently significant differences for both species (t-test for paired comparisons; for eight tests, $P>0.05$; for four tests, $0.01<P<0.05$) between the years for each sex. Therefore, all other analyses were carried out on the grouped data over 3 yr. Sexes were analysed separately as female growth and mortality rates were required in subsequent analyses.

Comparisons between back-calculated mean fork length at the same age for fish of the same sex and of the same cohort sampled in different years did not differ significantly ($0.01<P<0.05$, but in 90% of the analyses at $P>0.05$). For example, the back-calculated fork length at each age for female cisco of age 5 in 1979, 6 in 1980, and 7 in 1981 did not differ significantly. Thus, there was no evidence for Lee's phenomenon.

Von Bertalanffy growth curves calculated for each sex of both species indicated significant differences ($P<0.001$) in all parameters between the two species and between sexes within each species (Table 1). Asymptotic length was greater for lake whitefish than cisco and greater for females than males of both
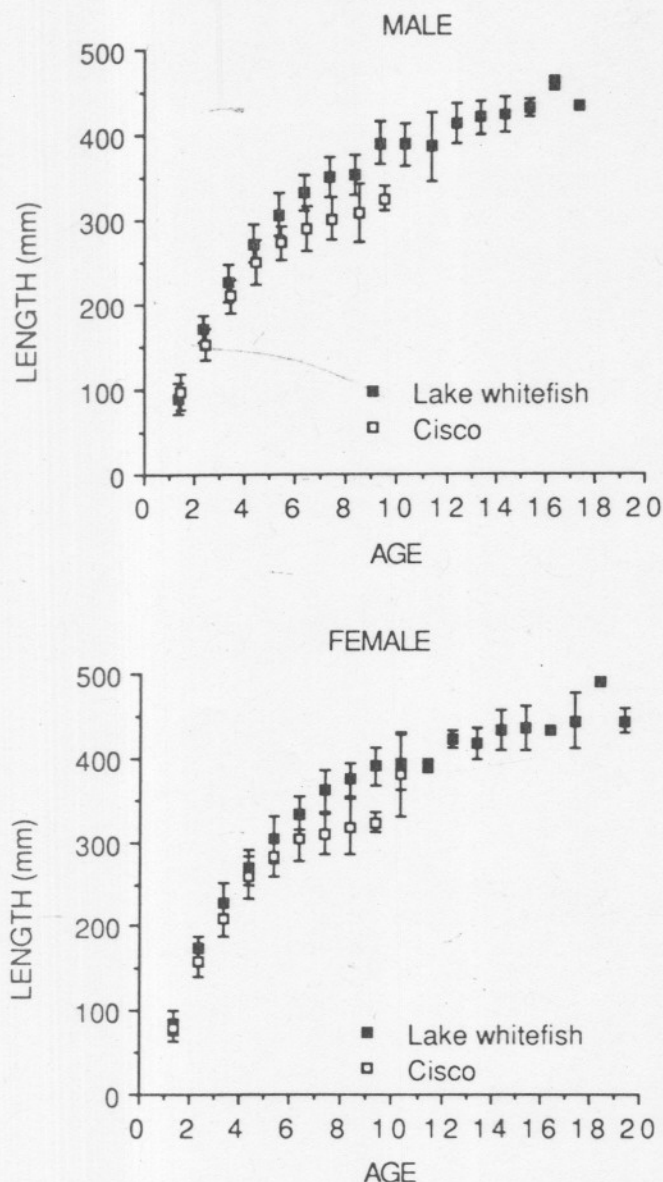
FIG. 2. Mean lengths at age of male and female cisco and lake white-fish for the grouped data of 1979 to 1981. Vertical bars indicate standard deviation.

species. Mean fork lengths at age were greater for lake whitefish and growth rate coefficient (K) was greater for cisco. Comparisons of mean fork lengths at age between the two species gave similar results (Fig. 2). Mean fork lengths at age of male and female cisco were significantly lower (t-test for paired comparisons; $P<0.01$) than those of lake whitefish. Such differences were not significant when comparing juvenile cisco and lake whitefish (age 1 to 4; $P>0.05$). However, mean fork lengths at age were not significantly different ($P>0.05$) between sexes within each species.

The age and length frequency distributions of spawning cisco and lake whitefish were evaluated using only fish caught after mid-July when maturity stage could be determined accurately. Only those fish showing a maturity stage of IV or V (classification of Nikolskii 1963) after mid-July were considered able to spawn in the fall. Cisco mature at a younger age and at a smaller size than lake whitefish and, in both species, males spawn earlier than females (Fig. 3). The age at first

reproduction was 4+ for male and 5+ for female cisco and 6+ for male and 7+ for female lake whitefish. In addition, no male and female lake whitefish were mature at the age of 4+ and 5+, respectively while in male and female cisco 60 to 77% of the fish were mature at these ages. In both species, males spawned at a smaller size than females (Fig. 3).

Cisco showed a significantly higher fecundity than lake whitefish (Fig. 4). The slopes of the two regressions did not differ significantly ($F=0.03$, $P>0.75$) but the adjusted mean fecundity was higher for cisco ($F=37.91$, $P<0.001$). Female cisco produced about 40% more eggs than female lake whitefish of the same length. However, considering the age at maturity, a 5-yr-old female cisco produced 34% fewer eggs than a 7-yr-old female lake whitefish.

The analysis of CPUE at age revealed a higher adult mortality rate for cisco than lake whitefish as demonstrated by the steeper slope of the catch curve for cisco (Fig. 5). Since those populations are only lightly exploited, we considered mortality rates as representing natural mortality. Comparisons between the slopes of the regressions lines (Table 2) indicated significant differences ($P<0.05$) between cisco and lake whitefish and no significant difference ($P>0.05$) between sexes within each species. Comparison of mortality rates for juvenile fish (Table 3) calculated with the mean CPUE at age (age 3 to 5; lower ages being incompletely sampled) indicated no significant difference between the two species (t-test; $P>0.05$). As juveniles, cisco and lake whitefish have similar mortality rates but as adults mortality rates are significantly higher in cisco than in lake whitefish (Table 3).

Lifetime Reproductive Potential

The CPUE of each age class for each year, combined with the proportion of spawning females in these age classes (Fig. 3) and their fecundity gave relative estimates of egg production for the two adult female populations. The number of eggs produced each year is $5.6 \cdot 10^4 \pm 1.7 \cdot 10^4$ for cisco and $1.9 \cdot 10^4 \pm 0.8 \cdot 10^4$ for lake whitefish. From these results and the mean estimates of CPUE at age 3 we obtain mean survival rates per year between age 0 and 3 of $5.5 \cdot 10^{-2} \pm 0.6 \cdot 10^{-2}$ for cisco and $4.9 + 10^{-2} \pm 0.6 \cdot 10^{-2}$ for lake whitefish.

With the schedule of survival, fecundity, and the proportion of spawners at each age, $l_t m_t$ is obtained for the female population of each species (Table 4 and 5). $l_t m_t$ at each age shows that the highest contribution in number of offspring for cisco is produced by age class 5 while the contribution is more equally distributed between ages 7 to 9 for lake whitefish with the highest contribution at age 8. The summation of the $l_t m_t$ products at each age indicate that both populations can be considered stable, as the summations give values close to one. The estimated rate of increase of populations numbers (Malthusian parameter r) is close to zero for both populations (0.002 for cisco and 0.026 for lake whitefish). The expected lifetime fecundity (F equation (2)) of individual females was estimated for different ages at maturity using the age-specific survival rates of juveniles and adults (Table 3), the estimates of fecundity and growth parmeters and a 2-yr interval between spawnings. The age at maturity maximizing expected lifetime fecundity corresponds to an age of 4.2 for female cisco which is lower than the observed age at maturity (Table 6). Within the standard errors of estimates for juvenile and adult survival rates and with other variables kept constant, the optimal age at maturity varies between 3 and 5.6 (Table 6). To predict an optimal
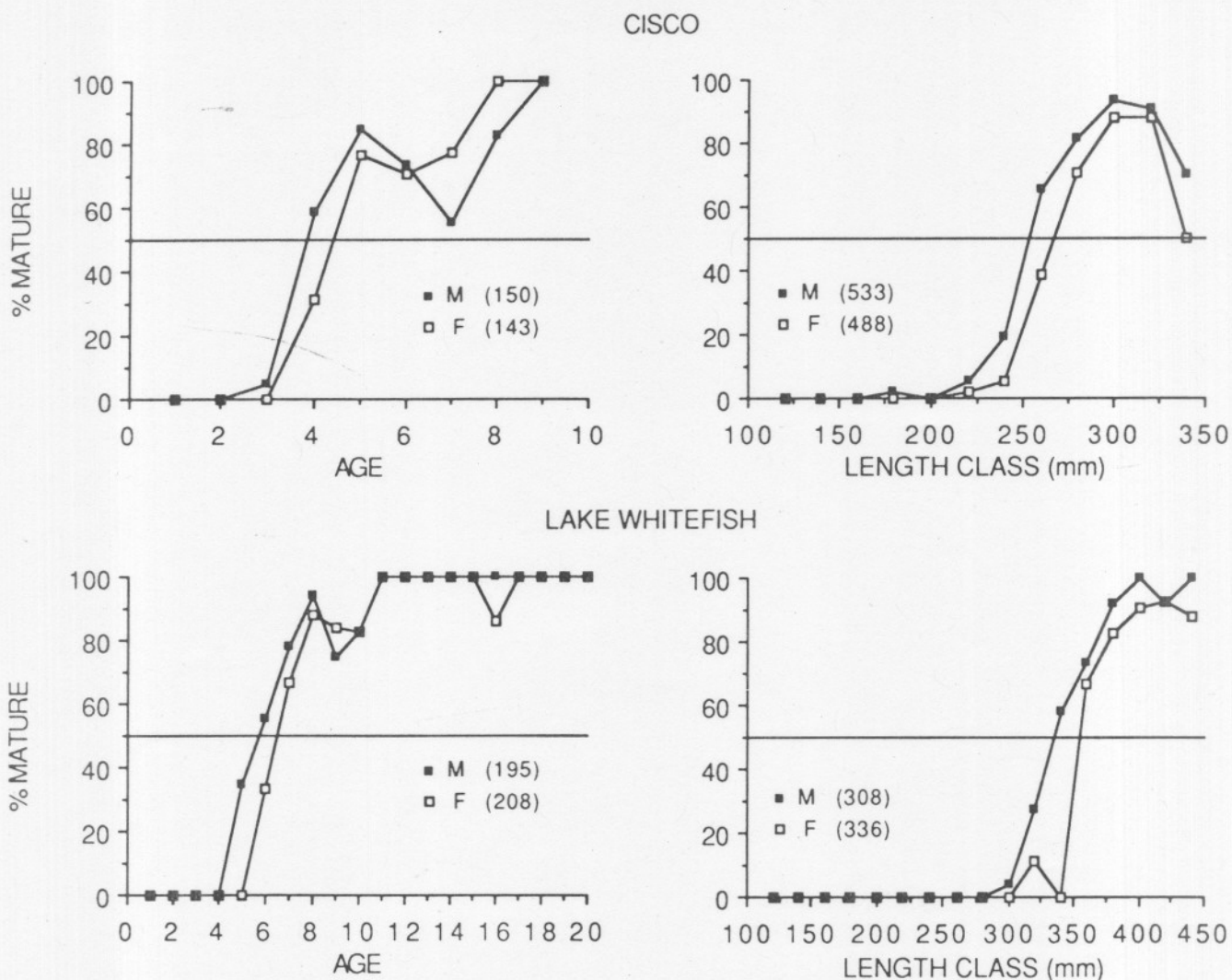
CISCO

LAKE WHITEFISH

FIG. 3. Percentages of mature male and female cisco and lake whitefish by age and length class. Horizontal line represents the 50% mature level. Numbers in parentheses represent the number of fish.

age at maturity equal to the observed age at maturity of female cisco (5), we must postulate a juvenile survival rate of 0.82 which is within the standard error of the estimate of juvenile survival rate (Table 3). For female lake whitefish, the combination of the mean estimates of the different variables do not result in an age where the expected lifetime fecundity is maximized. This is caused by the similarity between juvenile and adult survival rate. Within the standard errors of the estimates of juvenile and adult survival rates, the optimal age at maturity varies between no minimum value to a maximum value of 6.2 which is lower than the observed age at maturity (Table 6). To predict an optimal age at maturity equal to the observed age at maturity of female lake whitefish (7), we must postulate a juvenile survival rate of 0.89 and an adult survival rate of 0.71 (Table 6). These values are close to the range within the standard errors of the mean estimates of juvenile and adult survival rates (Table 3).

The sensitivity of optimal age at maturity to the estimation errors for different variables was examined for both female populations (Table 7). Age at maturity is very sensitive to changes in juvenile survival rate; an 8–10% change in juvenile survival rate producing changes between 0.8 and 3.4 yr in the optimal age at maturity (Table 7). Age at maturity is also sensitive, but

to a lesser degree, to changes in adult survival rate, growth rate (K) and the slope of the regression (b) of the fecundity–length function. However, for similar variations in the optimal age at maturity, lower coefficients of variation are observed for the growth rate parameter. Changes in mean juvenile survival rate between birth and age 3, in asymptotic length (L_∞) and in the parameter t_o of the growth curve had no effect on the optimal age at maturity (Table 7).

The age at first reproduction is important for both species as the contribution in fecundity by the first reproduction represents 67% (age 5) of the lifetime fecundity of cisco and 42% (age 7) of the lifetime fecundity of lake whitefish. The first two reproductive events in lake whitefish represent 68% of the lifetime fecundity. The number of reproductive events to realize the expected lifetime fecundity is also different between the two species; 97% of the lifetime fecundity is achieved in the first three spawnings in cisco whereas in lake whitefish this percentage is attained after the sixth spawning.

Discussion

Cisco and lake whitefish are closely related species and exhibit a wide range of variations and considerable overlap in
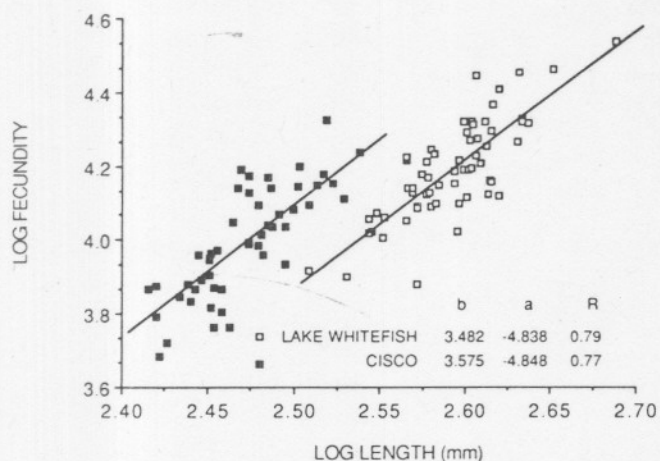
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FIG. 4. Regressions of the logarithm of fecundity on the logarithm of length for cisco and lake whitefish sampled from 1979 to 1981. Values *a* and *b* represent the intercept and the slope of the regression equations respectively and *r* the correlation coefficient.

their life history characteristics (Jensen 1981, 1985; Scott and Crossman 1974). However, in the same environment (Eastmain River) differences in life history characteristics are observed and result in different ages at maturity. Considering the East-main populations of cisco and lake whitefish stable, the age at maturity of cisco and lake whitefish corresponds, within the standard error of the estimates of the different life history characteristics, to the age at maturity maximizing their overall life-time reproductive potential (Table 6). As expected, the lower age at maturity of cisco is associated with a higher growth rate and a higher mortality than lake whitefish. Lake whitefish achieve expected lifetime fecundity (97%) with twice the number of spawnings (because of higher adult survival) than cisco. This may be viewed as a measure of the degree of iteroparity, with lake whitefish being more iteroparous than cisco.

Empirical studies using different approaches demonstrate the relative importance of different life history characteristics in determining the optimal age at maturity. For example, Jensen (1985) estimated that changes in the survival of immature fish and the age at maturity, which was related to length at maturity, growth rate and asymptotic length, were the only parameters that had a large effect on the net reproductive rate of lake white-fish. Jonsson et al. (1984) showed that the age maximizing overall lifetime reproductive potential in cutthroat trout (*Salmo clarki*) and Dolly Varden charr (*Salvelinus malma*) was sensi-tive to small changes in juvenile mortality rate, individual growth rate, and the malthusian parameter (*r*) but insensitive to variations in the other parameters. Roff (1984) modeled the important life history parameters determining the age at first reproduction. The analysis of the model with respect to the expected lifetime fecundity showed that age at first reproduc-tion was dependent on natural mortality rate, growth rate (*K*) and on the regression coefficient of the fecundity–length func-tion which was assumed constant (value of 3) in the model.

From the predictions of these models, the observed combi-nation of life history characteristics and the sensitivity of age at maturity to these different parameters, the difference in age at maturity between cisco and lake whitefish can be attributed to differences in juvenile and adult survival rate and growth
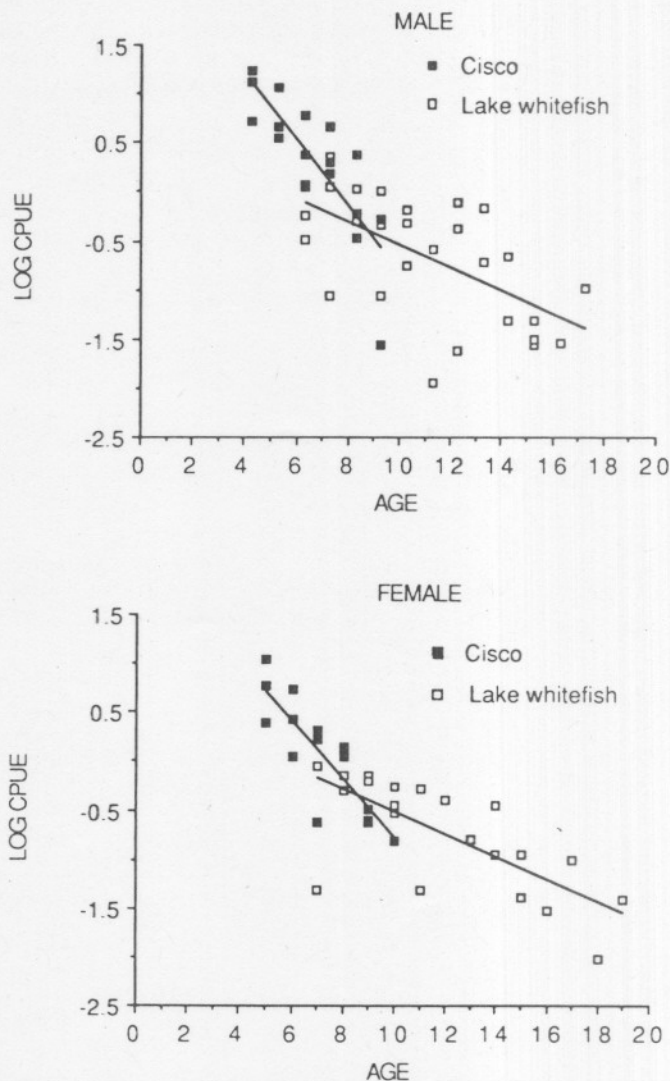

FIG. 5. Regressions of the logarithm of catch per unit of effort on age for male and female adult cisco and lake whitefish for the data of 1979 to 1981.

rate. The slopes of the regressions of the fecundity–length func-tions are not important in explaining the different age at matu-rity between the two species since no significant differences ($P>0.75$) in the slopes of the regressions were observed.

Juvenile Survival

Several studies have shown the influence of juvenile survival on life history patterns. For example, Stearns and Crandall (1981) obtained a correlation of 0.929 between predicted and observed age at maturity for nine populations of lizards and salamanders with a model based on the survival of juveniles. Glebe and Leggett (1981) concluded that predictability of the reproductive environment, through its influence on juvenile mortality, was the principal regulator of latitudinal differences in life history strategies in shad. Bell (1980), using models based on reproductive costs in time-varying environments, reached similar conclusions about the effect of juvenile survival. No significant differences in juvenile survival rates were observed between cisco and lake whitefish for either juveniles between age 0 and 3 or juveniles in prereproductive years (between 3 and age at maturity).

TABLE 2. Regressions of the logarithm of catch per unit of effort (Y) on age (X) for adult cisco and lake whitefish of each sex for the data of 1979 to 1981. $F = F$-value for the significance of the regression; P = probability level of significance; r = correlation coefficient; and n = number of observations. The instantaneous rate of mortality is obtained by changing the sign of the regression slope, and multiplying by 2.3026.

Species	Sex	Regression equation	F	P	r	n
Cisco	Male	$Y = 2.370 - 0.334\,X$	31.7	<0.001	0.82	17
	Female	$Y = 2.197 - 0.298\,X$	29.5	<0.001	0.84	14
Lake whitefish	Male	$Y = 0.520 - 0.117\,X$	16.8	<0.001	0.62	29
	Female	$Y = 0.638 - 0.115\,X$	24.6	<0.001	0.73	23

TABLE 3. Instantaneous rate of mortality (Z) with standard deviation (SD) and corresponding survival rate (S) for juvenile and adult cisco and lake whitefish. Standard deviation estimated from the mean CPUE at age for juveniles and from regression equations for adults.

	Z	SD	S	$\pm$ SD
Cisco				
Juvenile	0.234	0.084	0.792	0.728–0.860
(age 3 to age at maturity)				
Adult Male	0.769	0.136	0.463	0.405–0.531
Female	0.686	0.127	0.503	0.444–0.572
Lake whitefish				
Juvenile	0.271	0.151	0.763	0.656–0.887
(age 3 to age at maturity)				
Adult Male	0.269	0.067	0.764	0.715–0.817
Female	0.265	0.053	0.767	0.728–0.809

TABLE 4. Schedule of survival and fecundity for the female population of cisco and the contribution to female births of each age class with $l_o = 1$. l_t is the probability of surviving from birth to age t; R is the proportion of spawners in age class t; m_t is the number of female births at age t; and $l_t m_t (R)$ is the contribution of each age class to female births in the population.

Age	l_t	R	m_t	$l_t m_t(R)$
0	1.0	0.0		
1	$5.5 \cdot 10^{-2}$	0.0		
2	$3.1 \cdot 10^{-3}$	0.0		
3	$1.7 \cdot 10^{-4}$	0.0		
4	$1.3 \cdot 10^{-4}$	0.315	3479	0.146
5	$1.1 \cdot 10^{-4}$	0.765	4536	0.367
6	$5.3 \cdot 10^{-5}$	0.705	5432	0.204
7	$2.7 \cdot 10^{-5}$	0.775	6155	0.128
8	$1.4 \cdot 10^{-5}$	1.0	6719	0.091
9	$6.8 \cdot 10^{-6}$	1.0	7149	0.049
10	$3.4 \cdot 10^{-6}$	1.0	7473	0.026
11	$1.7 \cdot 10^{-6}$	1.0	7714	0.013
12	$8.7 \cdot 10^{-7}$	1.0	7891	0.007
			$\Sigma l_t m_t = 1.030$	

TABLE 5. Schedule of survival and fecundity for the female population of lake whitefish and the contribution to female births of each age class with $l_0 = 1$. l_t is the probability of surviving from birth to age t; R is the proportion of spawners in age class t; m_t is the number of female births at age t; and $l_t m_t (R)$ is the contribution of each age class to female births in the population.

Age	l_t	R	m_t	$l_t m_t(R)$
0	1.0	0.0		
1	$4.9 \cdot 10^{-2}$	0.0		
2	$2.5 \cdot 10^{-3}$	0.0		
3	$1.2 \cdot 10^{-4}$	0.0		
4	$9.3 \cdot 10^{-5}$	0.0		
5	$7.1 \cdot 10^{-5}$	0.0		
6	$5.4 \cdot 10^{-5}$	0.330	5064	0.090
7	$4.1 \cdot 10^{-5}$	0.665	6067	0.166
8	$3.2 \cdot 10^{-5}$	0.880	6967	0.194
9	$2.4 \cdot 10^{-5}$	0.840	7754	0.158
10	$1.9 \cdot 10^{-5}$	0.830	8427	0.130
11	$1.4 \cdot 10^{-5}$	1.0	8996	0.128
12	$1.1 \cdot 10^{-5}$	1.0	9470	0.104
13	$8.4 \cdot 10^{-6}$	1.0	9863	0.083
14	$6.5 \cdot 10^{-6}$	1.0	10185	0.066
15	$5.0 \cdot 10^{-6}$	1.0	10449	0.052
16	$3.8 \cdot 10^{-6}$	1.0	10663	0.041
17	$2.9 \cdot 10^{-6}$	1.0	10837	0.032
18	$2.2 \cdot 10^{-6}$	1.0	10978	0.025
19	$1.7 \cdot 10^{-6}$	1.0	11092	0.019
20	$1.3 \cdot 10^{-6}$	1.0	11184	0.015
21	$7.8 \cdot 10^{-7}$	1.0	11257	0.011
			$\Sigma l_t m_t = 1.313$	

lifetime fecundity. If r is the parameter maximized, the mean juvenile survival between age 0 and 3 (egg and larval survival) could then influence the age at maturity as demonstrated by the model of Roff (1984).

Juvenile survival rate in preproductive years (between 3 and age at maturity) has the largest influence on the optimal age at maturity; an 8–10% change producing changes from 0.8 to 3.4 yr in the optimal age at maturity (Table 7). Thus, the observed age at maturity of cisco and lake whitefish should be strongly influenced by juvenile survival rate in prereproductive years. However, differences in the age at maturity between cisco and lake whitefish cannot be attributed solely to differences in juvenile survival rate. The different juvenile survival rates (between 3 and age at maturity) of cisco and lake whitefish, although not statistically different (Table 3), contribute to the different ages at maturity of the two species. Based on the estimates of juvenile survival rates predicting the observed age at maturity of both species (Table 6), we observed that an increase in juvenile survival rate for cisco to a value equal to the predicted value

Variations in mean juvenile survival rate between age 0 and 3 (mostly the result of low egg and larval survival) have no effects on the age at maturity of both species (Table 7). Thus possible differences and year-to-year fluctuations in juvenile survival rates between age 0 and 3 will not affect the observed age at maturity unless mean juvenile survival rate changes in the long term, in which case the two populations would no longer be stable. In such a case, the malthusian parameter r would be a more suitable measure of fitness than the expected

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TABLE 6. Age at maturity maximizing the expected lifetime fecundity for the combination of the mean estimates of the life history parameters, minimum and maximum age at maturity within the standard deviations of juvenile older than 3 yr (S1) and adult (S2) survival estimates and juvenile and adult survival rate needed to predict an optimal age at maturity equal to the observed age at maturity.

	Survival rate	Optimal age at maturity
Cisco		
Mean estimates of parameters	S1 = 0.792 S2 = 0.503	4.2
Minimum within SD of survival rates	S1 = 0.860 S2 = 0.572	3.0
Maximum within SD of survival rates	S1 = 0.728 S2 = 0.444	5.6
Estimates of survival rates predicting the observed age	S1 = 0.844 S2 = 0.503	5.0
Lake whitefish		
Mean estimates of parameters	S1 = 0.763 S2 = 0.767	0
Minimum within SD of survival rates	S1 = 0.656 S2 = 0.809	0
Maximum within SD of survival rates	S1 = 0.889 S2 = 0.728	6.2
Estimates of survival rates predicting the observed age	S1 = 0.895 S2 = 0.705	7.0

for lake whitefish increased the optimal age at maturity for cisco by almost 1 yr (age 6). This change shows the importance of variations in juvenile survival rate on the age at maturity but also demonstrates that the difference in juvenile survival rate (between 3 and age at maturity) between cisco and lake whitefish is not a sufficient factor to explain their different age at maturity.

Growth Parameters

Variations in growth rate also explain the difference in age at maturity of cisco and lake whitefish. For example, decreasing cisco's growth rate to a value of 0.2223 (observed K for lake

whitefish) without changing fecundity and mortality increases optimal age at maturity by 1 yr.

As reported by the different studies reviewed by Roff (1984), growth has been related to physiological processes and environmental factors such as temperature and food and to different life history attributes. In the Eastmain River, cisco and lake whitefish (taxonomically close species) are present in the same temperature conditions and are opportunistic feeders, although showing different preference in their prey as adults (Lambert and Dodson 1982b). Cisco generally attain smaller maximum length than lake whitefish but can reach similar size. In Lake Ontario, cisco measure 41.4 cm at the age of 9 and a specimen of 57.2 cm has been captured in Great Slave Lake (Scott and Crossman 1974). The two species as juveniles have equal lengths, the growth curves only beginning to diverge when cisco reach maturity (Fig. 2). This suggests that the different population growth patterns of cisco and lake whitefish is principally associated with the cost of reproduction through its effect on growth and mortality. As both species are able to attain a comparable size, we conclude that differences in the cost of reproduction are responsible for the different population growth rates observed for the two species.

Adult Survival

The results presented for lake whitefish by Jensen (1985) indicate that an increase in mortality is associated with an increased growth rate and an earlier age and smaller size at maturity. A smaller size at maturity and lower growth after maturity results in a lower asymptotic size. In the present study lake whitefish reach a greater maximum age, a greater size, and a later age at maturity whereas cisco exhibit a greater growth rate and a higher fecundity. Morin et al. (1982) observed similar differences in the life history characteristics of the two species in La Grande River located 200 km to the north. Associated with the combination of these life history parameters, different mortality rates are observed in the Eastmain River. As juveniles, cisco and lake whitefish have the same mortality rate but as adults the mortality rate of cisco is significantly higher than that of lake whitefish.

Models of trade-off in energy allocation are based on the assumption that costs in survival are associated with reproduc-

TABLE 7. Sensitivity for estimation errors of the optimal age at maturity. In all estimations, one value is varied and the others are set equal to the population means except for juvenile (age 3 to age at maturity) and adult survival where mean values were replaced by the values predicting the observed age at maturity. For each value, the coefficient of variation (CV) for the estimate and the corresponding change in the optimal age at maturity are presented.

	Cisco		Lake whitefish	
Parameter	CV(%)	Change in the optimal age	CV(%)	Change in the optimal age
Juvenile survival (age 0 to 3)	10	—	13	—
Juvenile survival (age 3 to age at maturity)	8	0.8–1.2	10	2.6–3.4
Adult survival	13	0.2	5	0.2
Asymptotic length	2	—	1	—
Growth rate	6	0.2	3	0.2
Constant (t_o)	23	—	54	—
Fecundity (Regression slope-b)	12	0.2	10	0.2

tion. Apart from the study of Snell and King (1977) on rotifers, few studies give evidence of a direct connection between reproduction and survival probability. Nevertheless, evidence from bioenergetic studies supports the hypothesis. Glebe and Leggett (1981) for example, found a positive correlation between the energy expenditure by shad during freshwater migration and semelparity or iteroparity in these populations. Comparison of reproductive and nonreproductive cisco and lake whitefish indicate that reproduction results in somatic cost to both species but that cisco's higher reproductive effort results in a greater somatic cost in cisco than in lake whitefish (Lambert and Dodson 1990). A higher adult mortality rate for cisco is associated with this higher somatic cost (Table 3).

Using data on different anadromous species and populations, Glebe and Leggett (1981) noted differences in energy loss during freshwater migration associated with semelparity and iteroparity. Iteroparous species consumed less than 60% of their total energy reserves during migration. Semelparous species exhibited energy expenditures associated with migration that exceeded 70% of the total energy available. For example, St-Johns River shad consume 70–80% of their total energy reserves and all shad die following spawning. The 70% value may represent the minimum energy level below which no survival is possible. Cisco and lake whitefish are both iteroparous and, in both species, less than 60% (58% for female cisco and 35–44% for lake whitefish) of their energy reserves are consumed during migration and spawning (Lambert and Dodson 1989). However, if the cost of overwintering is included, cisco and lake whitefish consumed 61–67% of their energy reserves which approach expenditures typical of semelparous species. Assuming comparable energy expenditures for reproductive and nonreproductive fish during winter, reproductive female cisco would theoretically consume ≈84% of their energy reserves for migration, reproduction and overwintering compared with the observed value of 67%. Thus, we may hypothesize that cisco consuming more than approximately 67% of their energy reserves would not survive. The difference in mortality between cisco and lake whitefish may result from the different proportions of fish of each species that utilized more than a critical percentage of their energy reserves for migration, reproduction, and overwintering.

The higher somatic cost of reproduction in cisco will result in a greater proportion of cisco with an energy level close to the minimum level necessary to survive. Compared with lake whitefish, a higher proportion of cisco will experience energy expenditures greater than the critical limit. It is also reasonable to assume that annual mortality rate in reproductive cisco will be more likely to vary with fluctuations in environmental conditions. A small decrease in the accumulation of energy during the summer may, for example, increase the proportion of reproductive cisco that will exceed the minimum energy threshold. The lower proportion of lake whitefish near the minimum energy threshold may result in lower variations in the mortality rate of reproductive lake whitefish due to fluctuations in environmental conditions.

When fecundity increases with size, present reproduction involves an additional risk of failing to realize a greater future fecundity (fecundity cost) if reproduction increases mortality (Bell 1980). The somatic cost of reproduction also results in fecundity cost for both cisco and lake whitefish. Reproduction reduces future fecundity potential for the two species because the reduced energy level of reproductive fish after migration, reproduction, and overwintering obliges fish to miss the next

spawning season (Lambert and Dodson 1990), increasing the risk of mortality before the next reproduction. The fecundity cost will also be higher in cisco than in lake whitefish since reproduction results in a higher mortality in cisco.

The energy cost of migration is largely responsible for the higher somatic cost of reproduction in cisco compared with lake whitefish (Lambert and Dodson 1990). Consequently, the cost of migration contributes significantly to the observed species-specific adult mortality patterns.

Differences in the distance and difficulty of migration in the river systems of James and Hudson Bay may explain why intraspecific comparisons of life history traits of anadromous cisco and lake whitefish along the James and Hudson Bay coast do not clearly conform to the theory that predicts reduced fecundity, increased age at maturity, and more iteroparity northwards (Morin et al. 1982). Climatic data summarized by Morin et al. (1982) shows that climatic conditions are harsher at northern sites of Hudson Bay. We hypothesize that the differences in difficulty and distance of migration along the James and Hudson Bay coast can explain differences between observed and expected patterns of reproductive traits for cisco and lake whitefish. In the Eastmain river, migration extends 33 km, in which 7 km are rapids. For more northerly rivers, migration distance ranges from 13 km in the southern part of Hudson Bay to 3 km near the northern limit of distribution. There are no rapids before the spawning grounds in these rivers (Morin et al. 1980). Consequently, there is a decrease in the cost of migration with latitude and a decrease in the energy available because of shorter growing seasons with latitude. We propose that the observed reproductive traits may not be different from those expected theoretically if the cost of migration is included in the somatic cost of reproduction. For example, cisco exhibit delayed maturity and reduced growth in the north of James Bay and Hudson Bay (Morin et al. 1982). This implies that adult survival must increase or at least remain unchanged. As fecundity remains unchanged over the same range, comparable or improved adult survival can only be related to comparable or lower somatic costs of reproduction afforded by lower migration costs. However, in the absence of data on resource input, costs of migration and costs of reproduction for the observed fecundities, the adaptive significance of the age at maturity and fecundity observed over large latitudinal gradients cannot be interpreted in the context of life history theory.

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