

Life History Variations of Anadromous Cisco (*Coregonus artedii*), Lake Whitefish (*C. clupeaformis*), and Round Whitefish (*Prosopium cylindraceum*) Populations of Eastern James–Hudson Bay

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Differences in life history among three species of anadromous coregonines from La Grande River, James Bay, were significant with lake whitefish (*Coregonus clupeaformis*) and round whitefish (*Prosopium cylindraceum*) displaying reproductive patterns more typical of harsh northern environments and characteristic of "K-selection," relative to cisco (*Coregonus artedii*). Interspecific differences at La Grande River were more apparent than intraspecific differences in life history traits of cisco and lake whitefish over the James–Hudson Bay range. Although cisco exhibit decreasing reproductive effort independent of growth over the North American range, thus conforming to life history theory, both growth and reproductive effort are reduced northwards over their James–Hudson Bay range. The observations suggest that physiological constraints related to the shorter growing season at the northern limit of cisco's coastal Hudson Bay range may overwhelm expected coadapted life history traits. Lake whitefish exhibit reduced reproductive effort independent of variations in growth northwards over their North American and James–Hudson Bay coastal range; this suggests coadaptation of life history traits that permit survival at northern sites.

Key words: reproduction, growth, life history theory, anadromous coregonines, James–Hudson Bay

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Il existe, parmi trois espèces de corégoninés anadromes de la Grande-Rivière (baie James), des différences significatives, le grand corégone (*Coregonus clupeaformis*) et le ménomini rond (*Prosopium cylindraceum*) montrant des modalités de reproduction plus typiques d'un environnement boréal rigoureux et caractéristiques d'une « sélection K », comparativement au cisco de lac (*Coregonus artedii*). Les différences interspécifiques observées à la Grande-Rivière sont plus prononcées que les différences intraspécifiques des caractéristiques du cycle biologique du cisco de lac et du grand corégone dans toute l'aire baie James–baie d'Hudson. Bien que le cisco de lac exhibe un effort reproducteur amoindri indépendant de la croissance dans son aire nord-américaine, en conformité avec la théorie du cycle biologique, la croissance et l'effort reproducteur sont tous deux diminués vers le nord dans le secteur baie James–baie d'Hudson. Ces observations donnent à penser que les

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contraintes physiologiques liées à une saison de croissance plus courte à la limite septentrionale de l'aire de distribution côtière du cisco de lac dans la baie d'Hudson peuvent supplanter les caractéristiques d'adaptation anticipées. Le grand corégone montre une reproduction diminuée indépendante des variations de la croissance, à mesure qu'on progresse vers le nord dans toute leur aire nord-américaine et dans le secteur côtier des baies James et d'Hudson; ceci laisse supposer une coadaptation des caractéristiques du cycle biologique favorisant la survie dans le nord.

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COMPARISONS of fish populations have indicated geographic differences in fecundity (Paulson and Smith 1977), egg size (Marshall 1953; Blaxter and Hempel 1963), and age of maturity (Nikolskii 1963). A general trend in northern fishes to reduce fecundity and increase the lifetime frequency of spawning has been noted by Nikolskii (1970) and Leggett and Carscadden (1978). Several hypotheses have been proposed to explain these observations. Ricker (1954), Murphy (1966), Schaffer (1974), Schaffer and Elson (1975), and Leggett and Carscadden (1978) provided evidence for the selection of repeated spawning, late maturity, and decreased annual fecundity in fish inhabiting unstable environments as a means of reducing the probability of extinction in the face of wide fluctuations in juvenile mortality. Cody (1966), Holgate (1967), Gadgil and Bossert (1970), Charnov and Krebs (1973), and Mountford (1973) have variously hypothesized that there may be a trade-off in energy allocation among growth, maintenance, and reproduction that maximizes the individual's contribution to future genotypes. In the harsher, shorter, growing season of the north, reduced fecundity may be an adaptation to ensure an adequate allocation of energy from a restricted energy budget to maintenance and growth. Reduced fecundity may be balanced by increased longevity permitting more potential maturation cycles.

Evolutionary interpretations of observed life history variations, while conceptually appealing, are not uniformly held. Nikolskii (1969) and Bagenal (1978) have cautioned against assuming adaptive significance in life history variations within species in view of the effects of such proximate factors as temperature, light, and food on growth, fecundity, and maturity of fish. Stearns (1977) implies that there is little point in trying to match empirical results to current theories because they are based on such oversimplified assumptions and ambiguities, that contrasting models based on different assumptions produce similar predictions. In a subsequent paper (Stearns 1980), he suggests that life history tactics per se may be intrinsically organized in such a way that they do not respond similarly to selection and as a consequence, the direction of response to a particular set of conditions may not be predictable.

This paper describes the way in which anadromous stocks of cisco (*Coregonus artedii*), lake whitefish (*C. clupeaformis*), and round whitefish (*Prosopium cylindraceum*), occurring along 900 km of the eastern James-Hudson Bay coast, vary in life history. These populations, although subject to some exploitation by native subsistence fisheries (Berkes 1982), are believed to be in stable equilibrium with their physical and biotic environment. They thus provide an opportunity to verify whether shifts in life history traits along a south-north gradient conform to the pattern generally ob-

served and typed "K-selection": increased ages at maturity, fewer but larger young, a longer life expectancy, and smaller reproductive efforts.

This is the first synthesis of information on the biology of the anadromous stocks of whitefish in James-Hudson Bay. These stocks have assumed considerable importance in recent years because of the potential impacts of hydroelectric developments in progress or planned along this coast. The James Bay and Northern Quebec Agreement (1976), Section 24, provides for guaranteed levels of harvest of these species by native fishermen, where stocks permit. Published information on the present status of the stocks will be important when decisions have to be made on the management of native fisheries as conditions along the coast are modified by man.

Materials and Methods

STUDY AREA AND CLIMATE

Cisco, lake whitefish, and round whitefish were collected from the lower portions and estuaries of rivers and in bays along the east coast of James-Hudson Bay (Fig. 1, Table 1). The species are associated with freshwater discharges into the Bay and return to freshwater for reproduction and overwintering (Morin et al. 1981).

The climate of Hudson Bay is arctic; James Bay is milder, but its mean annual temperature is less than most of Canada at similar latitudes (Thompson 1968). The coastlines have continental, rather than maritime, climates as a result of extensive ice cover over several months. There are wide extremes of temperature between winter and summer. The growing season (mean daily temperature $>5.6^{\circ}\text{C}$) ranges from 140 d at Rupert's Bay to 80 d at Innuksuac River (Wilson 1971). The effects upon terrestrial vegetation are evident in the transition from boreal forest along the coast of James Bay and southern Hudson Bay to tundra to the north of Richmond Gulf. The coast is cool during spring and summer, especially in the north, as prevailing winds cross the ice-packed bay and extensive fog banks form along the coastal hills. James and Hudson bays are usually clear of ice from late August until late October (El-Sabh and Koutitonsky 1977; Larnder 1968).

SAMPLING

Most fish collections were made by gillnetting. The most frequently used gill nets measured 45.7×1.8 m and were formed of six panels of multifilament mesh graded 25, 38, 51, 64, 76, and 102 mm (stretched measure). Collections made in Richmond Gulf, Eastmain River, and in the upper La Grande

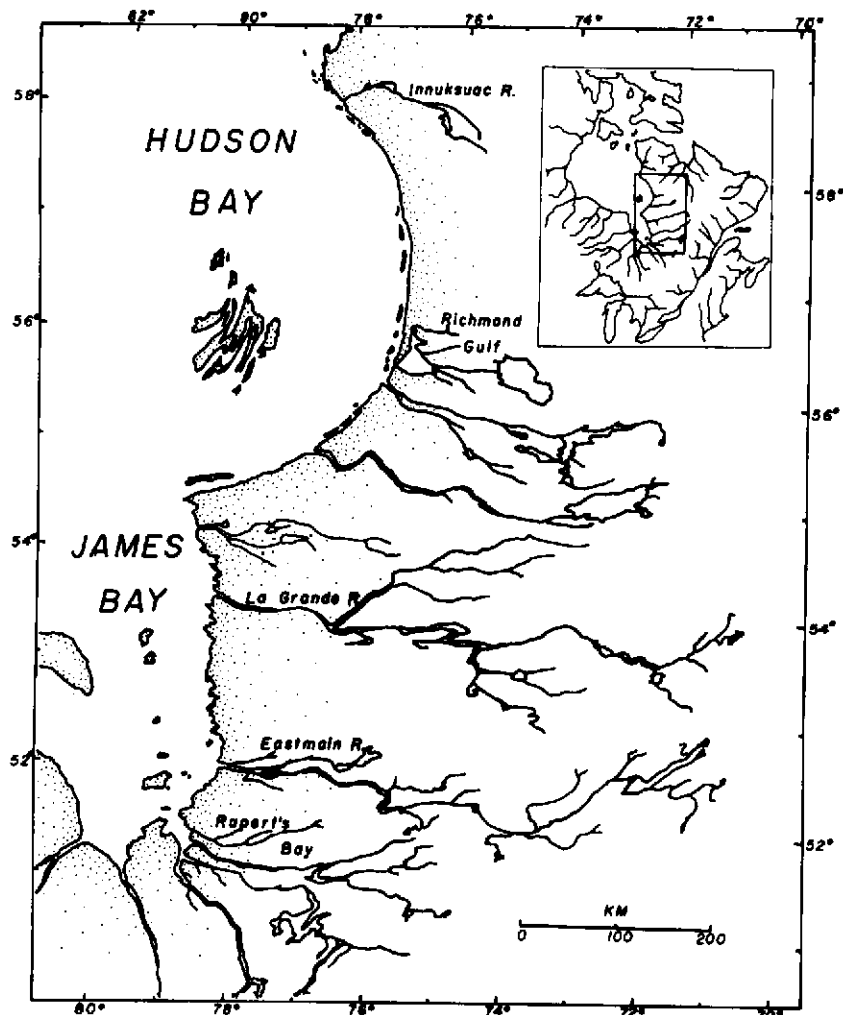


FIG. 1. East coast of James and Hudson bays, indicating the rivers and estuaries studied.

TABLE 1. The major physical characteristics of the rivers studied. Data for Rupert's Bay includes the Nottaway, Broadback, and Rupert rivers. Data for Richmond Gulf is based on measures of the l'Eau-Claire River. Mean breakup date is taken from Wilson (1971).

River	Latitude	Drainage area ($\text{km}^2 \times 1000$)	Mean annual flow ($\text{m}^3 \text{s}^{-1}$)	Mean date of breakup
Rupert's	51°40'	138.0	2549	May 1
Eastmain	52°15'	46.4	603	May 10
La Grande	53°50'	97.6	1700	May 20
Richmond Gulf	56°15'	4.5	86	June 1
Innuksuac	58°26'	11.4	101	June 20

River also included single-meshed gill nets of mesh sizes 38, 51, 64, 89, and 102 mm. Seining was conducted at the rapids of La Grande River for cisco and lake whitefish using the method described by Berkes (1976).

The Eastmain and La Grande rivers, and Richmond Gulf, were sampled from 1973 to 1975. Age, growth, and fecundity analyses for these three sites were based on 1974 data, while analyses of age at maturity and egg size were made by combining data for all years. The growth and age structure of

spawning coregonines in La Grande River are from samples taken at the La Grande River rapids in 1973. Rupert's Bay and the Innuksuac River were sampled in 1976 and 1977, respectively.

LIFE HISTORY VARIABLES

Age was determined from two independent readings for each specimen using scales and/or otoliths for fish aged 1+

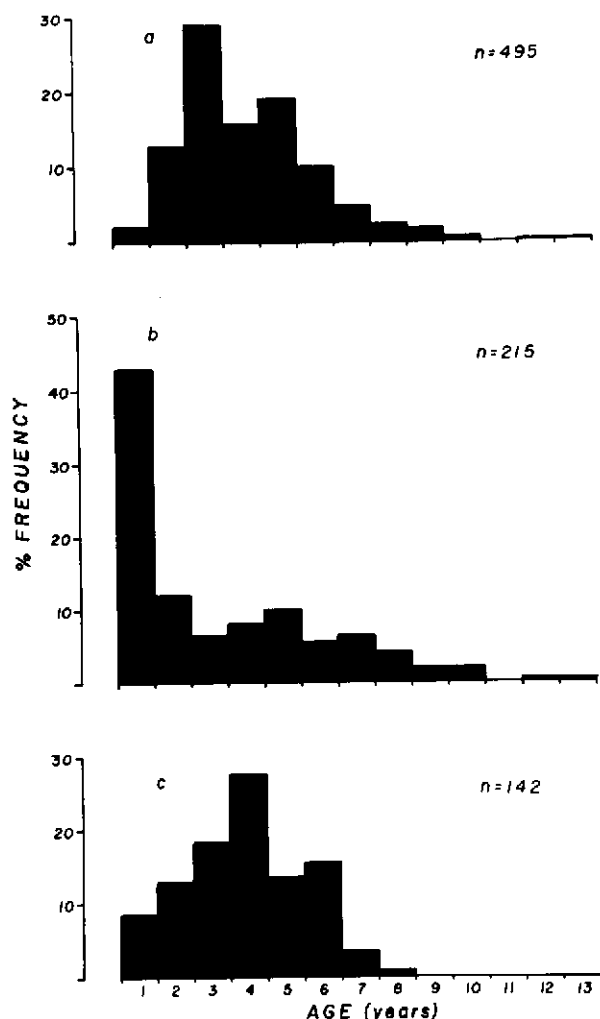


FIG. 2. Age-frequency distributions of (a) cisco, (b) lake whitefish, and (c) round whitefish captured in the lower La Grande River and estuary from July to October 1974.

to 8+ and sectioned otoliths for fish older than 8+. In case of disagreement between the first two readings a third reading was made to determine the age. All whitefish from Richmond Gulf and lake whitefish from the upper La Grande River were aged by scales alone. Age determination of lake whitefish by the scale method frequently underestimates the age of older specimens when compared with the corresponding age determined from otoliths (Power 1978). In the present study, comparisons of age determined by scales and by otoliths indicated that the scales of cisco and round whitefish may underestimate age by as much as 16 yr above a scale age of 8 yr. Caution must be exercised, therefore, in interpreting growth and population structure beyond the 8th year-class where scales only were used.

Back-calculated fork lengths at each scale annulus were fitted to a von Bertalanffy growth model (Abramson 1965) for cisco and lake whitefish of the La Grande River estuary. These data were examined for the presence of Lee's phenom-

enon which might indicate that growth curves were biased by size-selective mortality or by sampling bias (Ricker 1969). Lee's phenomenon was not detected in either the cisco or lake whitefish population of the lower La Grande River. Magnin and Clément (1979) fitted the same model to the back-calculated lengths of round whitefish in the lower La Grande River, and their pertinent results are presented.

Interpopulation comparisons of growth were made by comparing the observed fork lengths at each age-class over the range of estuaries sampled. This procedure was adopted to allow accurate comparisons of growth between young actively growing age-classes and to avoid possible errors from inaccurate age determination using scales for older fish. The Student-Newman-Keuls test (Sokal and Rohlf 1969) was used to test the significance of the differences between mean fork lengths.

All specimens captured were sexed and a descriptive evaluation of the stage of maturity was made. No reliable identification could be made of fish which had never previously spawned; however, maturing fish could be readily identified by mid-July using the criteria outlined by Nikolskii (1963). The complete ovaries of mature females sampled in the Est-main, La Grande, and Innuksuac rivers and Richmond Gulf were preserved in 10% formalin. In the laboratory, the ovaries were weighed to the nearest 0.1 g and rinsed and kneaded to separate the ovarian tissue. Egg diameter was measured taking the mean of four measurements of 10 eggs aligned on a millimetre ruler. Eggs were counted in a subsample of 25 to 30% (up to 5000 eggs), of each set of ovaries. The subsample and the balance of the ovaries were air-dried to a constant weight, then weighed to the nearest milligram, and the number of eggs determined by direct proportion. The comparison of this method with whole counts was made on four specimens, and the difference varied between -0.6 and 1.1%. Healey and Nicol (1975), using similar methods, reported an error of $\pm 2\%$.

Fecundity was regressed on net body weight (whole body weight minus weight of ovaries), and regression lines were compared by analysis of covariance (Snedecor and Cochran 1967). To evaluate the egg size of each species at similar stages of maturity, mean egg diameter was regressed on gonadosomatic index (GSI) and the regression lines compared by analysis of covariance. The gonadosomatic index, determined by dividing the weight of gonads by the total body weight of the fish, also provided a measure of sexual maturity.

The growth and reproductive characteristics of cisco and lake and round whitefish were first compared for La Grande River. La Grande River was chosen because it is located near the middle of the coastal range of sample sites and because the three species cohabit there. Secondly when possible, the same characteristics were compared separately for cisco and lake whitefish among sample sites along the coast. Data on the growth and reproduction of round whitefish were insufficient for a similar analysis of interpopulation variation.

Results

INTERSPECIFIC COMPARISONS — LA GRANDE RIVER

Age frequency — Age-frequency distributions of whitefishes sampled in La Grande River (Fig. 2) show that lon-

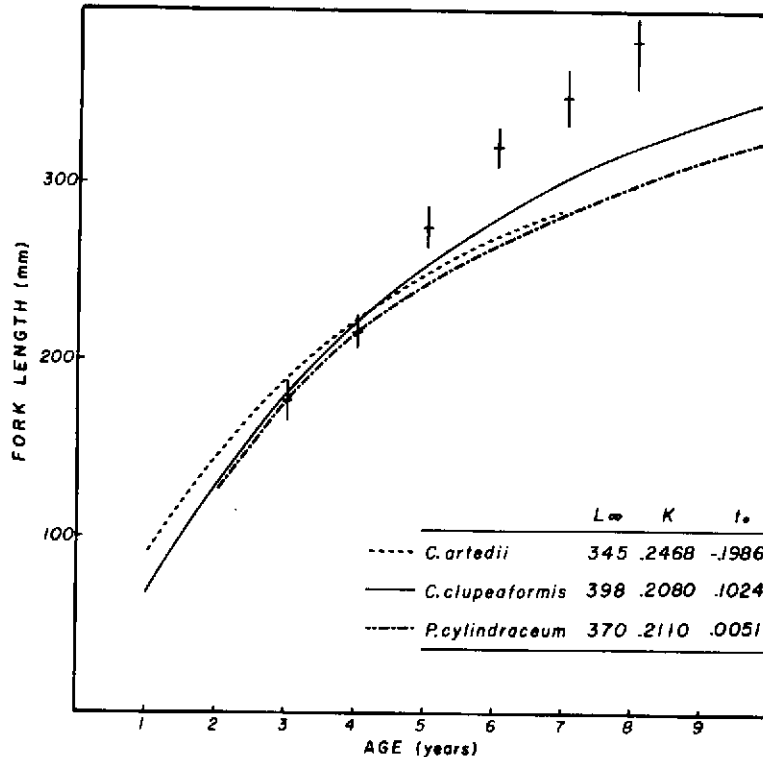


FIG. 3. Back-calculated growth of cisco, lake whitefish, and round whitefish captured in the lower La Grande River and estuary. Horizontal and vertical bars indicate the mean fork lengths and 95% confidence limits, respectively, of lake whitefish captured at the rapids of La Grande River. Curves were modeled according to the von Bertalanffy equation $L_t = L_{\infty} [1 - e^{-k(t-t_0)}]$, where L_t is the fork length at year t ; L_{∞} is the asymptotic fork length; k is a growth coefficient; and t_0 is the time when length would theoretically equal zero.

TABLE 2. Regressions of the logarithm of fecundity (y) on the logarithm of net body weight (x) for cisco, lake whitefish, and round whitefish from La Grande River. n = number of fish sampled; r = correlation coefficient obtained for the two variables x and y ; P = probability level of significance of r .

Species	Regression equation	n	r	P
Cisco	$y = 2.550 + 0.562x$	25	0.74	<0.01
Lake whitefish	$y = 1.973 + 0.787x$	20	0.79	<0.01
Round whitefish	$y = 1.179 + 0.934x$	18	0.73	<0.01

geivity is potentially greatest for lake whitefish followed by cisco and round whitefish. The maximum ages and corresponding fork lengths found over the entire 3-yr sampling period were for lake whitefish 17+ (446 mm), for cisco 13+ (367 mm), and for round whitefish 12+ (390 mm, Magnin and Clément 1979).

Growth — Back-calculated growth curves of the three species in the lower La Grande River and estuary indicate that cisco attain a slightly larger body size in their early years than either round or lake whitefish (Fig. 3). Growth of cisco subsequently diminishes and they reach the smallest asymptotic length.

The von Bertalanffy model of growth calculated for lake whitefish (Fig. 3) captured in the lower La Grande River and

TABLE 3. Regressions of the logarithm of egg diameter (y) on the logarithm of gonadosomatic index (x) for cisco, lake whitefish, and round whitefish from the La Grande River. n = number of fish sampled; r = correlation coefficient obtained for the two variables x and y ; P = probability level of significance of r .

Species	Regression equation	n	r	P
Cisco	$y = 0.912 + 0.280x$	41	0.86	<0.01
Lake whitefish	$y = 0.737 + 0.410x$	20	0.84	<0.01
Round whitefish	$y = 0.168 + 0.232x$	17	0.70	<0.01

estuary predicted an asymptotic fork length (389 mm) much smaller than the fork lengths commonly found in the river system. An analysis of the migrations of anadromous coregonines in La Grande River (Morin et al. 1981) indicated that lake whitefish collections at the river mouth were predominantly of small and juvenile fish with larger and more mature individuals migrating directly to the first rapids of La Grande River for the autumn spawning period. Migrating lake whitefish were not captured by gill nets at the river mouth. A comparison of the back-calculated lengths of lake whitefish captured at the rapids and at the river mouth (Fig. 3) revealed no significant differences for 3- and 4-yr-olds (t -test $P > 0.05$ for both ages). However, the mean fork lengths of 5- to 8-yr-olds captured at the rapids were significantly greater than the same age-groups captured at the mouth of the river (age

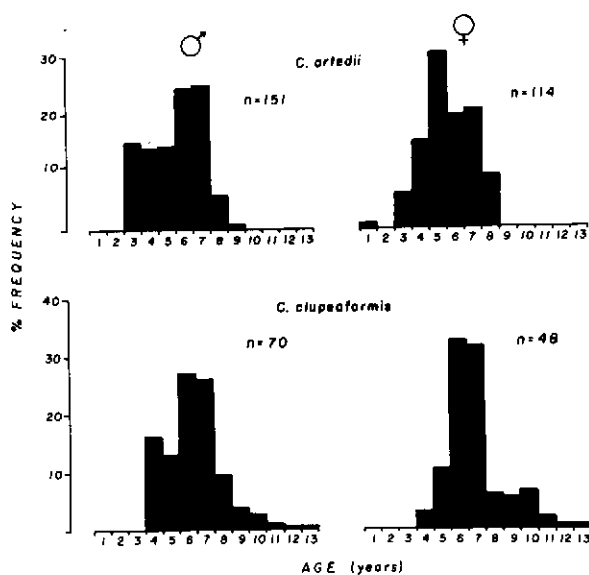


FIG. 4. Age-frequency distributions of spawning cisco (*C. artedii*) and lake whitefish (*C. clupeaformis*) captured at the first rapids of La Grande River, located 37 km upriver, during September and October 1973.

5: $P < 0.05$; age 6: $P < 0.001$; age 7: $P < 0.001$; age 8: $P < 0.001$). Therefore, samples of lake whitefish collected at the mouth of the river were biased towards smaller fish, also lake whitefish achieved the greatest asymptotic length of the three species, probably in the range of 450–500 mm.

Fecundity — No significant difference was observed among the slopes of the regressions of log fecundity on log net body weight in cisco, lake whitefish, and round whitefish (Table 2; analysis of covariance $P > 0.05$). The adjusted mean fecundities of cisco and lake whitefish did not differ significantly ($P > 0.05$), but were both significantly greater than that of round whitefish ($P < 0.001$).

Egg size — No significant differences were found among the slopes of the regression lines of log egg diameter on log gonadosomatic index (GSI) in cisco, lake whitefish, and round whitefish whereas differences between mean egg diameters were highly significant for each set of regressions tested (Table 3; analysis of covariance $P < 0.001$ in each comparison). For equivalent values of GSI, the egg diameter of round whitefish was greatest, that of cisco smallest, and lake whitefish intermediate.

Age at maturity — The ages of spawning cisco and lake whitefish populations, determined from samples taken at the rapids of La Grande River during September and October 1973 (Fig. 4), indicate that cisco mature earlier than lake whitefish. The most abundant age-group for female cisco was 5+, while 6+ and 7+ yr-old females were commonest among the lake whitefish. The most abundant age-classes of mature males for both species were 6+ and 7+ yr-olds. Similar data were unavailable for round whitefish.

In northern fish populations that do not spawn yearly, there is no simple criterion for identifying the age at maturity. There

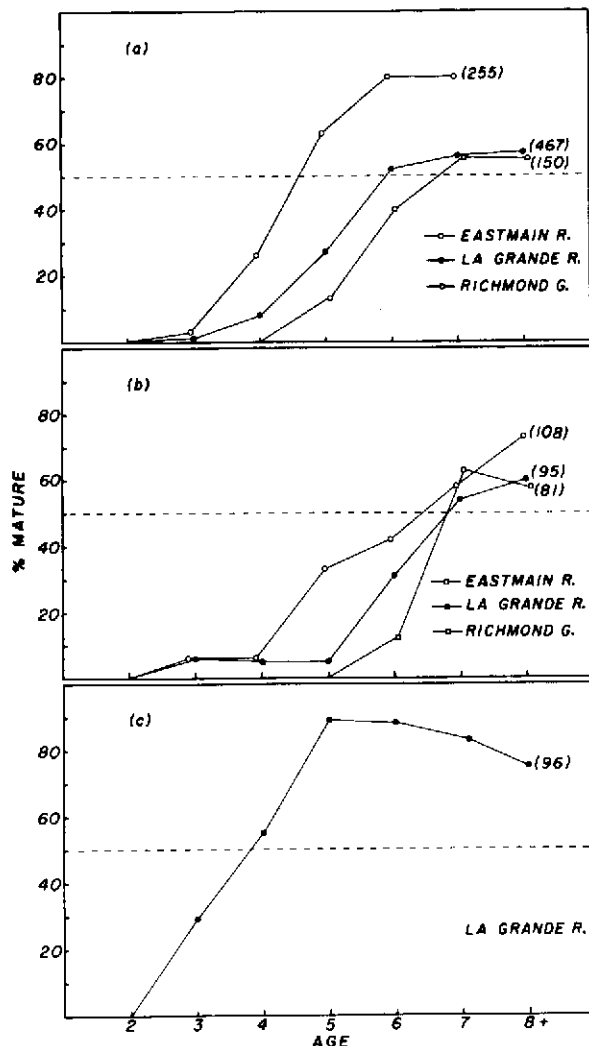


FIG. 5. Percent mature females in each age-class of (a) cisco, (b) lake whitefish, and (c) round whitefish from indicated sites along eastern James-Hudson Bay in 1974. Broken lines indicate the 50% mature level. Numbers in parentheses represent number of fish analyzed from each site.

is normally an increase in the percentage of maturing fish with age which peaks at an age and level set by the frequency of spawning, the age of first maturity, and the pattern of mortality. In this study, the youngest age-group in which at least 50% of the fish were maturing to spawn was adopted as the age of maturity. In La Grande River, round whitefish matured at age 4+, cisco at age 6+, and lake whitefish at age 7+ (Fig. 5).

INTRASPECIFIC COMPARISONS

The growth of cisco declined towards the north of their James-Hudson Bay range. The results of the Student-Newman-Keuls test applied to the observed mean fork lengths of cisco aged 1+ to 7+ (Table 4) indicated that the growth of cisco was significantly less in the Richmond Gulf

TABLE 4. Mean observed fork lengths (mm) of cisco for given age-classes and sampled rivers. Eastmain, La Grande, and Richmond Gulf data are from 1974 summer samples. Rupert's Bay data was taken in spring 1976 and Innuksuac data in summer 1977. Differences in mean fork lengths of ages 1-7 were tested by the Student-Newman-Keuls test, excluding Innuksuac data. Rivers in each age-class are arranged in descending order of mean fork length with horizontal bars underlining nonsignificantly different ($P > 0.05$) mean fork lengths.

Age	River and mean fork length (n)				
1	East	Rup B	La G	Rich G	
	130 (14)	126 (7)	121 (5)	102 (244)	
2	Rup B	East	La G	Rich G	
	190 (17)	187 (175)	186 (33)	175 (8)	
3	East	Rup B	La G	Rich G	Innuks
	241 (205)	231 (30)	227 (75)	195 (58)	196 (3)
4	East	Rup B	La G	Rich G	Innuks
	265 (137)	262 (15)	260 (43)	242 (41)	217 (2)
5	Rup B	East	La G	Rich G	Innuks
	288 (14)	285 (120)	276 (38)	267 (74)	241 (1)
6	Rup B	East	Rich G	La G	Innuks
	310 (10)	297 (74)	294 (47)	292 (17)	273 (1)
7	Rup B	East	La G	Rich G	Innuks
	343 (1)	305 (15)	301 (15)	300 (65)	244 (1)

TABLE 5. Mean observed fork lengths (mm) of lake whitefish for given age-classes and sampled rivers. Eastmain, La Grande, and Richmond Gulf data are from 1974 summer samples. Rupert's Bay data was taken in spring 1976 and Innuksuac data in summer 1977. Differences in mean fork lengths of ages 1-8 were tested by the Student-Newman-Keuls test. Innuksuac data were tested for age-classes 2-4. Rivers in each age-class are arranged in descending order of mean fork length with horizontal bars underlining nonsignificantly different ($P > 0.05$) mean fork lengths.

Age	River and mean fork length (n)				
1	Rup B	La G			Innuks
	126 (13)	121 (100)			122 (1)
2	Rup B	East	La G	Innuks	
	188 (8)	188 (61)	183 (33)	183 (16)	
3	Rup B	Innuks	Rich G	La G	East
	248 (16)	242 (29)	237 (34)	220 (27)	215 (95)
4	Innuks	Rup B	Rich G	La G	East
	304 (38)	285 (13)	260 (14)	257 (27)	257 (21)
5	Rich G	Rup B	La G	East	Innuks
	334 (6)	318 (10)	299 (12)	295 (13)	321 (2)
6	Rich G	Rup B	East	La G	Innuks
	330 (22)	327 (15)	323 (20)	278 (9)	334 (1)
7	Rich G	Rup B	East	La G	Innuks
	375 (12)	347 (11)	337 (46)	323 (17)	421 (1)
8	Rup B	La G	East	Rich G	Innuks
	375 (4)	363 (10)	362 (20)	362 (21)	361 (1)

population over four of the first five year-classes. Limited data presented for the Innuksuac River population (Table 4) suggest that the growth of cisco is further reduced in estuaries north of Richmond Gulf.

The growth of lake whitefish differed significantly in five of the eight year-classes tested over a range of sites (Table 5), but this variation could not be attributed to a latitudinal cline. Over all ages tested, the growth of lake whitefish in Rupert's

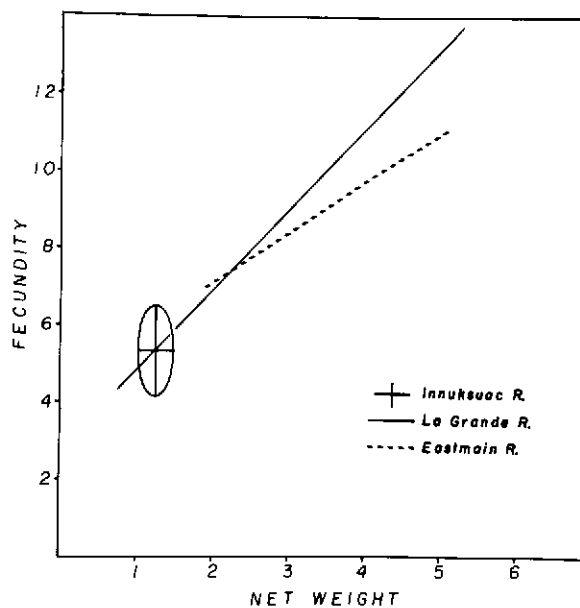


FIG. 6. Comparisons of fecundity (in units of 1000 eggs) net body weight (in units of 100 g) relations for different populations of cisco located along coastal James-Hudson Bay. The mean net weight and mean fecundity of Innuksuac River cisco are indicated by the intersection of horizontal and vertical bars, which also indicate the 95% confidence limits of net weight and fecundity.

Bay was similar to growth in Richmond Gulf or Innuksuac populations.

Female cisco attained 50% maturity at the age of 5+ in the Eastmain River, 6+ in La Grande River, and 7+ in Richmond Gulf indicating increased age of maturity with increasing latitude (Fig. 5). Furthermore, the more northerly cisco skip reproduction more frequently as there were lower percentages of maturing female cisco in the older age-groups from La Grande River and Richmond Gulf than from the Eastmain River.

The age of 50% maturity for female lake whitefish remained at age 7+ in all populations examined (Fig. 5), and percent maturity in the older age-groups remained more or less constant for all three populations. There were, however, more young mature females in the Eastmain population and fewer northwards.

Cisco show no evidence of latitudinal variation in fecundity along the James-Hudson Bay coast. Analysis of covariance indicated no significant difference ($P > 0.05$) between the slopes or elevations of fecundity on length for cisco from Eastmain and La Grande rivers (slopes: $df = 1,32$; $F = 1,319$; means: $df = 1,33$; $F = 0.567$) (Table 6) (Fig. 6). No apparent difference in fecundity can be seen between the Innuksuac sample and the Eastmain and La Grande River samples.

Fecundity of lake whitefish was lower in Richmond Gulf than in La Grande River which may reflect a northward decline in fecundity (analysis of covariance $P < 0.005$) (Table 6).

Because of heteroscedasticity in egg diameter data, the analysis of intraspecific variations in the egg size of cisco and lake whitefish by regression of egg diameter on GSI could not be

TABLE 6. Regressions of the logarithm of fecundity (y) on the logarithm of net body weight (x) for several James-Hudson Bay whitefish stocks. n = number of fish sampled; r = correlation coefficient obtained for the two variables x and y ; P = probability level of significance of r .

Species	Location	Equation	n	r	P
Cisco	Eastmain	$y=4528.7+12.9x$	11	0.60	<0.05
Cisco	La Grande	$y=2709.7+20.9x$	25	0.84	<0.01
Lake whitefish	Richmond Gulf	$y=491.6+18.9x$	23	0.91	<0.01
Lake whitefish	La Grande	$y=357.5+22.9x$	20	0.92	<0.01

carried out. Qualitatively speaking, no obvious differences in egg size between populations were evident.

Discussion

Interspecific comparisons of the life history traits of anadromous cisco and lake and round whitefish of La Grande River indicate patterns that generally conform to the predictions of life history theory when considered in relation to observed patterns of species dominance along James-Hudson Bay. Round whitefish exhibit a "K-selected" pattern of reproductive traits, with notably lower fecundity and larger egg size than cisco or lake whitefish. Round whitefish are more northern in distribution, being present in northern estuaries of James-Hudson Bay, but absent from estuaries of southern James Bay (Morin et al. 1980). In contrast, cisco dominate estuarine species assemblages in southern James Bay, but attain the limit of their distribution in northern Hudson Bay.

Intraspecific comparisons of the life history traits of anadromous cisco and lake whitefish along the James-Hudson Bay coast do not clearly conform to the pattern typed "K-selection." This would predict reduced fecundity, increased age at maturity, and more iteroparity northwards. Our data show that cisco grow more slowly (Table 4), mature older (Fig. 5), but do not exhibit reductions in fecundity (Table 6, Fig. 6) with increasing latitude. Limited evidence suggests that fecundity of lake whitefish diminishes northwards independent of variations in growth whereas age at maturity remains constant along the coast. These ambiguous patterns of reproductive traits may be due to physiological constraints overwhelming expected patterns of coadapted traits, as suggested by Stearns (1980), or be due to comparisons being made over too small a range of environmental conditions so that local variations confuse the general trends. To evaluate these possibilities, the following discussion deals with evidence for the selection of reduced reproductive effort independent of variations in growth within cisco and lake whitefish populations northwards over their North American range and compares such trends with patterns observed over the more-restricted James-Hudson Bay range.

Intraspecific comparisons of the growth and reproductive effort of cisco over their North American range reveal a pattern of decreased fecundity and delayed maturity northwards independent of variations in growth which conforms to the predictions of life history theory. Cisco fecundities decline towards the north of their range (Fig. 7), although limited data are available. Female cisco tend to mature later towards the north of their range, maturing at 1 and 2 yr of age in Clear

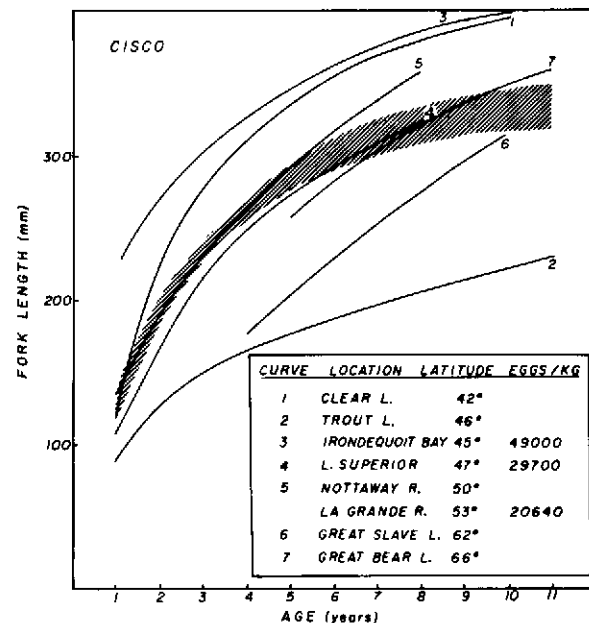


FIG. 7. Growth and fecundity of cisco at various latitudes in North America. Fecundity is expressed as the number of eggs produced by a 1-kg female. The hatched band indicates the range of observed growth of cisco along coastal James Bay. The fecundity of cisco in La Grande River is based on the relation: $\text{eggs} = 2530.2 + 18.1 \text{ body weight}$ ($n = 25$, $r = 0.88$, $P < 0.01$). Data sources are as follows: curves 1 and 2 — Hile (1936); curve 3 — Stone (1938); curve 4 — Dryer and Beil (1964); curve 5 — Magnin (1977); curve 6 — Bond and Turnbull (1973); curve 7 — Kennedy (1949). All curves were fitted by eye to mean fork length data.

Lake and Trout Lake (Hile 1936); at age 5 in Lake Ontario (Stone 1938); and at age 6 in La Grande River.

The growth of James Bay cisco is the same as that of non-anadromous populations at similar latitudes and not appreciably greater or less than more northerly or southerly populations, respectively (Fig. 7). Hile (1936) illustrated the importance of the interactions of biotic and abiotic factors in contributing to the widely varying growth rates of cisco in four Wisconsin lakes (Fig. 7). The growth rate in each lake was related to the length of the growing season and inversely related to the density of cisco in each lake. According to scale analysis, cisco grew during a period of over 5 mo in Clear Lake and 3 mo in Trout Lake. The reduced growing period in Trout Lake was attributed to less food availability and earlier gonad development, factors that might also be related to the

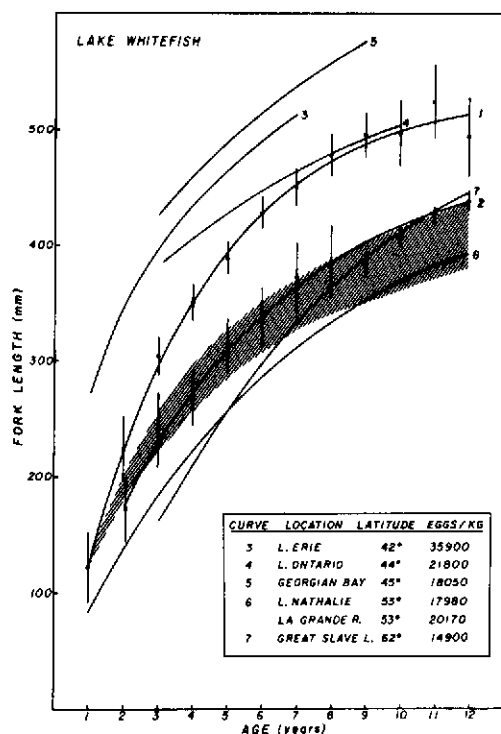


FIG. 8. Growth and fecundity of lake whitefish at various latitudes in North America and at different levels of exploitation. Curves 1 and 2 show the growth of lake whitefish at medium and low levels of exploitation, respectively, with mean fork length and standard error indicated for each year-class (based on Healey 1975). Fecundity is expressed as the number of eggs produced by a 1-kg female. The hatched band indicates the range of observed growth of lake whitefish along coastal James-Hudson Bay. The fecundity of lake whitefish in La Grande River is based on the relation: $\text{eggs} = 170.4 + 20.0 \text{ body weight}$ ($n = 20$, $r = 0.92$, $P < 0.001$). Data sources are as follows: curve 3 — Van Oosten and Hile (1947), (fecundity — Lawler 1961); curve 4 — Hart (1931); curve 5 — Cucin and Regier (1966); curve 6 — Dumont and Fortin (1978); curve 7 — Kennedy (1953). All curves were fitted by eye to mean fork length data.

higher density of cisco in Trout Lake. The anadromous cisco of James Bay have an approximate 4-mo growing period in estuarine and nearshore feeding conditions, and density effects such as found in lake populations probably do not operate in this environment.

The cisco populations of James-Hudson Bay do not exhibit the expected pattern of reduced reproductive effort independent of variations in growth with increasing latitude observed over their North American range. As cisco reach the northern limit of their coastal range in Hudson Bay (Morin et al. 1980), reduced growth may be due to colder temperatures and shorter growing seasons. The later maturity observed may result from reduced growth while the fecundity of cisco, which remains unchanged along the coast, may already be minimal. The observation that the more northerly cisco skip reproduction more frequently than the Eastmain population represents one way in which reproductive effort can be reduced beyond a minimal fecundity. Therefore, these changes along the James-Hudson Bay coast may not represent adap-

tive strategies, but responses to temperature stress whereby further trade-offs in energy allocation between reproduction and growth is physiologically not possible.

Intraspecific comparisons of the reproductive effort of lake whitefish over their North American range reveals a pattern of decreased fecundity and delayed maturity with increasing latitude and conforms to the pattern predicted by life history theory. Lake whitefish fecundities generally decline towards the north of their range (Fig. 8). Female lake whitefish tend to mature later towards the north of their range, maturing at age 4 in lake Erie (Lawler 1961), at age 5 in Georgian Bay (Cucin and Regier 1966), at age 7 in La Grande River, and at age 8 in Great Slave lake (Kennedy 1953).

The relationship between lake whitefish growth, fecundity, and latitude is ambiguous and confounded by the effects of exploitation. Healey (1975) reviewed the data on lake whitefish growth and found that growth in unexploited populations was inferior at the northern and southern limits of its range, with best growth occurring in regions with 890–1200 degree days above 5.6°C. Air temperatures along the eastern coast of James-Hudson Bay are below the optimal temperature range with 890 degree-days above 5.6°C at Rupert's Bay decreasing to 330 degree-days above 5.6°C at the Innuksuac river (Wilson 1971). Growth, however, is positively affected by exploitation (Healey 1975, 1980), and James-Hudson Bay lake whitefish exhibit growth similar to that in lake populations at low levels of exploitation and greater than that in unexploited lake populations at similar latitudes. Healey (1978) reported that increased fecundity in lake whitefish populations following exploitation was not apparently related to more rapid growth.

The lake whitefish populations of James-Hudson Bay exhibit reduced fecundity northwards independent of variations in growth, and this conforms to the pattern predicted by life history theory. These observations may constitute limited evidence for an adaptive strategy. This conclusion is supported by the observation that lake whitefish maintain their abundance along the coast of Hudson Bay (Morin et al. 1980).

In conclusion, predictions based on life history theory could not be consistently satisfied by the comparison of life history traits at the species and population levels. Interspecific comparisons generally conformed to predictions when considered in relation to observed patterns of coregonine species dominance along James-Hudson Bay. Intraspecific comparisons, while conforming to the predictions of life history theory over the North American range of cisco and lake whitefish, revealed only weak evidence for adaptiveness along James-Hudson Bay and more likely represent the physiological consequences of harsher climatic conditions at northern sites of James-Hudson Bay.

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