

Freshwater Migration as a Determinant Factor in the Somatic Cost of Reproduction of Two Anadromous Coregonines of James Bay¹

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We tested the hypothesis that the species-specific costs of migration differentially affect reproductive effort and somatic cost of reproduction in sympatric anadromous populations of cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) of James Bay. Reproductive effort, which includes the energy cost of migration, is higher for cisco. Female cisco allocate more energy to reproduction than its total energy gain. The energy invested by lake whitefish in reproduction is approximately equal to its seasonal energy gain. Reproduction results in large differences in the energy content of gonads, viscera, and carcass between reproductive and nonreproductive fish of the same length. Neither cisco nor lake whitefish are able to spawn two years in succession. The somatic energy increase of reproductive female cisco is 121% lower than the somatic energy increase of nonreproductive females; similar comparisons are 89% (female) and 103% (male) for lake whitefish. The energy cost of migration is largely responsible for the higher somatic cost of reproduction observed for cisco. These different somatic costs of migration are related to resource accumulation prior to migration and to differences in the aerobic cost of swimming between the two species in combination with the difficulty of the freshwater migration.

Nous avons testé l'hypothèse selon laquelle, le coût énergétique de la migration avait une influence importante dans la détermination de l'effort reproducteur et du coût somatique de la reproduction chez les populations sympatriques anadromes du cisco (*Coregonus artedii*) et du grand corégone (*C. clupeaformis*) de la baie James (Québec). L'effort reproducteur, qui inclut le coût énergétique de la migration, est supérieur dans le cas du cisco. Les femelles du cisco allouent plus d'énergie à la reproduction qu'elles n'en accumulent au cours de la saison alors que chez le grand corégone, l'énergie investie dans la reproduction est approximativement égale à l'augmentation totale en énergie pendant la saison. De larges différences dans le contenu énergétique des gonades, des viscères et de la carcasse entre les poissons reproducteurs et non-reproducteurs de même taille sont observées. Le cisco et le grand corégone sont incapables de se reproduire pendant deux années consécutives. Les femelles reproductrices du cisco ont un investissement somatique en énergie inférieur de 121% à celui des femelles non-reproductrices; par comparaison, on observe des valeurs de 89% (femelle) et 103% (male) chez le grand corégone. Le coût énergétique de la migration est en grande partie responsable du coût somatique plus élevé de la reproduction chez le cisco. Cette différence dans le coût de la migration est reliée à l'accumulation d'énergie avant la migration et au différent coût aérobique de natation entre les deux espèces, associé à la difficulté de la migration en eau douce.

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The energy cost of anadromous migration is potentially an important parameter of fish reproductive patterns. This cost may influence fecundity, growth, and maintenance because energy devoted to migration will reduce energy available for other functions (Glebe and Leggett 1981). The theoretical basis of our study on sympatric anadromous populations of cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) of James Bay (Québec) is that migration and reproduction are functionally related through partitioning of a limited energy resource. We hypothesized that the energy cost of freshwater migration, through its influence on reproductive effort and somatic cost of reproduction, is an important parameter in

determining different reproductive patterns of anadromous coregonine populations.

Accessory activities, like spawning behavior, territoriality on the spawning grounds or live bearing of young, may be more important in reproductive effort than the production of gonads. In anadromous species, migration affects the somatic cost of reproduction and survival. This is demonstrated by the extensive energy depletion and high spawning and postspawning mortality in many anadromous fish species (reviewed by Glebe and Leggett 1981). Bell (1980) provides evidence of a correlation between the degree of anadromy (migration distance) and the rate of adult survival. The most anadromous species that make extensive ocean migrations are semelparous whereas the least anadromous species with oceanic migrations that are short and confined to coastal and estuarine waters are all iteroparous. However, the correlation between gonad/total weight ratio and the rate of adult survival was weak. Similar gonad/total weight ratios were found in both semelparous and iteroparous species

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suggesting the importance of the degree of anadromy in determining adult survival.

The anadromous populations of cisco and lake whitefish in James Bay provide an excellent opportunity to study the contribution of migration cost to reproductive effort and somatic cost of reproduction. In the Eastmain River (Fig. 1), cisco and lake whitefish migrate the same distance and use the same spawning grounds. The cost of migration, based on weight loss studies, is apparently high for both species largely due to the long period (2–3 mo) fish spend in the river without feeding prior to spawning (Dodson et al. 1985). In addition, the 7-km section of rapids fish must ascend to reach the spawning grounds may represent a major difficulty for both cisco and lake whitefish. A low metabolic scope for activity combined with a high net aerobic cost of swimming led Bernatchez and Dodson (1985) to conclude that the swimming performance of cisco and lake whitefish was poor compared with most salmonids. The higher net aerobic cost of swimming for cisco (Bernatchez and Dodson 1985) and its smaller size should result in a higher cost of migration compared with lake whitefish.

The purpose of this study was to test the hypothesis that the species-specific costs of migration differentially affect reproductive effort and the somatic cost of reproduction for cisco and lake whitefish. Because of their smaller size and greater swimming costs, we proposed that cisco's migration costs should be higher than those of lake whitefish resulting in a higher somatic cost of reproduction.

The specific objectives of this study were: a) to estimate the somatic cost of reproduction, first by estimating seasonal energy increase in reproductive and nonreproductive fish and second by estimating the reduction in somatic energy increase caused by reproductive effort; b) to estimate the importance of the energy cost of migration in the somatic cost of reproduction and; c) to calculate if the energy cost of migration was higher in cisco resulting in a higher somatic cost of reproduction compared with lake whitefish.

Materials and Methods

Sampling

Seasonal migration patterns of cisco and lake whitefish were documented between 1979 to 1981 by recording changes in catch per unit effort and length composition of gill net samples obtained from mid-May (spring thaw) to late October (winter freeze-up) in the Eastmain River and adjacent areas (Lambert and Dodson 1982a,b).

Seasonal changes in energy content associated with migration and reproduction were documented by quantifying absolute changes in weight and energy content for reproductive and nonreproductive fish sampled along their general migratory route. As neither cisco nor lake whitefish appear to spawn yearly once maturity is reached (Morin et al. 1982), reproductive and nonreproductive fish of similar lengths are common in the populations of both species. Sampling was conducted between May 1982 and May 1983 and concentrated on adult fish. Adult fish were defined as fish which exceeded the length at which 50% of the fish were mature (>26 cm for cisco and >34 cm for lake whitefish). Ten reproductive and 10 nonreproductive adults of each sex and each species were sampled whenever possible according to the following schedule: (a) spring break-up (15–30 May 1982) at the mouth of the Eastmain River (Fig. 1) during seaward migration of both species following

overwintering; (b) mid-July to the end of July along the coast and in the vicinity of islands situated 15–20 km north of the river during the feeding migration of both species; (c) mid-August to the end of August at the mouth of the Eastmain River for the return migration of spawning adults and along the coast north of the river for nonreproductive adults; (d) mid-September at the base of the first rapids (Fig. 1) for reproductive adults and along the coast for nonreproductive adults; (e) mid-October to the end of October on the spawning grounds for reproductive adults and below the rapids and at the river's mouth for nonreproductive adults entering into freshwater for overwintering; (f) early November below the rapids for spent fish; (g) spring break-up (May 1983) at the river's mouth to complete one annual cycle. Fish identified as reproductive individuals represent fish that were spawning in 1982.

Nonreproductive females were identified in the spring of 1982 by the presence of unresorbed eggs and flaccid appearance of the ovaries. These fish spawned in fall 1981 but were unable to spawn in 1982. The identification of nonreproductive males in the spring of 1982 was more subjective and was based on the flaccid appearance of the testes. Between July and November, maturity stages using the classification of Nikolskii (1963) and the gonadosomatic index (weight of the gonads as a proportion of body weight) were used to identify reproductive and nonreproductive fish. It is probable that fish identified as nonreproductive individuals between July and November include repeat spawners that had skipped spawning and late maturing virgin fish that never spawned as the two groups are indistinguishable during this period.

Sampling was done with experimental gill-nets measuring 45.7 m by 2.4 m and comprising six panels graded from 25 to 102 mm mesh size (stretched measure). After capture, fish were kept on ice and were processed within 5 h. For each fish, fork length was measured to the nearest 0.1 cm and otoliths removed for age determination. Gonad, viscera, liver, and carcass weight (whole eviscerated body, including head, skeleton and muscle) were recorded to the nearest 0.01 g and each tissue was individually frozen for further analysis of energy content in the laboratory. A total of 672 fish were processed and kept for energy content analysis.

Proximate Analysis

Energy content of each fish was determined by the energy equivalence of protein and fat content of gonad, liver, viscera and carcass. Determinations of protein, fat, and moisture content were made for each tissue that had been previously homogenized (whole tissue). Determinations were performed in duplicate (two homogenized tissue samples) and a mean value was calculated except for tissues weighing less than 1 g where only one determination each was made. The mean difference between duplicate samples as percent of wet weight was less than 1% for carcass fat, protein, and moisture content. For other tissues, the mean difference between duplicate samples for fat, protein, and moisture content was less than 2%.

Moisture content was determined by drying 1 to 25 g samples to a constant weight at 80°C. Fat content was determined by the method of Bligh and Dyer (1959) with samples of 25 g for carcass tissue. Gonad, viscera, and liver fat contents were determined for 2-g samples by the combination of two methods: extraction according to Bligh and Dyer (1959) and determination of fat content by the colorimetric method by Kibrick and Skupp (1953) as modified by Fales (1971). Total nitrogen con-

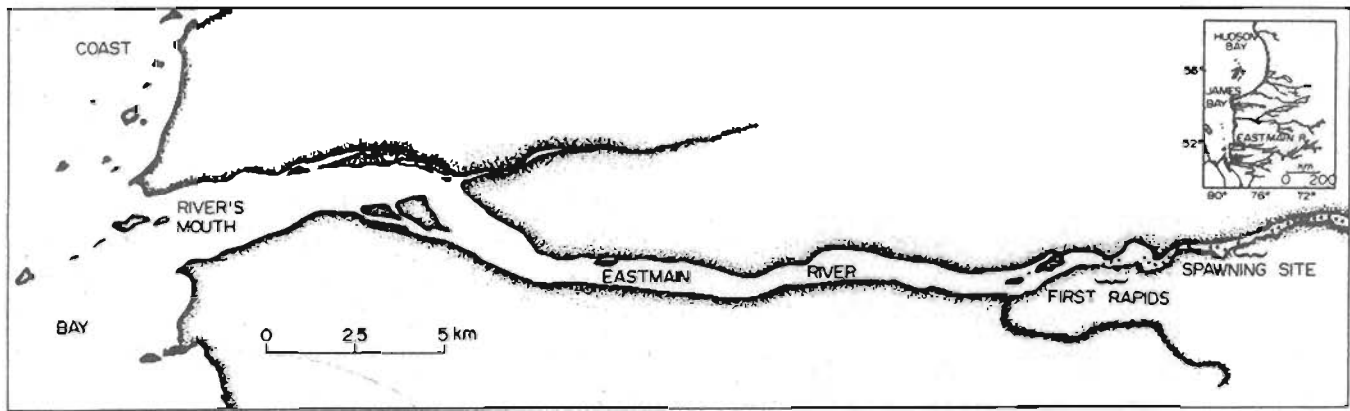


Fig. 1. Location map of the Eastmain River along the Eastern coast of James and Hudson bays with the indication of the spawning grounds for cisco and lake whitefish and position of the rapids.

tent was determined by micro-Kjeldahl digestion of 1-g samples followed by the Berthelot reaction (Haslemore and Rougham 1976; Dutil 1982). Correction for nonprotein nitrogen was done for the carcass (Niimi 1972). Protein content was estimated by multiplying nitrogen values by 6.25 (Dowgiallo 1975).

Energy contents were determined by applying the energy equivalents $2.4 \cdot 10^4 \text{ J} \cdot \text{g}^{-1}$ for protein and $4.0 \cdot 10^4 \text{ J} \cdot \text{g}^{-1}$ for fat (Kleiber 1975).

Energy Changes

Changes in energy content of different tissues at successive stages of migration were quantified by deriving linear regressions of tissue energy content on length (logarithmic transformed data) for reproductive and nonreproductive fish of each sex and species at each sampling site along the migratory route. Comparisons of the appropriate significant linear regressions were done by analysis of covariance (Sokal and Rohlf 1981). When the linear regression was not significant (slope 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 energy content from linear regressions for the same length were done with *t*-test (Zar 1974).

Fat, protein, and energy of carcass and viscera utilized during freshwater migration and overwintering were estimated for both sexes and species. Calculations were made from observed values at the end of freshwater migration and overwintering and calculated values from linear regressions before freshwater migration and overwintering. Relative levels of fat, protein, and energy content between reproductive and nonreproductive individuals at the end of the season (October) were also calculated from observed values of reproductive individuals and calculated values from linear regressions for nonreproductive individuals. Interspecific comparisons were done with Mann-Whitney U-test (Sokal and Rohlf 1981).

Absolute energy changes for each tissue were determined from linear regressions at each sampling site for a standard fish of each species. The length of a standard reproductive or nonreproductive fish corresponds to the observed mean length of reproductive adults of each species at the time of spawning; 29.0 cm for cisco and 36.5 cm for lake whitefish. Otoliths were used to calculate seasonal increase in length and the length of standard fish at different periods of the season in order to take into account the growth of the "standard" fish. Methods for

age determination and calculations of seasonal increase in length are described in Lambert and Dodson (1990).

Cost of Reproduction and Migration

Comparisons between somatic and reproductive investments of "standard" reproductive fish captured along the migratory route with those of "standard" nonreproductive fish were used to estimate reproductive effort, cost of reproduction, and cost of migration. These terms were estimated with the basic parameters defined by Tuomi et al. (1983):

I_n = the somatic energy increase of nonreproductive fish (which is equivalent to the total energy gain of nonreproductive fish)

I_s = the somatic energy increase of reproductive fish

I_r = the reproductive investment of reproductive fish

I_a = the total energy gain of reproductive fish ($I_s + I_r$).

Total energy gain represents the proportion of ingested energy (from feeding) available for growth and reproduction. The difference in total energy gain between reproductive and nonreproductive fish (R_a) was estimated by the difference between total energy gain of reproductive fish and somatic energy increase (total energy gain) of nonreproductive fish. Reproductive effort (R_e) was defined as the ratio of energy investment in reproduction on the maximum somatic energy content of reproductive fish. The absolute cost to somatic energy increase caused by reproduction (R_c) was estimated as the difference between somatic energy increase of reproductive and nonreproductive fish. The somatic cost of reproduction (RE_c) was measured by the extent to which reproduction reduced the somatic energy increase of reproductive fish below the level of nonreproductive fish.

The importance of the reproductive migration on somatic energy increase was estimated by evaluating migration effort and by comparing energy loss for migration and energy investment in the gonads. Migration effort (MG_e) was defined as the ratio of the energy loss for migration (MG) on the maximum somatic energy content of reproductive fish.

The basic parameters were estimated by energy changes of "standard" reproductive and nonreproductive fish. The somatic energy increase of nonreproductive fish (I_n) was calculated as the somatic energy increase (sum of carcass, viscera, and liver energy content) of nonreproductive fish between May and October 1982. The somatic energy increase of reproductive fish (I_s) was calculated as the net somatic energy increase of repro-

TABLE 1. Mean increase in length (mm) of reproductive (R) and non-reproductive (NR) cisco and lake whitefish of each sex of the same age. Cisco, 5 to 6 yr, lake whitefish, 6 to 7 yr.

		Mean (mm)	SD	n
Cisco				
Female	R	8.7	3.6	27
	NR	9.9	5.0	24
Male	R	10.9	5.7	36
	NR	11.2	3.3	10
Lake Whitefish				
Female	R	14.1	5.5	26
	NR	15.1	6.0	23
Male	R	15.8	7.0	33
	NR	18.0	6.3	9

ductive fish between May and early November 1982 (after spawning) following somatic energy depletion caused by reproduction. The reproductive investment of reproductive fish (I_r) was calculated as the sum of the energy increase in the gonads (I_g) between May and October 1982, the energy loss during spawning (due to spawning behavior and return of fish below the rapids after spawning) and the energy loss for migration (MG). The energy loss for migration was calculated as the difference between the somatic energy loss during freshwater migration (August to October for cisco and July to October for lake whitefish) and the energy increase in gonads during the same period of time (I_{gm}). The energy loss for migration between August and October was also calculated for lake whitefish (Mg) in order to compare the energy loss of both species during the period which fish ascend the rapids. Finally, the total energy gain of reproductive fish (I_a) was estimated as the sum of somatic energy increase and reproductive energy investment of reproductive fish.

The energy cost of overwintering (energy loss from November 1982 to May 1983; W_a for reproductive fish and W_n for nonreproductive fish) was also calculated as a proportion of the maximum energy content for both reproductive and nonreproductive fish. The total energy expenditures for migration, reproduction, and overwintering (TEC_r) were also expressed as a proportion of the maximum energy content.

Results

Increase in Length and Energy Changes

Within species, reproductive and nonreproductive individuals of both sexes of the most abundant age classes (cisco, 5 to 6 yr, lake whitefish 6 to 7 yr) showed similar increases ($P > 0.05$) in length over the growing season (Table 1). Nonreproductive individuals did not appear to devote any of their surplus energy to increase their length. However, differences ($P < 0.05$) in energy content between reproductive and nonreproductive individuals were observed during the growing season (Fig. 2). In May 1982, nonreproductive individuals of each sex (except for female lake whitefish) had lower energy content ($P < 0.05$) than reproductive individuals measuring the same length. By the end of October nonreproductive fish had higher energy content ($P < 0.05$) than reproductive fish due to the later's energy loss associated with freshwater migration and gonad maturation.

Cisco

In cisco, a significant increase ($P < 0.05$) in total and somatic energy content was observed between May and August for reproductive fish prior to freshwater migration (Fig. 2). From August until November, when the fish spawn, there was a significant decline ($P < 0.05$) in somatic energy content. During the same period, the energy content of the gonads increased to reach a maximum at the end of October (Fig. 3). Finally a decrease ($P < 0.05$) in somatic energy content was observed during the winter (beginning of November to the end of May). In nonreproductive cisco, energy content increased ($P < 0.05$) between May and October followed by a decline ($P < 0.05$) during the winter.

In nonreproductive fish, no changes in gonad energy content ($P > 0.05$) were observed during the season (Fig. 3). In reproductive females, maximum gonad energy content was reached near the end of October prior to spawning (387 kJ). Gonad development was not complete at river entry. An increase of 217 kJ (128%) in gonad energy content was observed between the end of August and the end of October during freshwater migration for females (Fig. 3). In males, the energy investment in the testes was much less (6 kJ) and the energy increase during freshwater migration was lower (32%).

Associated with maturation and freshwater migration, significant differences in carcass and viscera energy content were observed between reproductive and nonreproductive fish. In nonreproductive fish, increases in carcass and viscera energy content ($P < 0.05$) occurred during the summer and energy levels remained relatively stable until the end of October (Fig. 3). In reproductive fish, carcass and viscera energy ($P < 0.05$) increased during the summer with the maximum level observed at the end of August. During the freshwater migration, carcass and viscera energy content declined ($P < 0.05$). In female cisco (Fig. 3) carcass energy content decreased by 901 kJ (48%) and viscera energy content by 66 kJ (63%).

Carcass was the main source of energy used to complete gonad maturation and to fuel the freshwater migration. In female cisco, carcass energy decrease represented 92% of the total energy loss compared with 7% for viscera and only 1% for liver. In male cisco, the carcass energy decrease was 381 kJ (22%) but spent fish could not be sampled because the lower part of the Eastmain River froze before the end of spawning. As spawning activities can be costly, carcass energy decrease for male cisco was underestimated because the spawning period was missed. Even though underestimated, carcass energy was the main source of energy used during freshwater migration for male cisco and represented 83% of the total energy loss. The decline in viscera energy (67 kJ) for male cisco was similar to that of females following spawning suggesting that most of the energy available had been used prior to spawning. In fact, the energy level in male viscera did not change ($P > 0.05$) from October 1982 to May 1983 (Fig. 3).

Comparisons between reproductive and nonreproductive cisco show that fish that did not reproduce reached ($P < 0.05$) higher carcass and viscera energy levels in October even though they had significantly lower carcass and viscera energy in May (Fig. 3). After spawning (November), carcass and viscera energy reserves of reproductive females represented 58 and 17%, respectively of the carcass and viscera energy content of nonreproductive females. In males, carcass and viscera energy of reproductive individuals prior to spawning in October were also lower (72% of carcass energy and 23% of viscera energy) than those of nonreproductive males (Fig. 3).

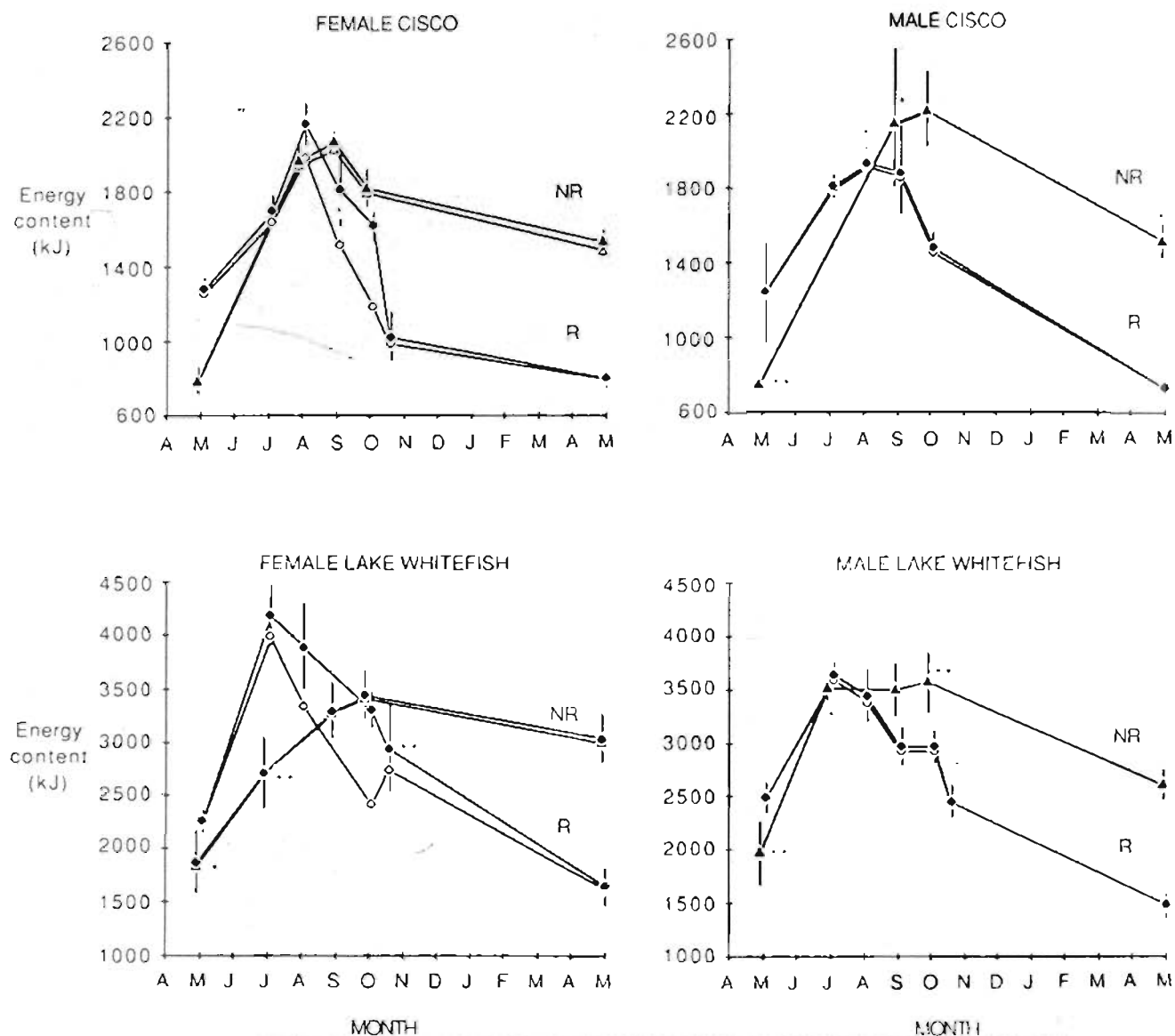


FIG. 2. Total and somatic content of standard reproductive (R) and nonreproductive (NR) cisco and lake whitefish sampled from May 1982 to May 1983 along their migratory route. Upper line (closed dots) indicates total energy content and lower line (open dots) indicates somatic energy content. Vertical bars indicate standard errors of total energy content derived from regression analysis. Regressions were significant at $P < 0.05$ level except as indicated by + where $0.05 < P < 0.10$ and by ++ where the regression was not significant; in such a case the mean value was presented. This convention is repeated in subsequent figures.

During overwintering, nonreproductive cisco rely on their carcass and viscera energy reserves but reproductive fish draw energy from their carcass energy reserves only (Fig. 3). In nonreproductive female and male cisco, 19 and 20%, respectively of the energy lost during winter came from the viscera energy reserves.

Lake whitefish

In lake whitefish, the same general pattern of total and somatic energy changes were observed (Fig. 2). The only difference with cisco was that the maximum energy level of reproductive fish was reached at the end of July instead of August. The analysis of variations in energy content of the different tissues (Fig. 4) indicate that female lake whitefish invested energy in gonads during freshwater migration. The increase in energy content of gonads between August and October was 347 kJ representing an increase of 66%. In males, the maximum

energy content in the testes was observed before the freshwater migration (Fig. 4). The apparent energy decrease in testes during freshwater migration was not significant ($P > 0.05$).

In nonreproductive males and females, significant increases in carcass and viscera energy content ($P < 0.05$) occurred between May and October 1982.

In reproductive males and females, carcass reserves were also the main source of energy to complete gonad maturation and freshwater migration. Carcass energy decrease of male and female lake whitefish represented 78% (895 kJ) and 75% (1172 kJ), respectively of the total energy lost during freshwater migration (Fig. 4). Viscera energy reserves used by male and female lake whitefish represent 19% (218 kJ) and 22% (345 kJ) of the total energy expended during freshwater migration. The liver was not an important organ for storage of energy, representing only 3% (48 kJ) of the energy used during freshwater migration.

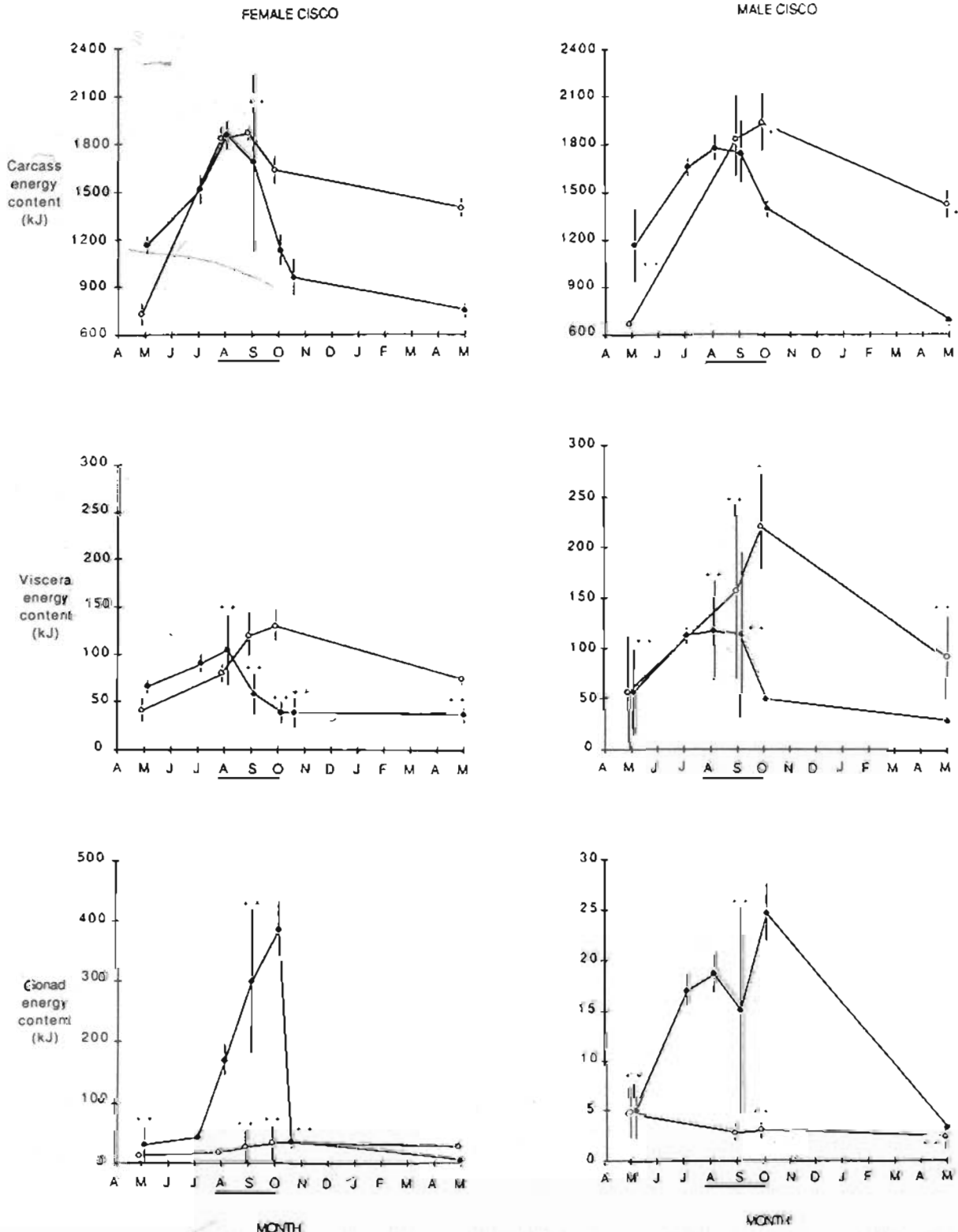


FIG. 3. Energy content (kJ) in the different tissues of standard reproductive (-♦-) and nonreproductive (-○-) cisco sampled from May 1982 to May 1983 along their migratory route. Solid horizontal lines represent the period of time between the beginning of migration and the beginning of spawning.

While overwintering, nonreproductive lake whitefish used both their carcass and viscera energy reserves whereas reproductive individuals used only carcass energy reserves. Viscera energy reserves represent 16 (male) and 33% (female) of the total energy loss during the overwintering period for nonre-

productive lake whitefish (Fig. 4).

Interspecific comparisons

Female lake whitefish used a smaller proportion of their carcass energy reserves and a greater proportion of their viscera

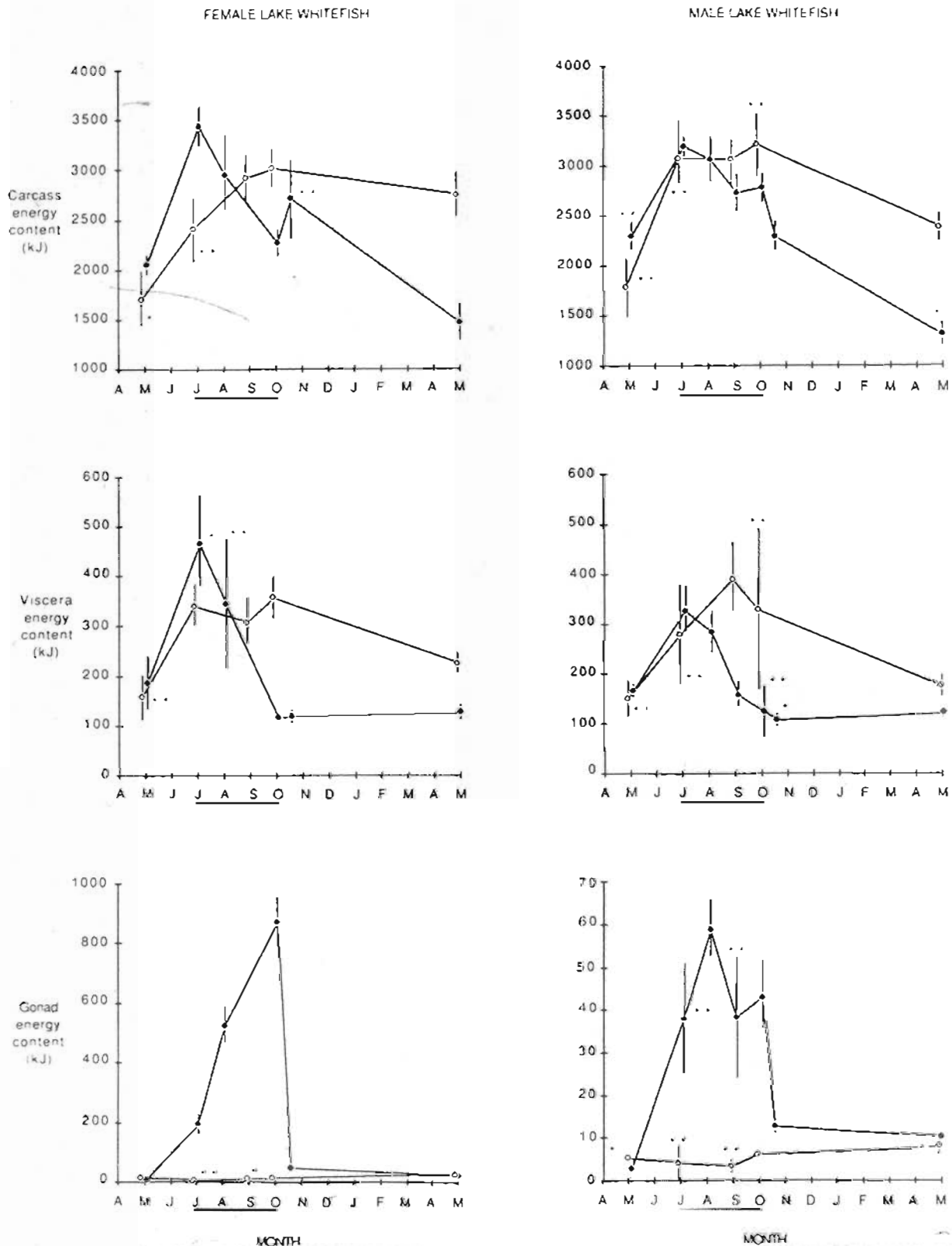


FIG. 4. Energy content (kJ) in the different tissues of standard reproductive (\blacklozenge) and nonreproductive (\circ) lake whitefish sampled from May 1982 to May 1983 along their migratory route. Solid horizontal lines represent the period of time between the beginning of migration and the beginning of spawning.

energy reserves than did female cisco. Based on tissue energy content following freshwater migration and spawning (Fig. 5), female lake whitefish carcass and viscera energy decreased by 34 and 75%, respectively compared to 49 and 61% for female

cisco. Comparisons between males after spawning could not be made because of the incomplete sampling of male cisco. However, comparisons of the data before spawning (Fig. 5) indicate that male lake whitefish used a greater proportion of their vis-

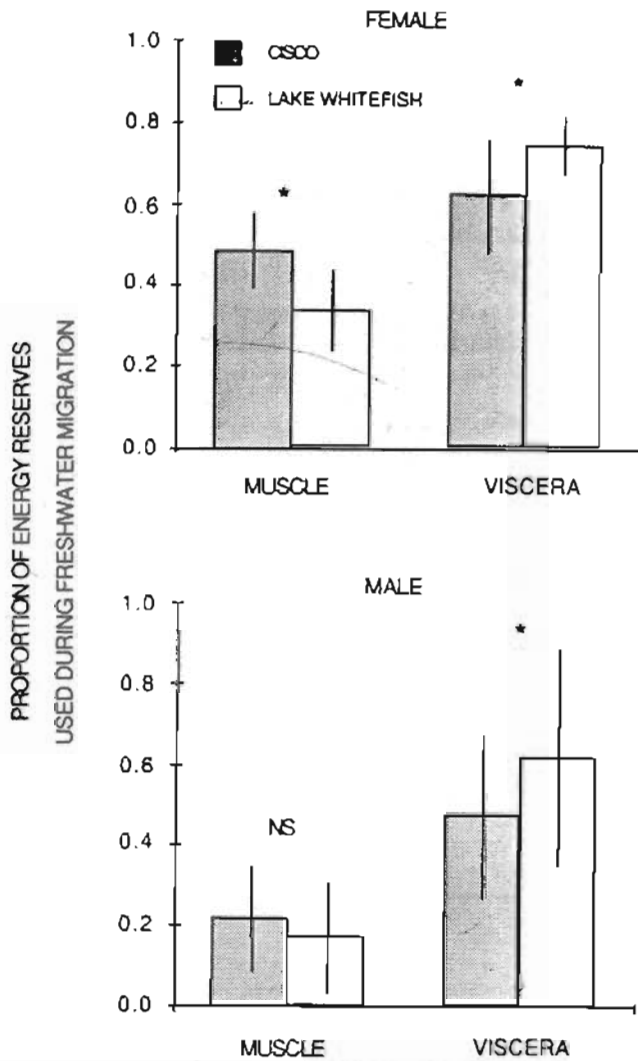


FIG. 5. Relative carcass and viscera energy decrease of reproductive cisco and lake whitefish during freshwater migration. Values are after spawning for females and before spawning for males. Significant differences between the two species are indicated by an asterisk (Mann-Whitney U-test; $P < 0.05$).

cera energy reserves (64% for lake whitefish compared with 47% for male cisco) and a comparable proportion of their carcass energy reserves.

As in cisco, nonreproductive lake whitefish reached significantly higher carcass and viscera energy levels by October (Fig. 4). The carcass energy content of reproductive female lake whitefish after spawning was only 75% of the carcass energy content of nonreproductive fish (Fig. 6). Viscera energy content was also lower representing 33% of the viscera energy content of nonreproductive fish (Fig. 6). Compared with female cisco, the proportional loss of carcass and viscera energy of reproductive fish compared with nonreproductive fish was smaller for lake whitefish. The carcass energy content of reproductive female cisco represented 58% of the carcass energy content of nonreproductive females and viscera energy content only 17% of the viscera energy content of nonreproductive females. Comparisons for males before spawning also demonstrated a higher proportional loss of carcass and viscera energy of cisco in reproductive fish compared with nonreproductive fish (Fig. 6). However, the difference in the ratio of viscera energy of repro-

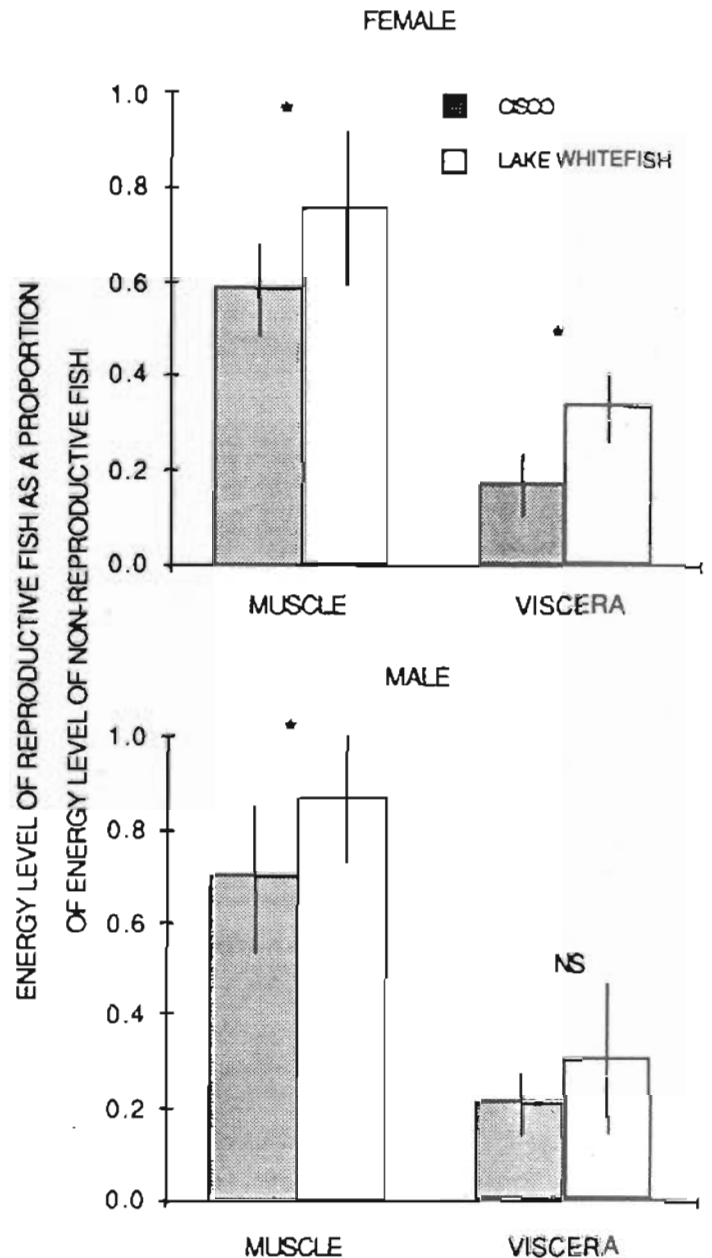


FIG. 6. Carcass and viscera energy content of reproductive male and female cisco and lake whitefish as proportions of carcass and viscera energy content of nonreproductive cisco and lake whitefish at the end of October. Values are after spawning for females and before spawning for males. Symbols as in Fig. 5.

ductive male on nonreproductive male was not significant between the two species.

During winter, reproductive fish of both species relied on their carcass energy reserves only whereas nonreproductive fish used both their carcass and viscera energy reserves (Fig. 3 and 4).

Proximate Composition

Gonads

While gonad fat and protein content of nonreproductive fish remained quite stable, gonad fat and protein content of reproductive fish increased significantly from May to October (Table 2). In reproductive females of both species, fat and protein con-

TABLE 2. Proximate composition of the gonads of standard reproductive (REP) and nonreproductive (NRP) cisco and lake whitefish from May 1982 to May 1983. Numbers in parentheses indicate standard errors.

Gonads			1982					(mid)	1983
			May	July	Aug.	Sept.	Oct.	Nov.	May
Cisco									
Percent moisture	Female	REP	72.7 (0.9)	66.6 (1.4)	59.3 (1.2)	58.7 (0.9)	61.4 (1.7)	84.7 (3.0)	83.8 (0.9)
		NRP	82.7 (2.3)	—	69.3 (1.6)	67.4 (1.7)	69.6 (1.2)	—	71.0 (1.3)
	Male	REP	77.7 (0.8)	79.5 (0.5)	79.2 (0.4)	72.0 (0.9)	77.8 (0.9)	—	77.6 (0.6)
		NRP	80.7 (0.8)	—	—	87.3 (6.2)	75.4 (0.4)	—	75.3 (0.8)
Fat content (g)	Female	REP	0.3 (0.1)	0.7 (0.1)	2.7 (0.2)	4.6 (2.1)	5.6 (0.3)	0.6 (0.1)	0.1 (0.1)
		NRP	0.1 (0.1)	—	0.3 (0.1)	0.4 (0.2)	0.4 (0.1)	—	0.2 (0.2)
	Male	REP	0.05 (0.02)	0.1 (0.1)	0.2 (0.1)	0.4 (0.1)	0.4 (0.3)	—	0.02 (0.02)
		NRP	0.04 (0.03)	—	—	0.05 (0.01)	0.04 (0.03)	—	0.01 (0.01)
Protein content (g)	Female	REP	0.3 (0.1)	0.6 (0.1)	2.2 (0.2)	4.9 (0.3)	7.1 (0.3)	0.4 (0.1)	0.2 (0.1)
		NRP	0.2 (0.1)	—	0.3 (0.1)	0.4 (0.1)	0.2 (0.1)	—	0.4 (0.1)
	Male	REP	0.1 (0.1)	0.4 (0.1)	0.5 (0.1)	1.0 (0.1)	0.5 (0.1)	—	0.1 (0.1)
		NRP	0.1 (0.1)	—	—	0.05 (0.04)	0.04 (0.02)	—	0.1 (0.1)
Lake Whitefish									
Percent moisture	Female	REP	82.3 (0.7)	66.4 (1.3)	61.2 (1.1)	—	60.6 (0.9)	84.3 (0.5)	85.2 (0.6)
		NRP	84.5 (0.8)	82.8 (0.2)	—	80.6 (0.8)	79.8 (0.6)	—	81.0 (0.8)
	Male	REP	82.0 (1.0)	79.8 (0.7)	77.8 (0.9)	72.5 (0.5)	72.9 (1.0)	81.8 (0.8)	81.0 (0.9)
		NRP	76.8 (2.4)	80.6 (0.2)	—	77.4 (0.2)	79.8 (0.6)	—	79.7 (0.7)
Fat content (g)	Female	REP	0.03 (0.02)	2.7 (0.3)	7.8 (2.2)	—	11.8 (0.7)	0.4 (0.2)	0.3 (0.1)
		NRP	0.1 (0.1)	0.02 (0.02)	—	0.1 (0.1)	0.1 (0.1)	—	0.4 (0.1)
	Male	REP	0.02 (0.02)	0.2 (0.1)	0.4 (0.1)	0.3 (0.1)	0.4 (0.1)	0.2 (0.2)	0.2 (0.1)
		NRP	0.04 (0.02)	0.04 (0.02)	—	0.05 (0.04)	0.1 (0.1)	—	0.1 (0.1)
Protein content (g)	Female	REP	0.3 (0.1)	3.4 (0.7)	10.8 (0.5)	—	16.1 (2.3)	1.0 (0.9)	0.4 (0.1)
		NRP	0.7 (0.1)	0.2 (0.1)	—	0.3 (0.1)	0.3 (0.1)	—	0.4 (0.1)
	Male	REP	0.1 (0.1)	1.2 (0.1)	1.9 (0.1)	1.0 (0.1)	1.2 (0.1)	0.3 (0.1)	0.1 (0.1)
		NRP	0.2 (0.1)	0.1 (0.1)	—	0.1 (0.1)	0.1 (0.1)	—	0.1 (0.1)

content increased ($P < 0.05$) during feeding (May to August) and freshwater migration (August and October). Conversely, percent moisture decreased ($P < 0.05$) during the same period. After spawning (beginning of November) gonad fat and protein content decreased ($P < 0.05$) and reached values similar to those of nonreproductive fish. In reproductive males of both species,

the maximum fat and protein content of the testes were attained earlier than in females. In male cisco, maximum fat and protein content were reached at the end of September whereas in male lake whitefish maximum values were attained at the end of August (Table 2). In reproductive males of both species, protein content decreased ($P < 0.05$) before spawning.

TABLE 3. Proximate composition of the carcass of standard reproductive (REP) and nonreproductive (NRP) cisco and lake whitefish from May 1982 to May 1983. Numbers in parentheses indicate standard errors.

Carcass			1982	July	Aug.	Sept.	Oct.	(mid	1983	
			May					Nov.	May	
Cisco										
Percent moisture	Female	REP	69.0 (0.7)	69.3 (1.0)	68.9 (0.6)	74.0 (2.4)	74.8 (0.6)	79.0 (0.1)	75.6 (0.5)	
		NRP	73.5 (1.7)	—	69.4 (0.6)	69.7 (0.8)	69.8 (0.3)	—	70.4 (0.3)	
	Male	REP	70.8 (1.2)	67.4 (0.9)	68.3 (0.5)	70.3 (1.6)	74.0 (0.3)	—	76.2 (0.3)	
		NRP	73.6 (0.7)	—	—	71.3 (0.7)	68.3 (0.9)	—	69.7 (0.8)	
Fat content (g)	Female	REP	10.1 (0.8)	13.8 (1.6)	21.4 (1.3)	13.4 (8.0)	7.1 (1.0)	3.6 (0.1)	2.3 (0.4)	
		NRP	3.9 (3.4)	—	20.0 (1.1)	19.4 (1.1)	15.5 (1.4)	—	12.3 (0.7)	
	Male	REP	8.3 (5.4)	16.4 (0.8)	20.9 (0.7)	21.6 (3.9)	11.0 (0.6)	—	1.7 (0.1)	
		NRP	2.0 (0.3)	—	—	21.1 (3.2)	21.6 (4.1)	—	14.0 (6.2)	
Protein content (g)	Female	REP	30.7 (1.0)	38.7 (1.1)	41.3 (1.6)	36.5 (2.8)	33.5 (1.9)	35.2 (2.9)	27.1 (0.9)	
		NRP	23.4 (2.2)	—	42.9 (1.2)	45.4 (1.2)	41.4 (0.9)	—	37.3 (1.3)	
	Male	REP	31.7 (0.9)	41.2 (1.1)	39.2 (2.8)	43.4 (1.6)	39.3 (1.9)	—	25.8 (1.2)	
		NRP	24.2 (1.1)	—	—	40.9 (0.7)	45.2 (2.3)	—	36.0 (1.0)	
Lake Whitefish										
Percent moisture	Female	REP	69.9 (0.5)	67.0 (0.6)	71.3 (1.0)	—	75.1 (0.7)	74.0 (0.6)	74.5 (0.7)	
		NRP	73.4 (1.3)	71.5 (1.3)	—	71.5 (1.0)	71.4 (0.7)	—	69.7 (0.5)	
	Male	REP	70.3 (0.6)	67.7 (0.5)	72.0 (0.5)	73.8 (0.7)	72.9 (0.3)	73.7 (0.6)	74.9 (0.5)	
		NRP	74.5 (1.2)	70.8 (0.1)	—	71.9 (0.7)	71.5 (0.4)	—	72.2 (0.6)	
Fat content (g)	Female	REP	16.2 (5.4)	33.8 (1.6)	26.6 (3.3)	—	17.2 (6.1)	18.7 (5.8)	5.1 (1.8)	
		NRP	9.3 (6.9)	21.3 (6.9)	—	27.0 (2.6)	28.0 (3.3)	—	26.5 (3.4)	
	Male	REP	17.9 (12.1)	32.3 (1.6)	26.4 (3.3)	19.1 (3.8)	19.2 (3.4)	12.8 (1.2)	7.5 (4.2)	
		NRP	6.5 (2.0)	28.7 (1.1)	—	28.0 (2.6)	25.7 (7.5)	—	15.3 (5.8)	
Protein content (g)	Female	REP	59.2 (2.5)	86.6 (5.2)	74.9 (7.1)	—	70.6 (1.7)	73.7 (3.4)	51.6 (4.5)	
		NRP	59.0 (3.1)	64.8 (6.1)	—	76.3 (3.8)	76.5 (6.4)	—	68.5 (4.9)	
	Male	REP	67.9 (1.9)	80.8 (3.8)	81.2 (6.2)	80.2 (4.1)	82.0 (1.9)	74.0 (2.1)	43.9 (2.9)	
		NRP	63.7	82.0	—	84.1	89.9	—	70.6	

Carcass

Carcass fat and protein increased ($P < 0.05$) during the season for nonreproductive male and female cisco with peaks at the end or near the end of October (Table 3). In reproductive female cisco, carcass fat and protein reached their maximum values in August prior to river entry. During freshwater migra-

tion, both carcass fat and protein were utilized. However, fat represented 83% of the carcass energy reserves that were used. As a result of the extensive use of carcass fat for gonad maturation and migration, carcass protein was the main source of energy for the overwintering period for reproductive females, representing 94% of the somatic energy reserves that were used.

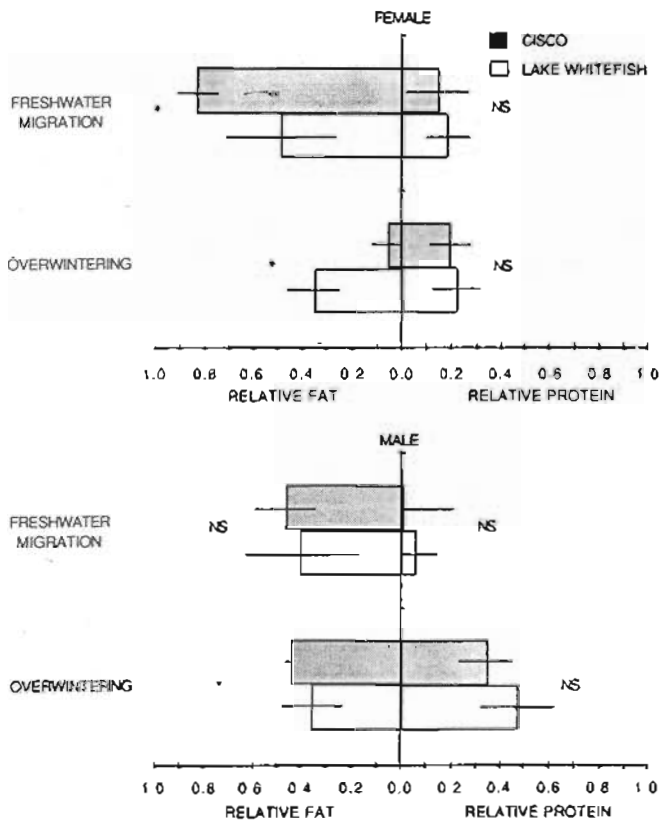


FIG. 7. Relative carcass lipid and protein decrease for cisco and lake whitefish during freshwater migration (after spawning for females and before spawning for males) and overwintering. Significant differences between the two species are indicated by an asterisk (Mann-Whitney U-test; $P < 0.05$).

In nonreproductive females carcass fat and protein were utilised to the same extent during the overwintering period. The decline in energy produced by the decrease of carcass fat represented 53% of the carcass energy loss for nonreproductive females.

In reproductive male cisco, only carcass fat was used during freshwater migration, carcass protein content remaining almost constant during the same period (Table 3). By the following spring, both carcass fat and protein had decreased ($P < 0.05$). Nonreproductive males also used both carcass fat (58% of the carcass energy loss) and protein during the overwintering period.

In nonreproductive lake whitefish, carcass fat and protein increased ($P < 0.05$) from May to October. In reproductive females, the maximum levels of fat and protein were reached in July and decreased ($P < 0.05$) during gonad maturation, freshwater migration and spawning (Table 3). Carcass fat represented 66% of the carcass energy reserves that were used. However, no differences ($P < 0.05$) in carcass protein content were observed between reproductive and nonreproductive females in October. Conversely, the carcass fat level of reproductive females was lower ($P < 0.05$) than that of nonreproductive females. During the overwintering period, carcass fat and protein were used by both reproductive and nonreproductive females.

In reproductive male lake whitefish, carcass protein content did not change ($P > 0.05$) during gonad maturation and freshwater migration but decreased ($P < 0.05$) during spawning (Table 3). Carcass fat decreased ($P < 0.05$) during freshwater migration and spawning. Carcass fat and protein levels in repro-

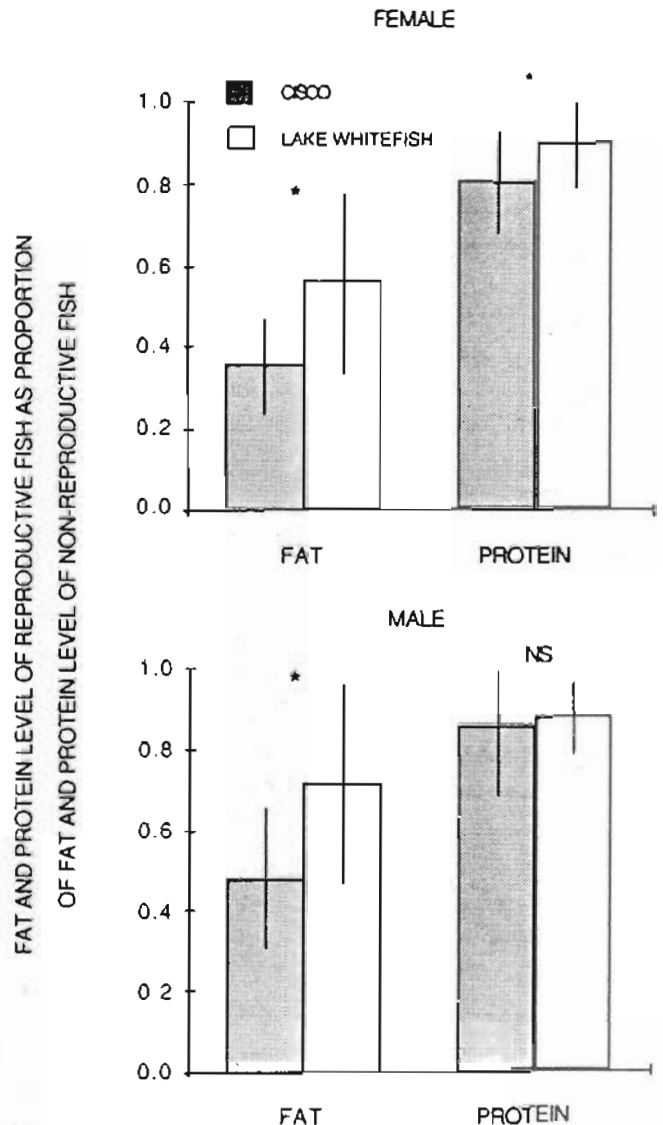


FIG. 8. Carcass lipid and protein content of reproductive male and female cisco and lake whitefish as proportions of carcass lipid and protein content of nonreproductive cisco and lake whitefish at the end of October. Values are after spawning for females and before spawning for males. Symbols as in Fig. 7.

ductive males after spawning were lower ($P < 0.05$) than in nonreproductive males. Like females, reproductive and nonreproductive males used both carcass fat and protein during the winter.

Interspecific comparisons indicate that female lake whitefish used a smaller proportion of their carcass fat reserves than female cisco during migration and reproduction (Fig. 7). Female lake whitefish used 49% of their carcass fat reserves compared with 83% for female cisco. As a consequence, reproductive female lake whitefish still had carcass fat reserves that could be used during winter. Carcass fat decreased by 36% during winter in lake whitefish whereas in cisco, carcass fat reserves decreased by only 6% (Fig. 7). Compared with nonreproductive females, the depletion in carcass fat and protein after spawning was less acute for female lake whitefish than for female cisco (Fig. 8). Carcass fat and protein content of reproductive females as a proportion of carcass fat and protein content of nonreproductive females were significantly lower for cisco (Fig. 8).

No significant differences in carcass fat and protein used during freshwater migration were observed between male cisco and

TABLE 4. Proximate composition of the viscera of standard reproductive (REP) and nonreproductive (NRP) cisco and lake whitefish from May 1982 to May 1983. Numbers in parenthesis indicate standard errors.

Viscera			1982 May	July	Aug.	Sept.	Oct.	(mid) Nov.	1983 May
Cisco									
Percent moisture	Female	REP	71.5 (1.2)	71.3 (2.0)	68.7 (1.5)	74.8 (1.7)	78.9 (0.6)	82.4 (0.8)	78.9 (0.8)
		NRP	77.9 (2.2)	—	64.8 (2.1)	64.2 (1.9)	64.3 (3.7)	—	77.4 (5.8)
	Male	REP	75.8 (2.4)	66.1 (1.7)	62.6 (1.8)	64.6 (4.0)	70.2 (0.7)	—	79.2 (0.5)
		NRP	81.2 (0.5)	—	—	67.3 (7.0)	55.6 (7.5)	—	62.8 (2.9)
Fat content (g)	Female	REP	0.9 (0.1)	1.5 (0.2)	1.6 (0.8)	0.6 (0.4)	0.3 (0.2)	0.2 (0.1)	0.1 (0.1)
		NRP	0.3 (0.2)	—	1.0 (0.2)	2.3 (0.9)	2.1 (0.3)	—	0.9 (0.3)
	Male	REP	0.3 (0.1)	2.1 (0.2)	1.9 (0.4)	2.1 (1.8)	0.7 (0.1)	—	0.02 (0.02)
		NRP	0.3 (0.2)	—	—	3.0 (2.0)	4.6 (1.1)	—	1.3 (1.0)
Protein content (g)	Female	REP	1.2 (0.1)	1.3 (0.1)	1.4 (0.1)	1.4 (0.1)	0.9 (0.1)	0.7 (0.1)	1.0 (0.1)
		NRP	1.3 (0.3)	—	1.3 (0.3)	2.2 (0.5)	1.7 (0.2)	—	1.6 (0.5)
	Male	REP	1.1 (0.1)	1.2 (0.1)	1.3 (0.3)	1.2 (0.1)	0.9 (0.1)	—	1.1 (0.1)
		NRP	1.0 (0.1)	—	—	1.9 (0.2)	1.6 (0.7)	—	1.5 (0.4)
Lake Whitefish									
Percent moisture	Female	REP	76.3 (0.6)	67.7 (6.3)	65.0 (4.0)	—	79.3 (0.7)	78.6 (0.4)	79.0 (0.4)
		NRP	79.0 (1.4)	69.7 (2.4)	—	60.8 (3.8)	59.6 (3.3)	—	70.7 (1.1)
	Male	REP	75.1 (3.7)	68.4 (1.4)	70.2 (0.8)	79.2 (0.8)	77.6 (0.8)	78.3 (0.7)	79.3 (0.4)
		NRP	80.5 (1.0)	68.4 (2.0)	—	70.6 (1.8)	64.6 (1.9)	—	75.0 (1.5)
Fat content (g)	Female	REP	1.7 (0.9)	9.0 (4.2)	4.1 (3.4)	—	1.1 (0.7)	0.6 (0.5)	0.3 (0.1)
		NRP	0.7 (0.6)	4.6 (0.7)	—	4.7 (1.0)	5.9 (0.8)	—	2.8 (0.7)
	Male	REP	1.7 (1.2)	5.9 (3.3)	3.7 (0.6)	2.0 (1.8)	1.2 (0.9)	0.9 (0.8)	0.3 (0.2)
		NRP	0.9 (0.7)	4.4 (0.4)	—	3.8 (1.8)	4.0 (1.0)	—	1.3 (1.1)
Protein content (g)	Female	REP	4.4 (0.3)	6.3 (0.8)	5.3 (0.5)	—	2.9 (0.2)	3.8 (0.3)	4.8 (0.2)
		NRP	4.1 (0.5)	5.8 (0.6)	—	4.3 (0.4)	4.7 (0.3)	—	4.2 (0.2)
	Male	REP	4.2 (0.3)	5.9 (0.3)	4.9 (0.4)	4.1 (0.1)	3.0 (0.2)	3.1 (0.2)	4.6 (0.2)
		NRP	3.6 (0.3)	4.2 (0.2)	—	7.5 (1.0)	3.9 (1.0)	—	4.9 (0.3)

lake whitefish (Fig. 7). However, during the period covering spawning and overwintering, carcass fat reserves declined to a greater extent in male cisco (Fig. 7). Carcass fat reserves of reproductive male cisco as a proportion of carcass fat reserves of nonreproductive male cisco were also significantly lower than in male lake whitefish (Fig. 8).

In both species, significant variations in percent moisture of the carcass were observed. Changes in percent moisture were the inverse of changes in carcass fat and protein levels (Table 3).

Viscera

In reproductive cisco, both viscera fat and protein were used during the freshwater migration (Table 4). Reproductive females

used 90% of their viscera fat and 63% of their viscera protein. In reproductive males, these percentages were lower (64% of viscera fat and 27% of viscera protein) but these values are probably underestimated. As a consequence, viscera fat and protein content of reproductive cisco were lower ($P < 0.05$) than in nonreproductive cisco at the end of October except for viscera protein content of reproductive and nonreproductive male cisco. The viscera fat content of nonreproductive cisco is used to cover a part of the energy demands of overwintering while viscera protein did not vary significantly (Table 4). In reproductive cisco, slight changes in viscera fat and protein content

TABLE 5. Energy gain, reproductive effort, somatic cost of reproduction, and overwintering cost for male and female cisco and lake whitefish. For the definition of terms see text.

Total and somatic energy gain	Cisco		Lake Whitefish	
	Female	Male	Female	Male
I_r (kJ)	1273.	1471.	1566.	1608.
I_s (kJ)	-271.	<218.	166.	-48.
I_p (kJ)	1144.	>469.	1747.	1274.
I_a (kJ)	873.	688.	1912.	1226.
R_a (kJ)	-401.	-784.	346.	-382.
Reproductive effort and somatic cost				
R_r (%)	58.	>25.	44.	35.
(kJ/kg)	3727.	>1597.	2885.	2008.
R_s (kJ)	1544.	>1253.	1401.	1656.
RE_s (%)	121.	>85.	89.	103.
Overwintering cost				
TEC_r (%)	67.	63.	64.	61.
W_a (%)	9.	—	20.	26.
W_n (%)	26.	32.	12.	27.

between November and May were observed but these variations were not significant.

In lake whitefish, viscera fat and protein were also used extensively by reproductive individuals during gonad maturation and migration (Table 4). Male and female lake whitefish used 85 and 93% of their viscera fat, respectively and 47 and 39% of the viscera protein, respectively. By the end of October, viscera fat and protein content were lower in reproductive fish compared with nonreproductive ones ($P < 0.05$) except for viscera protein content of male lake whitefish. As in cisco, nonreproductive lake whitefish used their viscera fat reserves to cover part of the energy cost of overwintering. The decrease in viscera fat represents 91 to 100% of the viscera energy loss during overwintering. Viscera protein content did not change during that period. In reproductive lake whitefish, changes in viscera fat and protein during the winter were not significant. The changes in percent moisture of viscera for cisco and lake whitefish were the inverse of changes in viscera fat and protein.

Reproductive Effort and Somatic Cost of Reproduction

Differences in total energy gain and somatic energy increase between reproductive (I_r , I_s) and nonreproductive (I_n) cisco and lake whitefish were observed (Table 5). The somatic energy increase of nonreproductive fish (I_n ; equivalent to total energy gain) was higher than the total energy gain of reproductive fish (I_r) except for female lake whitefish where somatic energy increase of nonreproductive females was lower than total energy gain of reproductive females.

Reproductive effort (R_r) indicates that the energy investment in reproduction by female cisco represented 58% of their somatic energy content and for males, 25% of their somatic energy content (Table 5). In male cisco, however, reproductive effort was underestimated because the energy cost of spawning activities could not be estimated. In lake whitefish, the energy invested in reproduction represented 44% (female) and 35% (male) of their somatic energy content.

On a comparative basis, reproductive effort in female cisco was higher than male and female lake whitefish. Female cisco allocated more energy to reproduction (I_r) than their total energy

TABLE 6. Relative importance of energy investment in migration and migration effort for male and female cisco and lake whitefish. MG represents the energy loss for migration between August and October for cisco and between July and October for lake whitefish. Mg representing the energy loss for migration between August and October for lake whitefish was also calculated in order to compare the two species for the period during which fish ascend the rapids. MG_s and Mg_s are calculated from the corresponding MG and Mg values.

Relative importance of migration	Cisco		Lake Whitefish	
	Female	Male	Female	Male
MG (kJ)	585.	450.	883.	731.
Mg (kJ)			557.	467.
MG/I_r	1.64	22.78	1.02	12.99
MG/I_{gm}	2.70	75.53	1.30	146.07
Migration effort				
MG_s (%)	29.	24.	22.	20.
(kJ/kg)	1907.	1530.	1459.	1153.
Mg_s (%)			14.	13.
(kJ/kg)			940.	745.

gain (I_a) whereas in lake whitefish the energy invested in reproduction was less or almost equal to the total energy gain during the season.

The energy investment in reproduction (I_r) in all cases was higher than the difference in total energy gain between reproductive and nonreproductive fish (R_a). Therefore, energy investment in reproduction was at the cost of somatic energy increase (Table 5). The somatic cost of reproduction indicates that somatic energy increase of reproductive fish was in all cases lower than the somatic energy increase of nonreproductive fish. Expressed in relative terms (RE_s), reproduction of female cisco resulted in a reduction of somatic energy increase equal to 121% of the somatic energy increase of nonreproductive fish (Table 5). In the case of female lake whitefish, reproduction reduced somatic energy increase by 89% of the somatic energy increase of nonreproductive fish.

Considering the energy cost of overwintering, reproductive males and females of both species consumed 61 and 67% of the somatic energy content they reached before migration to meet the energy demands of reproduction and overwintering (TEC_r , Table 5). The energy loss during winter was lower for reproductive female cisco (W_a) than for nonreproductive female cisco (W_n). In lake whitefish, the energy loss during winter of reproductive and nonreproductive individuals was comparable.

Cost of Migration

During the freshwater migration of both species, the energy cost of migration was higher than the energy invested in gonads and higher in female cisco than in female lake whitefish (MG/I_{gm} , Table 6). In males of both cisco and lake whitefish, the energy cost of migration was almost the only cost of reproduction representing respectively 76 and 146 times more energy than the energy invested in the testes.

The energy cost of migration was higher than the total energy investment in the gonads (164%) for female cisco and equal to the total energy investment in the gonads (102%) for female lake whitefish (MG/I_r , Table 6). The energy cost of migration represented 20 to 29% of the somatic energy content of reproductive fish of both species. The migratory effort (MG_s) also indicates that cisco expended more energy for migration than

lake whitefish, the difference between males and between females being respectively 17 and 24%. This difference is even larger if we consider the same period of time (August to October), the period during which fish ascended the rapids and moved to the spawning grounds. During this period of time, cisco expended two times more energy for migration than lake whitefish (Table 6). On an equivalent weight basis the results are the same.

Discussion

Differences in seasonal energy increase between reproductive and nonreproductive cisco and lake whitefish, as well as energy expenditures associated with reproduction, result in somatic loss for reproductive fish of both species (Table 5). However, the somatic depletion for reproduction is higher in cisco than in lake whitefish. Migration alone appears responsible for the higher somatic depletion for reproduction in cisco (Table 6).

Energy Allocation to Growth and Reproduction

Resource input

No significant differences in the increment in length between reproductive and nonreproductive fish were observed for cisco and lake whitefish suggesting that nonreproductive fish do not devote more energy than reproductive fish to growth in length (Table 1). In the laboratory, the length of guppies (*Poecilia reticulata*) did not differ significantly between reproducing and nonreproducing fish but nonreproducing females had significantly more energy in their somatic tissues than reproducing females (Reznick 1983). However, other workers have demonstrated significant differences in growth between reproductive and nonreproductive fish. For example, in male bluegill sunfish, Gross and Charnov (1980) estimated that within an age group, males with mature testes had a significantly smaller linear growth increment than equal-aged males with immature testes, in the season they were captured. These differences were explained by two distinct reproductive pathways, cuckoldry and parental strategy. Hirshfield (1980) observed that reproduction and growth of the Japanese medaka (*Oryzias latipes*) were in general negatively correlated suggesting that individuals reproducing the most were not able to grow as rapidly as individuals reproducing less. In these studies however, alternative reproductive strategies were implied as opposed to one reproductive strategy where years of reproduction alternate with years of nonreproduction.

The significantly higher energy content of nonreproductive cisco and lake whitefish in October (Fig. 2), due to the fact that no energy was allocated to reproduction, indicates that surplus energy was devoted to energy storage, as opposed to increase in length. By calculating the energy increase in nonreproductive fish if no growth had occurred between May and October, we estimated that 65% (52 and 72%) of the total energy gain in nonreproductive fish during that period was due to energy storage. The remaining 35% was due to growth. Energy content estimated for juvenile fish (Y. Lambert, unpubl. data) indicated that 27% (23 to 38%) of the total seasonal energy increase was due to storage. Thus growth was responsible for most of the energy increase (73%) in juvenile fish. As juveniles, fish grow in length and energy and as they approach the age of maturity more energy is accumulated as energy reserves to the detriment of growth.

As fish reach maturity, differences in total energy gain are observed. The total energy gain of reproductive fish is lower than the somatic energy gain of nonreproductive fish except for female lake whitefish which exhibited the opposite pattern (Table 5). Thus, reproduction appears in most cases to reduce energy gain during the summer. This may be related to the fact that reproductive individuals leave the feeding grounds in August to move to the river while nonreproductive fish stay on the feeding grounds until September. Although some reproductive lake whitefish captured in the estuarine portion of the freshwater migration had food in their stomachs (Dodson et al. 1985), it does not appear that feeding reduces greatly the energy lost during the freshwater migration. This could be the result of lower food availability in the river and/or lower intensity of feeding. The cost of migration per unit of distance ($42.8 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$) for lake whitefish in relation to the relative migration distance in body lengths ($9\cdot 10^4$) and weight (0.625 kg) is within the range of other anadromous species that stop feeding during migration (Bernatchez and Dodson 1987). This suggests that feeding in lake whitefish during the estuarine part of the migration is not energetically important. However, reproductive female lake whitefish show a higher resource input than nonreproductive females. This difference seems related to a higher intensity of feeding between May and July. The energy increase during this period is higher in reproductive females than in nonreproductive females and males (Fig. 2). Dabrowski (1982b), reporting data of Szyplula (1965) indicated that the feeding intensity of female vendace (*Coregonus albula* L.) was greater than that of males during gonad maturation.

During freshwater migration cisco and lake whitefish rely mostly on their energy reserves as they stop feeding before or soon after river entry. Even if cisco and lake whitefish move to the spawning grounds at the same time (Dodson et al. 1985), the maximum somatic energy content before migration is observed sooner in lake whitefish than in cisco (Fig. 2). Sampling interval and difference in energy increase in gonads can partly explain this difference. Because of the 1-mo interval between the July and August sampling dates, a difference of up to 4 wk in time of arrival of the two species at the river mouth is possible. If lake whitefish move to the river mouth earlier than cisco, as suggested by the data of 1979 to 1981 (Lambert and Dodson 1982a,b), the energy costs associated with entry into freshwater would be observed earlier in lake whitefish than in cisco. These costs include physiological changes associated with osmoregulation and a higher standard metabolism associated with the higher water temperatures in the river than in the bay (Dodson et al. 1985). The higher rate of displacement in the river of cisco (Dodson et al. 1985) suggests that cisco move later to the river mouth and migrate more rapidly than lake whitefish explaining why the two species are observed together during the upriver migration. The greater energy increase in gonads in lake whitefish by the end of August may also be partly responsible for the earlier decrease in energy because of energy transfer to the gonads.

Resource expenditures

Both carcass and viscera energy reserves are used during freshwater migration (Fig. 3 and 4). However, more than 75% of the total energy expenditures for migration and reproduction come from the utilization of carcass energy reserves. Dabrowski (1982a,b) observed that in vendace (*Coregonus albula* L.) and pollan (*Coregonus pollan* Thompson) muscle was the principal source of energy for gonad maturation. Both carcass fat and

protein decreased during freshwater migration (Table 3) but the comparison between males and females suggests that the decrease in carcass protein is mainly associated with gonad maturation. The decrease in carcass fat is associated with both gonad maturation and migration in females and almost exclusively with migration in males. Male cisco and lake whitefish deposit little energy in their testes (less than 6 kJ) during freshwater migration suggesting that most energy lost during that period is associated with migration. For males, no significant decrease in carcass protein occurs before spawning (Table 3) suggesting that carcass fat is the principal source of energy for migration in males. In females of both species, decrease in carcass protein is associated primarily with gonad maturation as gonad protein increase represents 80% of the carcass protein decrease. This result is consistent with the study of Dabrowski (1982a) who showed that the decrease in different amino acids in the muscle of pollan (*Coregonus pollan* Thompson) was closely related to their increase in gonads. The decrease in carcass fat for females may be associated with both gonad maturation and migration resulting in a higher carcass fat decrease in females than in males (Table 3).

Viscera energy reserves, although less important than carcass energy reserves, contribute 7% of the energy used during freshwater migration for cisco and 20% for lake whitefish. Reproductive fish use a large proportion of their viscera fat and protein during freshwater migration (Table 4). As a consequence, they rely mostly on their carcass energy reserves during winter. In contrast, nonreproductive fish derived 19 to 33% of the energy they need to overwinter from their viscera energy reserves, principally in the form of fat, thus reducing their loss of carcass reserves during the winter. The difference in the viscera energy reserves used during the winter supports the proposition that the stress of overwintering will be greater in reproductive fish because their carcass reserves, already lower than those of nonreproductive fish, will be reduced to an even greater extent during winter.

The large use of viscera fat and protein in migration and reproduction results in visceral atrophy. The atrophy of the digestive system is known to result in a lower efficiency of digestion since it increases gastric retention times (Jobling 1980) and reduces the ability to synthesize and secrete digestive enzymes (Windell 1966). In contrast, nonreproductive fish use only their viscera fat reserves which are accumulated around the digestive system and no atrophy is observed.

The large energy depletion associated with reproduction and overwintering (Fig. 2) suggests that surviving fish that reproduce one year must skip at least the next reproductive season in order to accumulate sufficient energy reserves to spawn again. Following the overwintering period, surviving cisco and lake whitefish that spawned the previous fall have 50% less energy (48 to 57%) than fish that did not spawn. Moreover reproductive fish have less energy in May 1983 after spawning and overwintering than in the previous spring (Fig. 2). The difference in energy content between reproductive and nonreproductive individuals could even be larger as the energy cost of overwintering is probably underestimated because of selective mortality, with fish in the poorest condition suffering the greatest mortality. The similarity between the total energy loss for reproduction and overwintering in cisco and lake whitefish can be attributed to such a bias in the determination of the cost of overwintering in reproductive fish. It may be assumed that the energy cost of overwintering would be comparable between reproductive and nonreproductive fish if they were equally vul-

nerable to mortality. Applying the energy cost of overwintering of nonreproductive female cisco to reproductive female cisco, we obtain a higher total energy loss for reproduction and overwintering for female cisco (in the order of 84%) than that observed (67%). In the case of lake whitefish, a similar calculation produces values of total energy loss (62% for males and 57% for females) comparable with the total energy loss for reproduction and overwintering observed (61 and 64%, Table 5). The difference, at least in female cisco, would indicate a greater mortality of reproductive females relative to nonreproductive females with only spent fish in the best condition surviving the winter. In lake whitefish we would expect little or no difference in mortality between reproductive and nonreproductive fish if the energy cost of overwintering is comparable for the two groups.

Reshetnikov et al. (1970) concluded that in whitefish (*Coregonus lavaretus* L.) of Lake Chun in USSR, maturation of the gonads was not only dependent on the attainment of a definite size and age but also on the attainment of a definite level of fat reserves specific to each population. Assuming a minimum energy level for maturation of James Bay coregonines, fish that spawn must accumulate energy reserves the following season and sacrifice growth. Given the short period for feeding (less than 3 mo), it seems very difficult if not impossible for a fish to spawn in consecutive years. Fish skipping the next opportunity to spawn would then benefit from a longer feeding period during which they would accumulate sufficient energy reserves for the next spawning season.

Although having a similar gonad energy content in May (Fig. 3 and 4) gonad development is very different between reproductive and nonreproductive females. In females that spawned the previous fall, gonads have a flaccid appearance, still contain unresorbed eggs and have a high moisture content (Table 2). Females that did not spawn have a lower moisture content and show a more advanced maturity stage (Nikolskii's (1963) stage III) suggesting that the maturation process had already begun. This also supports the conclusion that cisco and lake whitefish spawning one year must skip at least the following spawning season. Kuklin (1979) showed that muksun (*Coregonus muk-sun*) of the Yenisey River in northern USSR were unable to spawn annually and that length of the maturation process could be responsible. In fish presenting characteristic signs of the postspawning state (flaccid appearance of ovaries, unresorbed eggs), he estimated that the period of rematuration should last no less than 1.5 yr, making yearly spawning impossible. This long period of rematuration was associated with ecological conditions and the physiological state of fish. In James Bay, the low energy stores in reproductive cisco and lake whitefish after spawning (Fig. 2) may prevent the resorption of the gonads before spring and thus retard the rematuration process.

Several studies of northern populations of Arctic charr, brook charr, lake trout, cisco, and lake whitefish also report that fishes intermittently skipped reproduction (Kennedy 1949, 1953; Sprules 1952; Johnson 1972, 1980; Dutil and Power 1980; Morin et al. 1982). Dutil (1982, 1986) using energy content analysis, demonstrated that anadromous Arctic charr in the Northwest Territories were unable to spawn every year and could skip more than 2 yr between reproductive events. He observed that in spring, postspawners had about 46% less energy than maturing fish which is very comparable with the values we observed for cisco and lake whitefish. In all these studies, the restricted energy budget caused by short growing seasons seems to be one of the major factors limiting the pos-

sibilities of reproduction. Bull and Shine (1979) reporting data on amphibians, reptiles, and fishes, also concluded that lower frequency of reproduction (once every two or more years) was found in habitats of low quality or short growing seasons. They also noted that such situations are often characterized by a major accessory activity associated with reproduction such as migration, egg brooding, or live bearing.

Somatic cost of reproduction

The energy invested in reproduction (I_r) is high in both cisco and lake whitefish (Table 5) being almost equal to or higher than the total energy gain (I_a) of reproductive fish. Reproductive effort in both cisco and lake whitefish produced somatic cost (Table 5) such that the energy invested in reproduction reduced the somatic energy gain that would have been expected if fish had not reproduced. The trade-off in energy allocation between reproduction and other functions in cisco and lake whitefish is clearly shown by comparing reproductive and nonreproductive fish. Our results demonstrate that energy gain in nonreproductive fish is higher than in reproductive fish for males and females of both species with the exception of female lake whitefish which exhibited the opposite pattern.

Somatic energy increase of nonreproductive fish could be biased by the fact that individuals classified as nonreproductive fish between July and November include repeat spawners missing an opportunity to spawn and late maturing virgin fish that never spawned. However, if the energy content of repeat spawners and late maturing virgin fish were very different, we would expect much larger variance in the energy content of individuals classified as nonreproductive fish in October. However, within the standard errors of energy content and mean increase in length for nonreproductive individuals, the estimations of the somatic cost of reproduction for the two species changed by only 1 to 3%. Although comparable in their energy content in October, repeat spawners and late maturing virgin fish could nevertheless show differences in their seasonal pattern of growth and energy storage.

Relative Importance of the Energy Cost of Migration

Migration incurred somatic costs in both species and was largely responsible for the higher somatic cost of reproduction in cisco. In females of both species, the proportion of the total energy gain invested in gonads is comparable (41% for cisco; 45% lake whitefish). Migration resulted in somatic cost in two ways. As already mentioned, reproductive fish migrate to the river several months before nonreproductive fish. Thus, the reproductive migration reduced feeding. In the case of female lake whitefish, reproductive fish exhibit greater energy gain than nonreproductive fish despite their early departure from the feeding grounds. Thus, the lower somatic cost of reproduction in female lake whitefish is partly due to their ability to accumulate reserves in excess of nonreproductive fish prior to migration.

Migration also results in somatic cost due to the cost of displacement in freshwater. The energy loss for migration as a proportion of the somatic energy content before freshwater migration (MG_e) is higher in cisco and twice as high in cisco than in lake whitefish if we consider only the period during which fish ascend the rapids and move to the spawning grounds.

The difference in energy expenditure associated with swimming activity represents one of the major factors explaining the higher energy cost of migration for cisco. At low swimming speeds (29 to 35 $\text{cm}\cdot\text{s}^{-1}$ which is equivalent to 0.9 to 1.2 body

lengths $\cdot\text{s}^{-1}$) the energy expenditures (joules per kilogram per hour) for standard metabolism and swimming activity are comparable between "standard" cisco and lake whitefish (Bernatchez and Dodson 1985). However, at higher swimming speeds energy expenditures increase more rapidly in cisco than in lake whitefish. At a swimming speed of 40 $\text{cm}\cdot\text{s}^{-1}$, the energy expenditure of cisco is 1.12 times higher than in lake whitefish. At 70 $\text{cm}\cdot\text{s}^{-1}$ the energy expenditure of cisco is 2.2 times higher and at 80 $\text{cm}\cdot\text{s}^{-1}$, 2.7 times higher. Correcting for differences in body weight, cisco swimming at 40 $\text{cm}\cdot\text{s}^{-1}$ would expend 0.9 times the energy expended by lake whitefish but at speeds of 70 to 80 $\text{cm}\cdot\text{s}^{-1}$, the energy expended by cisco would be 1.7 to 2.1 times greater than that of lake whitefish. The high sustained swimming speeds needed to ascend the 7 km of rapids in the Eastmain River where current velocities vary from 0.7 to 1.5 $\text{m}\cdot\text{s}^{-1}$ will necessarily result in a higher energy expense in cisco. This conclusion is supported by the fact that metabolic adjustments to increase the aerobic capacity of the swimming musculature are more dramatic for cisco compared with lake whitefish in the Eastmain River (Guderley et al. 1986). The smaller size of cisco will also increase the energy cost of migration. Glebe and Leggett (1981) demonstrated in American shad (*Alosa sapidissima*) a higher energy cost of migration in smaller fish.

These results demonstrate that an energy cost is associated with reproduction for both cisco and lake whitefish in the Eastmain River and that the energy cost of migration is mostly responsible for the different somatic costs of reproduction observed between the two species. The energy cost of migration is important in determining the reproductive pattern of both species and results in differences in the life history characteristics exhibited by the two species (Lambert and Dodson 1989).

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