*Journal of Fish Biology* (1998) **53,** 1231–1242
Article No. jb980789

# A study of trophic niche partitioning between larval populations of reproductively isolated whitefish (*Coregonus* sp.) ecotypes

A. CHOUINARD AND L. BERNATCHEZ*

*Département de biologie, GIROQ, Université Laval, Sainte-Foy, Québec, G1K 7P4 Canada*

(*Received 19 May 1998, Accepted 25 July 1998*)

The abundance, spatio-temporal distribution, and feeding of larvae were compared from two reproductively isolated dwarf and normal ecotypes of whitefish (*Coregonus* sp.) to test the hypothesis that larval ecotypes should reduce competition by using different resources. Contrary to a priori expectations, trophic niche partitioning between larval populations was much less pronounced than previously reported for the adult stages of fish ecotypes, presumably due to the lack of competition acting at this stage, and related to non-limiting food resources. Because this study was conducted in a single year and a single lake, we cannot however, strictly rule out the possibility that resource-based competition and resulting niche partitioning may occur at the larval stage in these species complexes. Nevertheless, this suggests for the first time, that resource-based selection at the larval stage may be relatively unimportant compared to that occurring at older life-history stages in driving the divergence and the development of reproductive isolation in sympatric fish ecotypes.

Key words: ecotypes; trophic resources; speciation; competition; adaptive radiation; mitochondrial DNA; *Coregonus*.

## INTRODUCTION

Ecological speciation refers to the evolution of reproductive isolation as a result of processes driving ecological and phenotypic changes, i.e. resource-based divergent selection and resource competition (Schluter, 1996*a*). In this theoretical framework, the understanding of species formation is intimately related to that of ecological mechanisms allowing distinct populations to coexist in sympatry and to how such processes may be involved in the development of their reproductive isolation.

Studies of sympatric fish ecotypes found in postglacial lakes of the northern hemisphere have contributed substantially to the understanding of the role of ecological processes in population divergence (Skulason & Smith, 1995). These revealed that similar patterns of morphological, behavioural and life-history polymorphisms associated with specializations for exploiting distinct trophic niches have evolved in numerous species groups (Schluter & McPhail, 1993). Such polymorphisms are found in lakes that were created following glacier retreat <15 000 years ago which implies that they evolved rapidly, most likely as a consequence of relaxed competition and/or availability of open niches

---

*Author to whom correspondence should be addressed. Tel.: (418) 656 3402; fax: (418) 656 2043; email: louis.bernatchez@bio.ulaval.ca

0022–1112/98/121231+12 $30.00/0

(Smith & Todd, 1984). Experimental studies revealed that selection for trophic efficiency may have promoted both ecological divergence and postmating reproductive isolation between sympatric ecotypes (Schluter, 1996*b*). The demonstration that similar evolutionary changes evolved in parallel among populations of independent lineages within same-species complexes provided indirect evidence for the role of ecological selection in promoting their divergence (Taylor & Bentzen, 1993; Taylor *et al*., 1996; Pigeon *et al*., 1997).

One important caveat in studies of resource partitioning among sympatric fish ecotypes is the almost complete lack of consideration of the importance of ontogenic shifts in trophic niches (Persson & Greenberg, 1990; Snorasson *et al*., 1994). Thus, most, if not all studies focused on adult stages, although current knowledge of larval fish ecology suggests that selective pressures for developing adaptations to occupy distinct trophic niches could be stronger in earlier life-history stages. Namely, as density-dependent mortality is maximal at the larval stage (Cushing, 1975), the greatest contributions to fitness in many fishes may be reached by maximizing survival at this stage, which could be achieved partly by relaxing competition for resources (Mayr, 1963). Ecological processes maximizing survival at the larval stage are also considered to play a major role in determining population subdivision and abundance in fishes (Sinclair & Iles, 1988).

Sympatric pairs of lake whitefish *Coregonus clupeaformis* Mitchill species complex ecotypes have been reported in several lakes of North America (Fenderson, 1964; Bodaly, 1979; Fortin & Gendron, 1990; Vuorinen *et al*., 1993; Chouinard *et al*., 1996). Several lines of evidence suggest that resource-based divergent selection and/or resource competition have played an important role in their radiation. Adults of these ecotypes, referred to as dwarf and normal, display differences in life-history parameters, and differ in behavioural and morphological traits associated with the alternate use of limnetic (dwarf) and benthic (normal) trophic niches (Fenderson, 1964; Bernatchez *et al*., unpubl.). Phylogeographical studies revealed their polyphyletic origin whereby the evolution of a dwarf phenotype derived from an ancestral normal form occurred in at least three independent evolutionary lineages (Pigeon *et al*., 1997). The fact that it is only found in sympatry with normal fish also indicated that the dwarf ecotype may have evolved repeatedly as a consequence of character displacement. Finally, the observation of a correlation in the amount of gene flow between whitefish ecotypes within different lakes and the extent of their morphological differentiation associated with trophic ecology led Bernatchez *et al*. (1996) to hypothesize that the extent of reproductive isolation achieved between ecotypes may be driven by the intensity of natural selection that generated and is maintaining ecotypic adaptive divergence in each lake.

In order to address this general hypothesis, a comparative study of ontogenic resource partitioning was undertaken on the spatial, temporal and trophic niche axes among pairs of sympatric whitefish ecotypes of the St John River drainage of northern Maine, U.S.A. and southern Québec, Canada, that have reached different levels of reproductive isolation. This paper compares the abundance, spatio-temporal distribution, and feeding of dwarf and normal larvae in a situation of maximal reproductive isolation (Pigeon *et al*., 1997) and adult morphological differentiation (Fenderson, 1964; Chouinard, unpubl. data). This was achieved in order to test the hypothesis that larval ecotypes should reduce competition by using different resources, and to identify the mechanisms used to achieve resource partitioning. Given the presumed importance of ecological processes maximizing survival at the larval stage to determine population richness and abundance in fishes, we predicted that trophic niche partitioning should be at least as important at the larval as at the adult stage. The alternate scenario of no niche partitioning in a situation of maximal reproductive isolation and adult morphological differentiation would suggest that resource-based selection at the larval stage may have played little role in driving population divergence in these fishes compared to that occurring at the adult stage.

## MATERIALS AND METHODS

### STUDY AREA AND SPATIO-TEMPORAL DISTRIBUTION

The study was performed in Cliff Lake (Maine, U.S.A.; 46°24′N, 69°15′W), located at the headwater of the Allagash River system in the St John River drainage. The lake has a surface area of 543 ha, mean and maximum depths of 5·8 and 19·7 m, respectively. Cliff Lake has a fish community typical of small north temperate lake species, where lake whitefish, white sucker *Catostomus commersonii* (Lacépède), and brook charr *Salvelinus fontinalis* (Mitchill) are the most abundant species. The main predators are lake trout *S. namaycush* (Walbaum), and burbot *Lota lota* (L.). Lake cisco *Coregonus artedi* Lesueur and rainbow smelt *Osmerus mordax* (Mitchill), two potential competitors and/or predators of whitefish (Scott & Crossman, 1973; Loftus & Hulsman, 1986), are absent from the lake.

Sampling was conducted in 1994 during four periods, extending from spring ice break-up to juvenile metamorphosis: 16–19 May, 23–26 May, 6–9 June and 20–23 June. The lake was stratified into nine tow-stations to cover all depths and distances from shoreline. At each station and depending on maximum depth, larvae were sampled at three vertical strata; surface (0–3 m), 3–6 m, and >6 m, during both day-time and night-time. All stations were sampled twice a week with a pelagic trawl (mouth area 1 $m^2$, length 2 m, mesh size 0·5 mm) towed 50 m behind an outboard motor boat at a speed of 3–5 kn. Volume of filtered water was quantified with a flow meter (General Oceanics, model 2030R) to estimate larval density (number 1000 $m^{-3}$). The heterogeneity of horizontal larval density among stations was evaluated using randomization tests with 1000 randomizations (Roff & Bentzen, 1989), whereas vertical heterogeneity among depths and time period was estimated by Fisher's exact tests. The correlation of both horizontal and vertical distributions between dwarf and normal ecotype larvae was assessed by Spearman's correlations. By definition, the term larvae used in this study refers to life-history stages prior to metamorphosis into the juvenile form which more resembles the adult phenotype. Although morphology was not detailed in this study, it was obvious that the main trophic features, such as gillraker numbers and length which differ between ecotypes at the juvenile and adult stages are not developed at the larval stages we analysed.

### GENETIC IDENTIFICATION OF LARVAE

Total DNA was extracted following Bernatchez *et al.* (1992) after larvae had been measured and their stomach contents and otoliths preserved for further analyses. In Cliff Lake, sympatric dwarf and normal whitefish ecotypes can be discriminated unambiguously by their mtDNA composition since they are fixed alternatively for diagnostic haplotypes (Bernatchez & Dodson, 1990; Pigeon *et al.*, 1997). The cytochrome *b* gene/control region (D-loop) (2·1 kilobase pairs) was amplified by the polymerase chain reaction (PCR) as described in Bernatchez *et al.* (1995). The PCR amplified segment was digested with *Hae*III which generates diagnostic fragment patterns between the two ecotypes (Pigeon *et al*., 1997). Electrophoresis and detection procedures were as described in Chouinard *et al*. (1996).

### LARVAL AGE AND HATCHING DATES

Sagittal otoliths were used for age determination and back-calculation of larval hatching dates. Otoliths were mounted and fixed on microscope slides using thermoplastic glue. Larval age in days was estimated by the number of daily growth increments (Stevenson & Campana, 1992) counted under an optical microscope (magnification: 400–1000 × ). Hatching dates were determined by subtraction of larval age from the date (in julian days) of sampling. Two counts were made for all individual larvae analysed, with a third count in cases of discordance. Validation of daily increments has been performed previously in the *C. lavaretus*/*clupeaformis* species complex (Eckmann & Rey, 1987). Heterogeneity in the frequency distribution of hatching dates between both larval forms was estimated by a *t*-test.

### DIET ANALYSIS

Larval diet was evaluated by dissecting the entire gut contents, identifying and counting prey items under a binocular microscope (magnification: 40–200 × ). A non-parametric Wilcoxon matched-pairs test was used to compare the proportion of food items consumed by each ecotype. Diet overlap was estimated by Schoener's (1970) resource overlap index. The index varies between 0 and 1, 0 corresponding to a completely distinct diet and 1 to complete diet overlap with respect to proportional food category composition. We also computed competition coefficients (varying between 0 and 1) as additional indicators of potential for competition between larval populations both for spatial and trophic resources (MacArthur & Levins, 1967). Coefficients for spatial distribution were quantified from the relative frequencies of larvae of each ecotype found at different depths (vertical distribution) or stations (horizontal distribution), whereas coefficients for diet were computed using the fractions of different prey items in each population.

## RESULTS

### HATCHING DATES

A total of 996 larvae was captured during the overall sampling campaign. Restriction digests of the cytochrome *b*/control region mtDNA segment with *Hae*III revealed that larvae of the dwarf ecotype dominated in abundance ($n$=950) compared to normals ($n$=46). The otolith microstructure of a random subsample of 110 dwarf and all but six (unreadable) normal ecotype larvae ($n$=40) was analysed for age determination. Ages observed during the entire study varied between 2 and 45 days old for dwarf, and between 3 and 40 days old for normal ecotype larvae, respectively. The frequency distribution of hatching dates based on backcalculations of individual otolith larvae revealed no differences between dwarf and normal larval groups ($t$-test, $t$=1·52, d.f.=148, $P$=0·129), with the majority of larvae hatching between 12 and 18 May independently of the form (Fig. 1).

### HORIZONTAL DISTRIBUTION

A strong heterogeneity in horizontal larval distribution was observed among sampling stations within each form during the first week of sampling (dwarf:

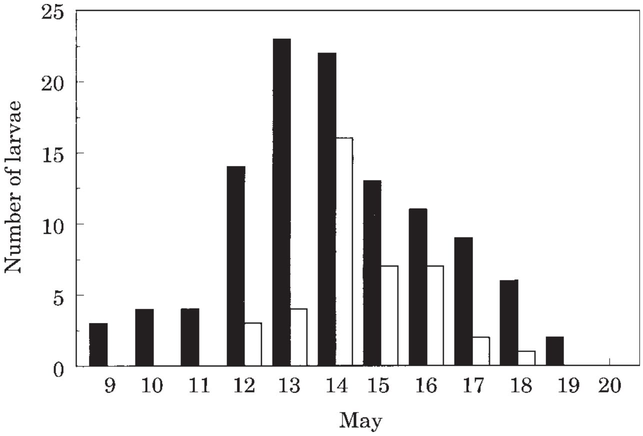


FIG. 1. Hatching date–frequency distribution for dwarf (■) and normal (□) ecotype larvae based on otolith backcalculations.

$\chi^2=437{\cdot}3$, d.f.$=8$, $P<0{\cdot}000001$; normal: $\chi^2=28{\cdot}3$, d.f.$=8$, $P=0{\cdot}00416$) [Fig. 2(a)]. There was, however, a strong correlation between the horizontal distribution of both ecotypes (Spearman correlation $r=0{\cdot}8814$, $P=0{\cdot}0017$). The highest densities were observed for both ecotypes at stations 5 (dwarf: 423 larvae 1000 $m^{-3}$; normal 41 larvae 1000 $m^{-3}$) and 8 (dwarf: 732 larvae 1000 $m^{-3}$; normal 36 larvae 1000 $m^{-3}$) located near the shore, suggesting the sympatry of spawning grounds for both forms at both ends of the lake. Mean larval densities of all other stations were <25% of those observed at stations 5 and 8 during the same period (dwarf: 151 larvae 1000 $m^{-3}$; normal 7 larvae 1000 $m^{-3}$). During the 3 following weeks of sampling, both ecotypes were distributed more uniformly among stations [Fig. 2(b); data pooled for weeks 2–4 due to limited sample sizes for the normal ecotype]. Larvae of both forms were observed at all stations although there was no correlation in their distribution (Spearman correlation, $r=0{\cdot}162$, $P=0{\cdot}676$).

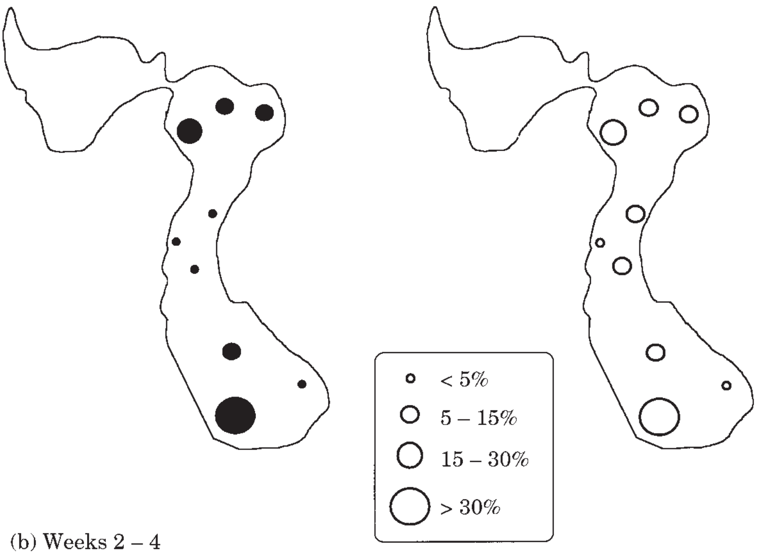
## VERTICAL DISTRIBUTION

No apparent difference in the vertical distribution was observed between ecotypes (Table I). Thus, larvae of both forms exhibited a similar pattern of vertical distribution either in day-time (Fisher's exact test$=1{\cdot}6$, d.f.$=1$, $P=0{\cdot}2056$) or night-time (Fisher's exact test$=0{\cdot}001$, d.f.$=1$, $P=0{\cdot}9483$), both forms being captured predominantly in the surface layer during the day and in deeper water at night (dwarf: exact test$=518{\cdot}77$, d.f.$=1$, $P<0{\cdot}0001$; normal: exact test$=17{\cdot}42$, d.f.$=1$, $P<0{\cdot}0001$). Consequently, the spatio-temporal distribution of larval density of both forms was highly correlated (Spearman correlation $r=0{\cdot}943$, $P=0{\cdot}0048$).

## DIET

No statistical differences were observed between diets of both larval forms for a given sampling period (Wilcoxon test, $P=0{\cdot}790$). During the first 3 weeks, cyclopoids dominated in the diet of all larvae, averaging 97·9% (week 1, 2, 3=99%, 95%, 98%) and 97·4% (week 1, 2, 3=99%, 89%, 99%) of the prey consumed by dwarf and normal larvae, respectively (Fig. 3). The secondmost

(a) Week 1



(b) Weeks 2 – 4

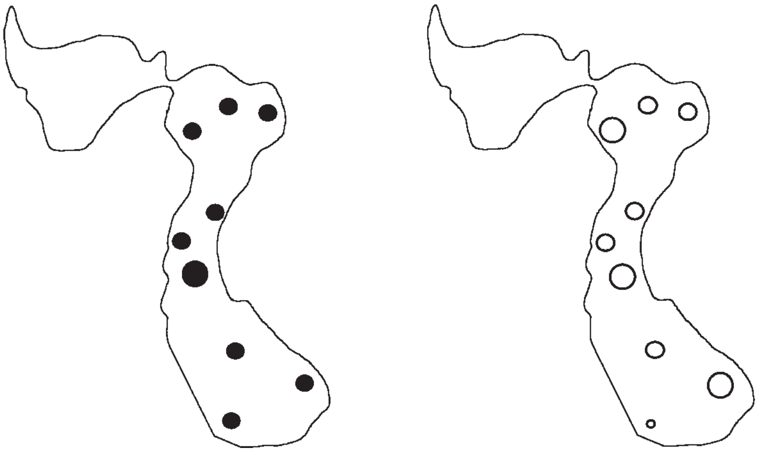


FIG. 2. Horizontal distribution in categories of relative abundance (%) for dwarf (■) and normal (□) ecotype larvae for (a) sampling week 1 and (b) pooled sampling weeks 2–4. Symbols are positioned at midpoint of trawling length for each of the nine stations sampled. The non-sampled area corresponds to a shallow-water, marshy area unsuitable for whitefish, and separated from the main lake.

important food items consisted of cladocerans (*Daphnia* sp. and *Bosmina* sp.) which represented 1 and 2% of the prey consumed by dwarf and normal larvae, respectively, resulting in a very high diet overlap index ($a$=0·956). An obvious shift occurred in the diet of both forms between the last week and the first 3 weeks of sampling ($P$<0·0001 for both dwarf and normal larvae). Cyclopoids became much less important at this time, being replaced by a relatively high occurrence of rotifers, calanoids, and cladocerans that resulted in a very low diet overlap index between sampling periods for both dwarf ($a$=0·1224) and normal ($a$=0·0240) larvae. The proportion of these food items, however, was quite

TABLE I. Total and relative abundance (%) of dwarf and normal whitefish larvae at three vertical depth strata during day-time and night-time

| Ecotype | Day-time | | | Night-time | | |
|---|---|---|---|---|---|---|
| | 0–3 m | 3–6 m | >6 m | 0–3 m | 3–6 m | >6 m |
| Dwarf | 454 | 24 | 0 | 105 | 333 | 34 |
| Normal | 19 | 3 | 0 | 6 | 17 | 1 |
| Dwarf (%) | 94·98 | 5·02 | 0·00 | 22·25 | 70·55 | 7·20 |
| Normal (%) | 86·36 | 13·64 | 0·00 | 25·00 | 70·83 | 4·17 |

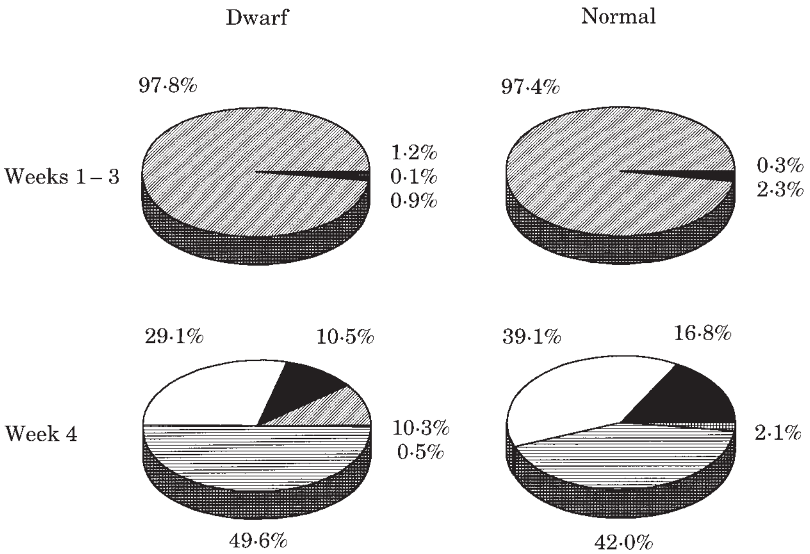


FIG. 3. Diet composition expressed as percentage of prey items for dwarf and normal ecotype larvae for weeks 1–3 (pooled) and week 4. Cross-hatched, cyclopoida; black, cladocera; horizontal-hatched, rotifera; white, calanoida; grill-hatched, others.

similar for both forms, still resulting in a high diet overlap index ($\alpha$=0·820), although lower than observed for the first 3 weeks.

Estimates of competition coeffcient were near maximal, either for spatial distribution or diet. Values for vertical distribution were 0·914 in day-time and 0·992 for night-time, whereas those for horizontal distribution were 0·972 for either the first week or pooled weeks 2–4. Competition coefficient estimate for diet was near maximal for the first 3 weeks (0·997), and slightly lower for week 4 (0·965).

## DISCUSSION

The main objective of this study was to test the hypothesis that larvae of sympatric fish ecotypes reduce competition by using different resources. This was achieved by comparing trophic resource use in time and space between dwarf and normal whitefish ecotypes in a situation of maximal reproductive isolation and adult morphological differentiation encountered within this species complex. Admittedly, the low number of normal larvae sampled imposed limitations to data interpretations, preventing a detailed comparison of trophic use at each sampling station and sampling period. Three lines of evidence indicated that low numbers of normal relative to dwarf larvae was not due mainly to the fact that they concentrated at locations not sampled here, although this cannot be ruled out entirely. Sampling was performed at all depths, from shore to central parts of the lakes, and distributed horizontally to cover most of the lake surface area. During the first week of sampling, when larvae were less mobile, the highest concentration of normal ecotype larvae was observed at the exact same locations as dwarf ecotype larvae of similar age (range: 2–12 days old), indicating that both forms use the same spawning grounds. Finally, the lower proportion of normal larvae correlated with lower numbers of adult normal whitefish compared to dwarf consistently observed in Cliff Lake (Chouinard, unpubl. data). Once correlated for differential fecundity between ecotypes, Chouinard (unpubl. data) estimated that the relative numbers of eggs produced by the whole population of normal ecotype females should be at least five times less than that of the dwarf population. Despite sample size limitations for detailed comparisons of resource partitioning between larval forms, statistical power obtained when pooling data from different sampling periods was demonstrated by the possibility of detecting highly significant differences in horizontal distribution among stations, vertical distribution between circadian time periods, and diet shift between sampling periods in both normal and dwarf ecotypes.

All estimates of resource partitioning revealed very high overlap between both forms, which refuted our working hypothesis. A strong correlation was observed in the horizontal distribution during the first week of sampling, and larvae of both forms were distributed almost uniformly among stations during the following weeks. Similarly, the vertical distribution of both forms was highly correlated and followed an identical pattern of circadian migration. Their diet was very homogeneous during the first 3 weeks of sampling and a similar shift in diet occurred in both during the fourth week, resulting in high diet overap indices at all times. This resulted in estimates of competition coefficients that were all near maximal (>0·95), indicating that the potential for competition on both spatial and trophic axes was important but that no obvious mechanisms existed to reduce it. High larval diet overlap in cage experiments between closely related coregonids has also been reported, although the potential effects of prey size selectivity of the cages could not be ruled out in that study (Davis & Todd, 1992).

These observations are in contrast with previous studies of resource partitioning between whitefish ecotypes at the adult stage. In studies of two whitefish trophic ecotypes (HGR = high gillraker ecotype, LGR = low gillraker) from the Yukon, Canada, Bodaly (1979) and Bernatchez *et al.* (1996) observed a differential vertical distribution of both ecotypes within several lakes, which translated in competition coefficient averaging 0·51, and ranging from 0·071 to 0·845, depending on lakes. Bodaly (1979) also documented important differences in diet between these ecotypes at different periods of the growing season, the HGR and LGR ecotypes feeding mainly on planktonic and benthic prey, respectively. In Cliff Lake, Bernatchez *et al.* (unpubl.) observed consistently highly significant differences in the vertical distribution and diet between adults or dwarf and normal ecotypes, although this varied between sampling periods. Important differences in resource-based utilization have been reported also between adult fish of ecotypes in other species complexes (e.g. Sandlund *et al*., 1992; McPhail, 1994).

Several alternative explanations may account for the apparent lack of resource partitioning between whitefish ecotype larvae observed in this study despite high potential for competition. First, use of alternate diet between ecotypes may be limited by reduced prey diversity found in the lake early during the growing season. This is suggested partly by the fact that a single taxon (cyclopoids) composed >97% of prey items found in stomach contents of all larvae during the first 3 weeks of sampling, as previously reported in other studies on larval whitefish (Ponton & Müller, 1989; Rojas-Beltran *et al*., 1991). However, higher trophic diversity was observed during the last week of sampling without apparent segregation of prey between ecotypes. Even in situations of low trophic diversity, competition could be reduced by exploiting similar food resources at different times or places (Schoener, 1982), which was not observed here. Although it cannot be ruled out, these observations suggest that reduced trophic diversity alone does not account for the observed lack of resource partitioning between larval whitefish ecotypes in Cliff Lake.

Another explanation may be that the lack of resource partitioning reflects the absence or low intensity of resource based selection potentially driving ecological divergence at the larval stage. A prerequisite for the development of specific resource use is that this must be limited such that interspecific competition is intense enough to increase relative survival of individuals exploiting alternate resources (Schoener, 1982). Indeed, both experimental (Maret & Collins, 1997) and field studies (Boag & Grant, 1981; Smith, 1990) demonstrated a positive correlation between the potential for competition, either due to reduced resource availability or increased population density, and the extent of trophic niche partitioning. Although there are no available data on the amount of available trophic resource for whitefish in Cliff Lake, the low densities of larvae observed suggest that their numbers may be below the carrying capacity of their environment, in a state of plenty as far as trophic resources are concerned (Wiens, 1977). In such a situation, competition, and therefore selection for characteristics reducing competition, is expected to be much less intense or not to occur at all (Schoener, 1982). Additional evidence suggesting low intensity of resource-based competition between larvae of sympatric fish ecotypes is provided by Pigeon *et al*. (1998) who reported an almost complete spatial overlap in the distribution of larvae of two rainbow smelt populations occurring sympatrically in the estuary of the St Lawrence River. The authors associated the absence of spatial segregation between these two larval populations to the abundant food resources found in the estuarine system where they coexisted.

Because both of these studies on whitefish and smelt were conducted in a single year, we cannot rule out the possibility that resource-based competition and resulting niche partitioning may occur at the larval stage in these species complexes. Indeed, there is sound evidence that competition may vary in time as a function of trophic resource abundance, and that the sporadic episodes of high competitive intensity may be important in driving ecological and morphological divergence in matters of generations (Boag & Grant, 1981; Grant & Grant, 1993). Similarly, we cannot rule out that competition exists, but it is based on behavioural traits associated with size of the larvae and individual aggressiveness, which could force one ecotype into a suboptimal usage of the resource if the other ecotype is more abundant and successful at consuming the same resource (Todd & Davis, 1995). In comparison with previous studies of resource partitioning at the adult stage, however, this study and that of Pigeon *et al.* (1998) indicate that resource-based selection and niche partitioning may be much less pronounced at the larval stage. Because the present study was performed in a situation of maximal reproductive isolation and adult morphological specialization found in sympatric whitefish ecotypes, we suggest that resource-based selection at the larval stage has played little role in driving the divergence and reproductive isolation in this species complex.

The authors thank D. Bussière, S. Martin, and G. Moreau for field and laboratory assistance; J. Dodson, E. Taylor, J. Turgeon, T. Todd and one anonymous referee for their judicious constructive comments; and D. Basley, P. Bourque, D. Coté and the Department of Inland Fisheries and Wildlife of Maine for their logistic collaboration. This work was supported by NSERC (Canada) and FCAR (Québec) research grants to LB. AC was supported by FCAR scholarships. Contribution to the programme of GIROQ.

## References

Bernatchez, L. & Dodson, J. J. (1990). Allopatric origin of sympatric populations of lake whitefish (*Coregonus clupeaformis*) as revealed by mitochondrial-DNA restriction analysis. *Evolution* **44,** 1263–1271.

Bernatchez, L., Guyomard, R. & Bonhomme, F. (1992). DNA sequence variation of the mitochondrial control region among geographically and morphologically remote European brown trout *Salmo trutta* populations. *Molecular Ecology* **1,** 161–173.

Bernatchez, L., Glémet, H., Wilson, C. C. & Danzmann, R. G. (1995). Introgression and fixation of Arctic char (*Salvelinus alpinus*) mitochondrial genome in an allopatric population of brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* **52,** 179–185.

Bernatchez, L., Vuorinen, J. A., Bodaly, R. A. & Dodson, J. J. (1996). Genetic evidence for reproductive isolation and multiple origins of sympatric trophic ecotypes of whitefish (*Coregonus*). *Evolution* **50,** 624–635.

Boag, P. T. & Grant, P. R. (1981). Intense natural selection in a population of Darwin's finches (Geopizinae) in the Galapagos. *Science* **214,** 82–85.

Bodaly, R. A. (1979). Morphological and ecological divergence within the lake whitefish (*Coregonus clupeaformis*) species complex in Yukon territory. *Journal of Fisheries Research Board of Canada* **36,** 1214–1222.

Chouinard, A., Pigeon, D. & Bernatchez, L. (1996). Lack of specialization in trophic morphology between genetically differentiated dwarf and normal forms of lake whitefish (*Coregonus clupeaformis* Mitchill) in Lac de l'Est, Québec. *Canadian Journal of Zoology* **74,** 1989–1998.

Cushing, D. H. (1975). *Marine Ecology and Fisheries.* Cambridge: Cambridge University Press.

Davis, B. M. & Todd, T. N. (1992). Diet overap in larval lake herring (*Coregonus artedi*) and bloaters (*Coregonus hoyi*). In *Biology and Management of Coregonid Fishes* (Todd, T. N. & Luczynski, M., eds). *Polskie Archiwum Hydrobiologii* **39,** 279–287.

Eckmann, R. & Rey, P. (1987). Daily increments on the otoliths of larval and juvenile *Coregonus* spp., and their modification by environmental factors. *Hydrobiology* **148,** 137–143.

Fenderson, O. (1964). Evidence of subpopulations of lake whitefish *Coregonus clupeaformis*, involving a dwarfed form. *Transactions of the American Fisheries Society* **93,** 77–94.

Fortin, R. & Gendron, M. (1990). Reproduction, croissance et morphologie des Grands Corégones (*Coregonus clupeaformis*) nains et normaux du réservoir Outardes-2 (Québec). *Canadian Journal of Zoology* **68,** 17–25.

Grant, B. R. & Grant, P. R. (1993). Evolution of Darwin's finches caused by a rare climatic event. *Proceedings of the Royal Society of London B, Biological Sciences* **251,** 111–117.

Loftus, D. H. & Hulsman, P. F. (1986). Predation of larval lake whitefish (*Coregonus clupeaformis*) and lake herring (*C. artedi*) by adult rainbow smelt (*Osmerus mordax*). *Canadian Journal of Fisheries and Aquatic Sciences* **43,** 812–818.

MacArthur, R. H. & Levins, R. (1967). The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* **101,** 377–385.

Maret, T. J. & Collins, J. P. (1997). Ecological origin of morphological diversity: a study of alternative trophic phenotypes in larval salamanders. *Evolution* **51,** 898–905.

Mayr, E. (1963). *Animal Species and Evolution.* Cambridge, MA: Harvard University Press.

McPhail, J. D. (1994). Speciation and the evolution of reproductive isolation in the sticklebacks (*Gasterosteus*) of southwestern British Columbia. In *Evolution of the threespine stickleback* (Bell, M. A. & Foster, S. A., eds), pp. 399–437. Oxford: Oxford University Press.

Persson, L. & Greenberg, G. A. (1990). Interspecific and intraspecific size class competition affecting resource use and growth of perch, *Perca fluviatilis*. *Oikos* **59,** 97–106.

Pigeon, D., Chouinard, A. & Bernatchez, L. (1997). Multiple modes of speciation involved in the parallel evolution of sympatric dwarf and normal morphotypes of lake whitefish (*Coregonus clupeaformis*, Salmonidae). *Evolution* **51,** 196–205.

Pigeon, D., Dodson, J. J. & Bernatchez, L. (1998). A mtDNA analysis of spatio-temporal distribution of two genetically distinct sympatric larval populations of rainbow smelt (*Osmerus mordax*) in the middle estuary of the St Lawrence river, Québec, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, in press.

Ponton, D. & Müller, R. (1989). Alimentation et facteurs de mortalité des larves de corégones (*Coregonus* sp.). Exemple de deux lacs de niveaux trophiques différents: les lacs de Sarnen et de Hallwill (Suisse Centrale). *Aquatic Sciences* **51,** 67–83.

Roff, D. A. & Bentzen, P. (1989). The statistical analysis of mitochondrial DNA polymorphisms: $\chi^2$ and the problem of small samples. *Molecular Biology and Evolution* **6,** 539–545.

Rojas-Beltran, R., Balvay, G., Tunowski, J., Gerdeaux, D. & Guillard, J. (1991). Relations trophiques zooplancton-poissons dans le lac Leman: Première approche de l'alimentation des larves de *Coregonus lavaretus* en conditions naturelles et semi-naturelles. *Troisième Conférence Internationale des Limnologues d'Expression Francaise*, 128–131.

Sandlund, O. T., Gunarsson, K., Jonasson, P. M., Jonsson, B., Lindem, T., Magnusson, K. P., Malmquist, H. J., Sigujonsdottir, H., Skulason, S. & Snorrason, S. S. (1992). The arctic charr *Salvelinus alpinus* in Thingvalavatn. *Oikos* **64,** 305–351.

Schluter, D. (1996*a*). Ecological causes of adaptive radiation. *American Naturalist* **148,** S40–S64.

Schluter, D. (1996*b*). Ecological speciation in postglacial fishes. *Philosophical Transactions of the Royal Society of London B* **351,** 807–814.

Schluter, D. & McPhail, J. D. (1993). Character displacement and replicate adaptive radiation. *Trends in Ecology and Evolution* **8,** 197–200.

Schoener, T. W. (1970). Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* **58,** 408–418.

Schoener, T. W. (1982). The controversy over interspecific competition. *American Scientist* **70,** 586–595.

Scott, W. B. & Crossman, E. J. (1973). Freshwater fishes of Canada. *Bulletin of Fisheries Research Board of Canada* **184**.

Sinclair, M. & Iles, T. D. (1988). Population richness of marine fish species. *Aquatic Living Resources* **1,** 71–83.

Skúlason, S. & Smith, T. B. (1995). Resource polymorphisms in vertebrates. *Trends in Ecology and Evolution* **10,** 366–370.

Smith, T. B. (1990). Resource use by bill morphs of an African finch: evidence for intraspecific competition. *Ecology* **71,** 1246–1257.

Smith, G. R. & Todd, T. N. (1984). Evolution of species flocks of fishes in north temperate lakes. In *Evolution of Fish Species Flocks* (Echelle, A. A. & Kornfield, I., eds), pp. 45–68. Orono, ME: University of Maine at Orono Press.

Snorrason, S. S., Skúlason, S., Jonsson, B., Malmquist, H. J., Jónasson, P. M., Sandlund, O. T. & Lindem, T. (1994). Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces: Salmonidae): morphological divergence and ontogenetic niche shifts. *Biological Journal of the Linnean Society* **52,** 1–18.

Stevenson, D. K. & Campana, S. E. (1992). Otolith microstructure examination and analysis. *Canadian Special Publications in Fisheries and Aquatic Sciences* **117**.

Taylor, E. B. & Bentzen, P. (1993). Evidence for multiple origins and sympatric divergence of trophic ecotypes of smelt (*Osmerus*) in Northeastern North America. *Evolution* **47,** 813–832.

Taylor, E. B., Foote, C. J. & Wood, C. C. (1996). Molecular genetic evidence for parallel life-history evolution within a pacific salmon (sockeye salmon and kokanee, *Oncorhynchus nerka*). *Evolution* **50,** 401–416.

Todd, T. N. & Davis, B. M. (1995). Effects of fish density and relative abundance on competition between larval lake herring and lake whitefish for zooplankton. *Archivum für Hydrobiologie Special Issues in Advanced Limnology* **46,** 163–171.

Vuorinen, J. A., Bodaly, R. A., Reist, J. D., Bernatchez, L. & Dodson, J. J. (1993). Genetic and morphological differentiation between dwarf and normal size forms of lake whitefish (*Coregonus clupeaformis*) in Como Lake, Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* **50,** 210–216.

Wiens, J. A. (1977). On competition and variable environments. *American Scientist* **65,** 590–597.