JOURNAL OF Evolutionary Biology eseb European Society for Evolutionary Biology

doi: 10.1111/j.1420-9101.2010.02121.x

Role of epibenthic resource opportunities in the parallel evolution of lake whitefish species pairs (*Coregonus* sp.)

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Keywords:

community assemblages;
Coregonus clupeaformis;
ecological opportunity;
limnology;
parallel evolution;
seasonal variation;
speciation.

Abstract

Parallel evolution of a dwarf and normal whitefish has been documented in six post-glacial lakes. Here, we relate the structure and seasonal variations of the epibenthic invertebrate communities to the extent of phenotypic differentiation in these species pairs. The highest phenotypic differentiation occurs in lakes characterized by less overlap in size distribution between limnetic and epibenthic prey which could represent enhanced ecological opportunities for trophic specialization and adaptive divergence. Differences in community assemblages and seasonal variation of biotic and abiotic conditions may also play a role. Accumulating evidence indicates that strong directional selection acting on dwarf whitefish may be more important than divergent selection acting on both sympatric forms in driving whitefish phenotypic divergence and ultimately, ecological speciation. Along with Landry *et al.* (2007), this study supports the general hypothesis that parallelism in divergence among sympatric dwarf and normal whitefish is associated with parallelism in limnological adaptive landscape.

Introduction

Evolution by natural selection is strongly supported by parallel evolution of morphological, physiological, behavioural and life-history trait variations for the exploitation of similar resources and habitats in sympatric, closely related lineages (Taylor & McPhail, 2000; Nosil *et al.*, 2002; Bernatchez, 2004; Rolan-Alvarez *et al.*, 2004). Consequently, there is particular interest to improve our knowledge about ecological opportunities, i.e. available resources and habitats (reviewed in Schluter, 2000; sensu Simpson, 1953), for many independent sympatric populations wherein varying degrees of parallel divergence have been observed. This would allow the identification of the specific characteristics in ecological opportunity that could be involved in the emergence of polymorphisms, ecological speciation (Losos *et al.*, 1998; Robinson *et al.*, 2000; McKinnon *et al.*, 2004; Nosil & Reimchen, 2005) or lack thereof (Moore *et al.*, 2007; Hendry *et al.*, 2009).

In general terms, ecological opportunity may impose selective pressures that promote population divergence through both the availability and heterogeneity of exploited habitats and resources (Rainey & Travisano, 1998; Kassen *et al.*, 2004; Svanbäck & Bolnick, 2007). First, availability of ecological opportunity is dependent upon the density of specific resources, which in turn may be influenced by the density of competitors, and predators (Harmon *et al.*, 2009). Polymorphism as well as adaptive divergence potentially leading to ecological speciation could arise where ecological opportunity occurs, and intraspecific competition reduces fitness of relatively common phenotypes, thus promoting density-dependent directional or disruptive selection (see Bolnick & Lau, 2008). Second, heterogeneity of ecological opportunity seems essential for divergence and may impose selective pressures promoted by physical spatial structure (Rolan-Alvarez *et al.*, 2004; Savolainen *et al.*, 2006; Johannesson *et al.*, 2010). Heterogeneity itself can also be defined by spatial community assemblages of available prey or hosts diversity, such as the different

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predatory behaviour in the case of walking sticks that use different host plant species based on cryptic coloration (*Timema cristinae*; Nosil *et al.*, 2002), and Darwin's finches (*Geospiza* spp.) with different beak size that exploit different seed sizes of different plant species (Abbott *et al.*, 1977; Grant & Grant, 2006). Predator and competitor effects may also impose different selective pressure for the efficient exploitation of the least accessible resources or use of habitat structures for survival (Abrams, 2000; Reimchen & Nosil, 2002; Rundle *et al.*, 2003; Toju, 2007).

Since the post-glacial Pleistocene recolonization, independent evolution resulting in similar phenotypic divergence has occurred many times in diverse northern freshwater fishes (Hindar & Jonsson, 1982; Robinson *et al.*, 2000; Taylor & McPhail, 2000; Bernatchez, 2004). In lacustrine environments, phenotypic and genotypic replicate patterns have been hypothesized to emerge from the similar heterogeneous characteristics associated with the occurrence of planktonic and littoral (or benthic) habitats (reviewed in Robinson & Wilson, 1994; Bolnick & Lau, 2008). Thus, characterization of the differences in these lake habitats may permit the identification of features that could promote and maintain particular patterns of differentiation between two genetically distinct, yet closely related sympatric populations inhabiting them. Yet, little attention has been paid to documenting the 'limnological landscape' and its possible role in explaining patterns of ecological and morphological divergence between sympatric forms of freshwater fishes.

In lake whitefish, *Coregonus clupeaformis* (Mitchill.), the parallel evolution of a dwarf phenotype derived from an ancestral normal phenotype and remaining reproductively isolated while living in sympatry with it, has been documented in six post-glacial lakes of the St. John River basin (Québec, CA and Maine, USA) (Bernatchez, 2004). The dwarf whitefish is only found in sympatry with normal whitefish (Chouinard & Bernatchez, 1996; Pigeon *et al.*, 1997; Lu & Bernatchez, 1999), and in the absence of the lake cisco (*Coregonus artedii*), a direct competitor species that may limit exploitation of the planktonic habitat (Davis & Todd, 1998; Trudel *et al.*, 2001; Bernatchez, 2004). Dwarf and normal whitefish have specific predators in these lakes. Lake trout (*Salvelinus namaycush*) is more generally known to prey on the dwarf whitefish, similar to brown trout (*Salmo trutta*) in European whitefish systems (Kahilainen *et al.*, 2003), and the bottom-dwelling burbot (*Lota lota*) more generally consume normal whitefish (Carl & McGuiness, 2006). Typically, dwarf and normal sympatric whitefish mainly use pelagic and epibenthic habitats and resources, respectively (Bernatchez *et al.*, 1999). Each displays phenotypic associations with their respective habitats in regard to behavioural (e.g. foraging, swimming), life history (e.g. age at maturity), physiological (e.g. growth), morphological traits (e.g. gill raker number), as well as gene expression (Bernatchez *et al.*, 1999; Lu & Bernatchez, 1999; Trudel *et al.*, 2001; Rogers *et al.*, 2002; Rogers & Bernatchez, 2005; Derome *et al.*, 2006; St-Cyr *et al.*, 2008). Also, some of the latter traits have been linked with loci under divergent selection in natural conditions (reviewed in Bernatchez *et al.*, 2010).

Moreover, Lu & Bernatchez (1999) showed that the extent of phenotypic divergence varied among whitefish species pairs and that there is a positive relationship between phenotypic divergence and the extent of reproductive isolation likely driven by the intensity of divergent selection has been documented in this system. Recently, Landry *et al.* (2007) also showed that lakes harbouring sympatric whitefish pairs with different levels of phenotypic and genetic divergence (Lu & Bernatchez, 1999) also differed in their limnological landscapes characterized by several abiotic features as well as the zooplankton community. This provided further support to the hypothesis that different selective pressures imposed by distinct limnological landscapes were involved in driving the adaptive divergence and reproductive isolation between sympatric dwarf and normal whitefish through their role in promoting competitive interactions.

Here, we complement the earlier study of Landry *et al.* (2007) by documenting the structure of benthic invertebrate communities in the same system for the same years of study. First, we predicted that the density of the benthic invertebrate community should be lower in lakes with high differentiation between dwarf and normal whitefish. Although the causal vs. consequential links between density and divergence cannot rigorously be told apart in this study, lower prey density could potentially promote directional selection by increasing intraspecific competition and increasing the fitness potential of individuals of the dwarf species exploiting the pelagic habitat. Second, these lakes should also show, relative to lakes harbouring more weakly differentiated whitefish pairs, community assemblages of benthic invertebrates with higher individual length that would accentuate differential selective pressures between planktonic and epibenthic environment. We also predicted that these two lake groups should harbour different benthic prey diversity that could create different selective pressures, as well as different seasonal variation that would cause selection to fluctuate differently.

Materials and methods

Study sites

Six dimictic lakes of the St. John River watershed were selected for this study on the basis of prior work in the region (Lu & Bernatchez, 1999). Based on previous univariate and multivariate analyses of morphological and meristics traits, these rank in decreasing order of overall phenotypic differentiation between sympatric dwarf and normal whitefish: Cliff Lake, Indian Pond, Webster Lake, Crescent Pond, Témiscouata Lake and East Lake (Lu & Bernatchez, 1999). Thus, the first three lakes were assigned to group A (most differentiated species pairs) and the last three lakes to group B (least differentiated species pairs; see also details in Landry *et al.*, 2007). Lake cisco (*C. artedii*) is absent from all six lakes, but all harbour healthy populations of lake trout (*S. namaycush*) and burbot (*L. lota*; except in Crescent Pond).

Epibenthic invertebrate sampling and analyses

Five sampling stations were randomly selected in each lake between depths of 5 and 25 m, where both dwarf and normal whitefish are most typically found. Namely, both forms are known to avoid warmer waters of the littoral zone (< 5 m) during the growing season. At each sampling period, we recorded depth for each station, which were also positioned using a geographical positioning system and bathymetric maps. Stations were sampled early (16–26 June) and late (20–28 August) in 2003. Given that data were collected during a single growing season, results should be interpreted with caution. Benthic invertebrates were captured with an Ekman dredge and samples were passed through a 0.300-mm sieve. Samples were preserved in 95% ethanol until laboratory analyses. All individuals were classified into taxonomic groups (Table 1). For each sampling station, the number of individuals for each taxonomic group were counted, and a random sample of twenty individuals from each taxon were measured to the nearest 0.025 mm using a dissecting microscope with an ocular micrometer. These sub-samples were then divided into 1 mm length classes. For a given taxon, numbers of measured individuals of each length class were transformed to density by multiplying the frequency of individuals in a length class calculated over all measured individuals by the number of individuals per square metre of this taxon at a given station.

Statistical analyses

Density and length distribution of benthic invertebrates and seasonal variation

Lake group differences in resource availability, in terms of density and mean length of epibenthic invertebrates, were analysed using a two fixed factors (month and lake group) mixed procedure (Littell *et al.*, 2004). Mean values were calculated over the five stations surveyed in each lake. Lake was considered as a random factor and was nested in its respective lake group. For a better look at individuality of each lake in given lake group, we also estimated lake difference in availability in terms of density using a two fixed factors (month and lake) mixed procedure. Here, stations values were considered as a random factor and nested within lake (Littell *et al.*, 2004). All analyses were performed using SAS, v. 8.2.

Benthic invertebrate community structure and seasonal variation – species assemblage

Following Clarke (1993), we built a triangular similarity matrix of species composition (Bray-Curtis) between sample pairs. The samples were formed by the density of each taxon, in each station for every month in every lake. Data from each sample was square root transformed, to better account for contributions from rare species and standardized to correct for density differences between samples. Similarity matrices were used for testing differences in benthic invertebrate density taxa assemblage using ANOSIM. This analysis was carried out

Table 1 Summary of benthic invertebrate community characteristics of the lakes harbouring highly differentiated (Lake group A) and weakly differentiated whitefish pairs (Lake group B).

		Lake group A			Lake group B		
Variable	Month	CL	IP	WL	CP	TL	EL
Taxa	June	a,b.c,d,n,o,t,q	a,b,c,d,h,k,m-p,t	a,b,d,h,o,p	a,b,c,d,h,k,m-p	a,b,d,g,h,k,m-p	b,c,d,h,k,m,o
	August	a,b,c,d,h,k,m,o,p	a,b,d,h,k,m,o,p	a,b,c,h,k,m-p	a,b,c,h,k,m,o,p	a,b,h,k,m,gam,o,p	b,c,h,k,m-p
Density 103 ind m-2 (std)	June	3.2 (1.4)	4.7 (2.9)	1.7 (0.8)	2.6 (0.9)	10.6 (9.5)	1.4 (0.5)
	August	4.4 (2.2)	4.2 (3.1)	1.3 (0.6)	3.4 (1.8)	15.0 (5.2)	1.7 (0.8)
Range size (mm)	June	0.6–18.7	0.6–17.6	0.8–16.7	0.6–18.1	0.5–19.6	0.6–13.7
	August	0.5–21.2	0.6–19.3	0.5–17.2	0.4–11.8	0.5–23.0	0.5–13.3
Mean size mm (std)	June	5.5 (1.9)	4.2 (1.0)	6.8 (1.9)	4.4 (0.6)	2.0 (0.8)	3.7 (1.1)
	August	2.9 (0.6)	4.6 (0.8)	4.9 (2.4)	3.7 (0.5)	1.9 (0.3)	2.4 (0.8)
R between months (*P*)		0.544 (0.008)	0.436 (0.016)	0.531 (0.008)*	0.616 (0.008)	0.152 (0.143)	0.116 (0.222)

Taxa: a = chaoboridae larvae, b = chironomidae larvae, c = ceratopogonidae larvae, d = diptera pupae, e = annelida (always present), f = nematoda (always present), g = gasteropoda, gam = gamaridae, h = bivalvia, k = ostracoda, m = hydracarina, o = copepoda, p = cladocera, q = tricoptera larvae and t = others *without WL1A (see Materials and methods for details).

WL1A, Webster Lake in August.

to assess differences in various levels of comparisons, namely between: lake groups by month (two-crossed analysis), lake groups, months within each lake group, individual lakes, individual lakes by month (two-crossed analysis) and months within each lake. The resulting R statistic provided the estimated differences of mean rank similarities between and within assemblages. Assemblages were considered as different when within-lake similarity values are higher than between-lakes similarities, i.e when $R > 0$. R values were interpreted as showing a strong difference at $R > 0.75$, intermediate difference at $R > 0.5$, small difference at $R > 0.25$ and random grouping at $R = 0$ (Winkler *et al.*, 2005). *P* values were obtained by randomly relabelling all samples and recalculated R for each possible unique relabelling. Then, *P* values were estimated as the ratio between the numbers of random *R*-values exceeding the observed one over the total number of random *R*-values. We used a similarity of percentages routine, SIMPER, to assess the contribution in per cent of different taxa to the observed assemblage dissimilarities (Bray-Curtis) and to assess both the overall similarity in species assemblage within each pair and dissimilarity between pairs for each ANOSIM analysis described elsewhere. We then used nonmetric multi-dimensional scaling (NMDS) to graphically represent community relationships. The ranked average similarities provided by the previous triangular matrix between sample pairs can thus be used to reconstruct a bi-dimensional map of the 'distance' between samples. The algorithm, through iterative cycles, moves samples of community assemblages into positions in which the rank order of the inter-sample 'distances' becomes ever closer to the rank order in the original triangular matrix. A stress level was calculated to determine the extent to which the representation disagreed with rank similarities, in which 0 indicates perfect agreement and 0.2 defines the upper limit of disagreement corresponding to a suitable picture. In the NMDS plot of all samples, the first station of Webster Lake in August (hereafter WL1A) appeared as an outlier that could potentially bias all the analysis (see Results). Consequently, results shown are without this station; however, we present both analyses (with and without WL1A) when removal of this sample significantly changed the result. Bray-Curtis matrix calculation, ANOSIM, SIMPER and NMDS plotting were all performed using the PRIMER-E, v.5 (Clarke, 1993).

Results

Density of benthic invertebrates

The mixed ANOVA modelling revealed no significant difference of epibenthic invertebrate density between lake groups and month (lake group: $F_{1,4} = 0.19$, $P = 0.6860$; month: $F_{1,4} = 1.39$, $P = 0.3040$; lake group by month: $F_{1,4} = 2.79$, $P = 0.1702$). However, this analysis revealed a significant difference between individual lakes ($F_{5,24} = 15.30$, $P < 0.0001$). Témiscouata Lake was significantly different than any other lakes (Cliff Lake: $t_{24} = -4.16$, $P = 0.0003$; Indian Lake: $t_{24} = -3.68$, $P = 0.0012$; Webster Lake: $t_{24} = -7.58$, $P < 0.0001$; Crescent Pond: $t_{24} = -4.96$, $P < 0.0001$; East Lake: $t_{24} = -7.25$, $P < 0.0001$), also, significant differences were observed between Cliff Lake and East Lake ($t_{24} = 3.09$, $P = 0.0050$), Cliff Lake and Webster Lake ($t_{24} = 3.42$, $P = 0022$), Crescent Pond and East Lake ($t_{24} = 2.29$, $P = 0.0310$), Crescent Pond and Webster Lake ($t_{24} = 2.63$, $P = 0.0148$), East Lake and Indian Pond ($t_{24} = -3.57$, $P = 0.0015$), and Indian Pond and Webster Lake ($t_{24} = 3.90$, $P = 0.0007$).

Mean length of benthic invertebrates

The mixed ANOVA modelling of mean length revealed no significant difference in mean length between lake groups and months (lake group: $F_{1,4} = 4.41$, $P = 0.1035$; month: $F_{1,4} = 4.44$, $P = 0.1029$; lake group by month: $F_{1,4} = 0.14$, $P = 0.7265$). The ANOVA model for individual lakes showed significant differences between months (mean June: 4.4569, SD = 1.9307, mean August: 3.3945, SD = 1.5232, $F_{1,24} = 14.13$, $P = 0.0010$) and between individual lakes ($F_{5,24} = 13.61$, $P < 0.0001$). On average, however, *post hoc* analyses show marginally more differences between lakes from the different lake groups (8 on 9 cases) than between lakes within each group (3 on 6 cases), which was indicated by significant least square differences (see Fig. 1) in the following lake pair comparisons. Significant between-group comparisons were Cliff Lake and East Lake ($t_{24} = 2.26$, $P = 0.0335$), Cliff Lake and Témiscouata

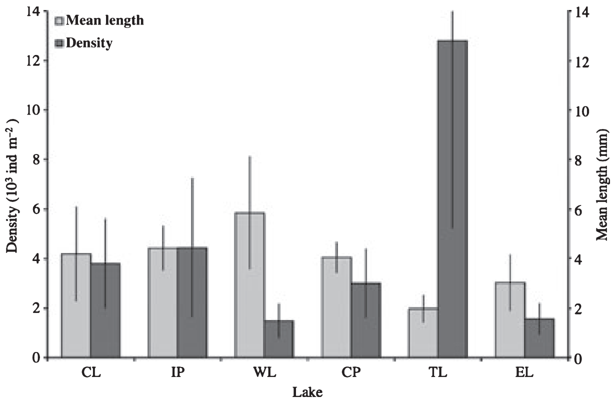

Fig. 1 Comparison of benthic invertebrates mean length (light grey) and density (dark grey) between individual lakes and lake groups. Lake group A: CL, Cliff Lake; IP, Indian Pond; WL, Webster Lake; Lake group B: CP, Crescent Pond; TL, Témiscouata Lake; EL, East Lake. A = lake group with highest phenotypic differentiation between sympatric dwarf and normal whitefish and B = lake group with lowest phenotypic differentiation.

Lake ($t_{24} = 4.91$, $P < 0.0001$), Crescent Pond and Webster Lake ($t_{24} = -2.43$, $P = 0.0227$), East Lake and Indian Pond ($t_{24} = -3.01$, $P = 0.0061$), East Lake and Témiscouata Lake ($t_{24} = 2.65$, $P = 0.0141$), East Lake and Webster Lake ($t_{24} = -4.82$, $P < 0.0001$), Indian Pond and Témiscouata Lake ($t_{24} = 5.66$, $P < 0.0001$), and Témiscouata Lake and Webster Lake ($t_{24} = -7.47$, $P < 0.0001$). Significant within-group comparisons were Cliff Lake and Webster Lake ($t_{24} = -2.57$, $P = 0.0170$), Crescent Pond and East Lake ($t_{24} = 2.39$, $P = 0.0252$), Crescent Pond and Témiscouata Lake ($t_{24} = 5.04$, $P < 0.0001$). Marginally significant difference between month in each lake was also observed ($F_{5,24} = 2.64$, $P = 0.0490$), and *post hoc* analyses show significant differences between month in Cliff Lake ($F_{1,24} = 13.60$, $P = 0.0012$), East Lake ($F_{1,24} = 6.58$, $P = 0.0170$) and Webster Lake ($F_{1,24} = 5.56$, $P = 0.0269$).

Community structure: species assemblages

The most pronounced differences in species assemblages were observed between individual lakes belonging to lake group A vs. those of lake group B. Thus, the three most pronounced differences were observed between Indian Pond (A) and East Lake (B; $R = 1.000$, $P = 0.001$; Average dissimilarity = 65.70 explained by 26.93% bivalvia taxa that was more abundant in East Lake), followed by Cliff Lake (A) and East Lake (B; $R = 0.980$, $P = 0.001$; Average dissimilarity = 64.18 explained by 30.62% bivalvia taxa that was more abundant in East Lake), and Indian Pond (A) and Témiscouata Lake (B); $R = 0.929$, $P = 0.001$; Average dissimilarity = 50.01 explained by 30.36% ostracoda taxa that was more abundant in Témiscouata Lake). Also, although an overall significant difference was observed between individual lakes community assemblages ($R = 0.726$, $P = 0.001$; Table 2), the smallest differences were observed between lakes harbouring the most highly differentiated whitefish pairs (lake group A). Thus, the smallest difference was between Indian Pond and Cliff Lake ($R = 0.070$, $P = 0.096$; Average dissimilarity = 31.15 explained by 16.53% copepoda taxa that was more prevalent in Indian Pond), the second between Cliff Lake and Webster Lake ($R = 0.238$, $P = 0.017$; Average dissimilarity = 40.53 explained by 20.33% copepoda taxa that was more prevalent in Cliff Lake), and the third was observed between Indian Pond and Webster Lake ($R = 0.350$, $P = 0.001$; Average dissimilarity = 36.36 explained by 23.44% copepoda taxa that was more abundant in Indian Pond).

A net significant difference in community assemblages was also detected between both lake groups, which can be considered 'intermediate' based on R value ($R = 0.595$, $P = 0.001$). The two-way crossed ANOSIM analysis of lake group by month also showed a significant intermediate difference when testing for differences between lake groups averaged over months ($R = 0.613$, $P = 0.001$), and a significant yet small difference between months averaged across lake groups ($R = 0.172$, $P = 0.001$). Average dissimilarity between lake groups was 52.13, which was first explained by the contribution of 19.70% of the bivalvia taxa which was more abundant in lake group B, then 16.50% explained by copepoda taxa which was more prevalent in lake group A, and third by 15.49% ostracoda taxa which was more abundant in lake group B. Average similarity between lakes within lake group A was 64.77, which was explained by 29.61% copepoda taxa, 28.67% chironomidae larvae taxa, and 27.61% chaoboridae larvae taxa. Average similarity within lake group B was 61.54 and explained by 29.64% chironomidae larvae taxa, 24.14% bivalvia taxa and 18.99% ostracoda taxa. NMDS plot illustrated three main differences between samples, and the intermediate level of stress (0.14) allowed interpreting the relationships depicted between samples (Fig. 2). First, as in the ANOSIM analysis, this plot revealed a difference between lake group A and B. Second, overlap between months appeared more prevalent in lake group B (see also below for more details) than lake group A. Third, samples from lake group A tended to be more similar among themselves, especially in August as shown by the SIMPER analysis (see also details given in the following paragraphs).

Table 2 Difference between lake groups from Bray-Curtis similarities of taxa density data (standardized and square-root transformed).

Lake group	Lake	R	P	SIMPER analysis	
	All pairwise	0.721	0.001	*Av. Dis.*	*Taxa (lake +)*
A – A	CL, IP	0.070	0.096	31.15	Copepoda (IP)
	IP, WL	0.350	0.001	36.36	Copepoda (IP)
	CL, WL	0.238	0.017	40.53	Copepoda (CL)
B – B	CP, TL	0.746	0.001	41.76	Ostracoda (TL)
	TL, EL	0.867	0.001	48.44	Bivalvia (EL)
	CP, EL	0.916	0.002	42.97	Bivalvia (EL)
A – B	CL, CP	0.723	0.001	44.79	Copepoda (CL)
	CL, TL	0.794	0.001	51.81	Ostracoda (TL)
	CL, EL	0.980	0.001	64.18	Bivalvia (EL)
	IP, CP	0.916	0.001	44.43	Copepoda (IP)
	IP, TL	0.929	0.001	50.01	Ostracoda (TL)
	IP, EL	1.000	0.001	65.70	Bivalvia (EL)
	WL, CP	0.501	0.001	40.16	Bivalvia (CP)
	WL, TL	0.688	0.001	48.69	Ostracoda (TL)
	WL, EL	0.895	0.001	59.94	Ostracoda (EL)

Within-lake similarity values are higher than between-lake similarities when > 0. Lake differences are significant when $P < 0.05$ (50 times over 999 relabelling times). SIMPER analysis showed average dissimilarity (*Av. Dis.*) for each pairwise lake comparison and the taxa explaining the higher percentage of average dissimilarity (*taxa*). *Lake* + was the lake where the given taxon was the most abundant.

Figure 3 presents the most common taxa in each lake group, their differences between months, as well as the different benthic invertebrate assemblage between lake groups and months. For lake group A, community

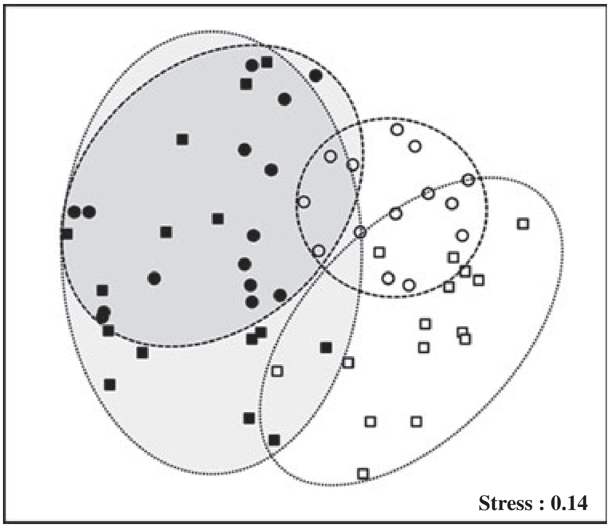

Fig. 2 Non-metric multi-dimensional scaling plot of benthic invertebrate community (density) represented by the five stations in June (square and arbitrary dotted line) and August (circle and arbitrary regular line) for A lake group (high differentiation between sympatric dwarf and normal whitefish; white and clear area) and B lake group (low differentiation; black and frosted area). See Material and methods for details on stress.

assemblages showed significant difference between months ($R = 0.279$, $P = 0.001$, Fig. 4). Average dissimilarity between months was 37.35 and explained by 17.79% copepoda taxon that was more abundant in August, 13.69% chironomidae larvae taxa, and 13.04% chaoboridae larvae, which were both more prevalent in June. Average similarity for June within lake group A was 68.12 and explained by 36.52% chaoboridae larvae taxa, 32.51% chironomidae larvae taxa and 24.17% copepoda taxa. Average similarity for August within lake group A was 68.04 and explained by 32.63% copepoda taxa, 22.89% chironomidae larvae taxa, and 19.99% chaoboridae larvae taxa. For lake group B, assemblage did not differ significantly between months ($R = 0.044$, $P = 0.175$). Average similarity among lakes within June for lake group B was 60.90 and explained by 31.99% chironomidae larvae taxa, by 25.82% bivalvia taxa, and by 15.05% ostracoda taxa. Average similarity in August within the same lake group was 63.66 and explained by 26.10% chironomidae taxa, 22.94% ostracoda taxa, and 21.51% ostracoda taxa. Separate NMDS plot of each lake group (Fig. 4) revealed two main observations, and stresses lower than 0.2 allowed interpreting these plots (lake group A = 0.19, lake group B = 0.10). First, as in the ANOSIM analysis, months tended to overlap more strongly in lake group B than in lake group A. Second, similarity within month for a given lake group tended to be greater in lake group A, as in the SIMPER analysis.

Similarity comparisons were also made between samples from each month within each lake, because two-crossed analysis of lake by month showed highly significant differences (lake, $R = 0.813$, $P = 0.001$; month, $R = 0.395$, $P = 0.001$). For lake group A, we observed differences between months in all three lakes: significant, small to intermediate differences were found in Cliff Lake ($R = 0.544$, $P = 0.008$), Indian Pond ($R = 0.436$, $P = 0.016$), and Webster Lake ($R = 0.531$, $P = 0.008$; with WL1A; $R = 0.228$, $P = 0.071$). For lake group B, significant difference between months was observed in Crescent Pond ($R = 0.616$, $P = 0.008$) but no significant differences were found for the other two lakes (Témiscouata Lake $R = 0.152$, $P = 0.143$; East Lake $R = 0.116$, $P = 0.222$; see Table 1).

Discussion

In a previous study, Landry *et al.* (2007) showed that lakes harbouring sympatric whitefish pairs with different levels of phenotypic and genetic divergence (Lu & Bernatchez, 1999) also differed in their limnological landscapes. Namely, lakes harbouring the most divergent phenotypes were characterized by a greater depletion of hypolimnetic oxygen during the growing season and narrower distribution of prey length. This provided further support to the hypothesis that different selective pressures imposed by distinct 'limnological landscapes' were involved in the phenotypic divergence between sympatric dwarf and normal whitefish through their role in promoting competitive interactions.

Here, our goal was to complement this study by testing whether biotic differences could also be observed between lake groups in terms of benthic invertebrate community characteristics. Although no significant difference in density of benthic prey was detected, we observed a marginally higher mean length of benthic invertebrates in lakes harbouring the phenotypically most divergent dwarf and normal whitefish populations. Significant differences between months in the assemblage of benthic invertebrate communities were also observed in these lakes, which was not the case in the three lakes harbouring the least differentiated whitefish pairs. Benthic invertebrate assemblages were also more similar among the most differentiated lakes than among the lakes with low differentiation or between lakes belonging to each group of lakes. Below, we discuss how these differences along with those previously documented for planktonic communities and abiotic factors by Landry *et al.* (2007) may explain the extent of phenotypic divergence observed between the two lake groups. In doing so, we realize that having included data with only normal whitefish could have rendered our interpretations more conclusive. For instance, we cannot rule out that lakes without sympatric pairs do not show similar level of differences in epibenthos characteristics. On the other hand, including lakes with only one form was complicated by the fact that the occurrence of lake whitefish species pairs is associated with a secondary

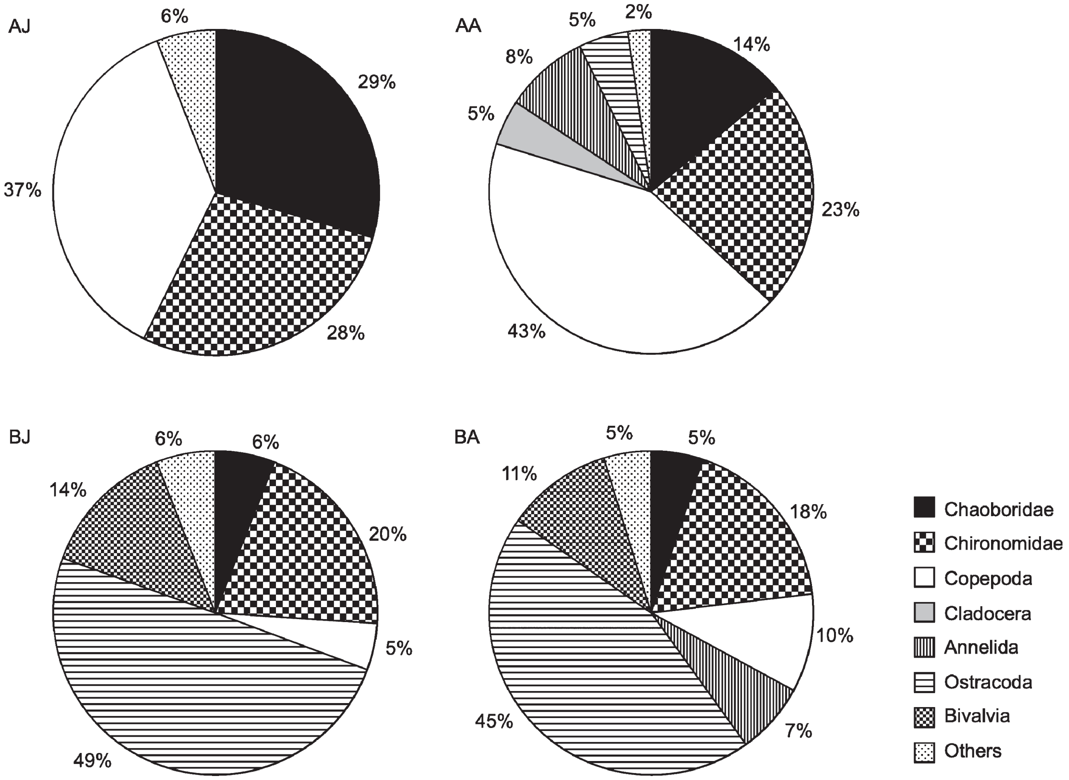

Fig. 3 Relative density of benthic invertebrates by taxon within lake group A (lake group with highest phenotypic differentiation between sympatric dwarf and normal whitefish) and B (weak differentiation) for each month (J = June and A = August). Values represent the contribution of each taxon (in per cent) for a given month within a lake group. Taxa representing < 5% were grouped in 'Others'.

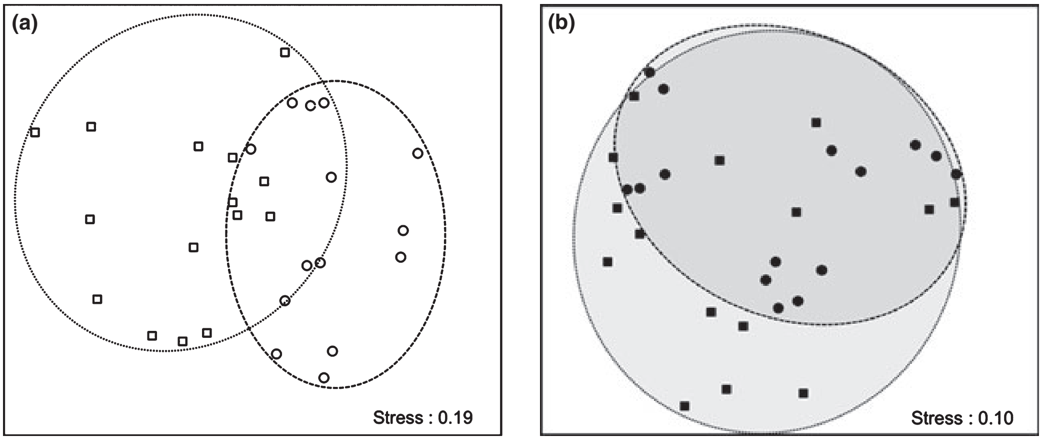

Fig. 4 Nonmetric multi-dimensional scaling plot of benthic invertebrate community (density) represented by the five stations in June (square and arbitrary dotted line) and August (circle and arbitrary regular line) for A lake group (white and clear area) and B lake group (black and frosted area). Analyses for each lake group were carried out separately. See Material and methods for details on stress.

contact in lakes that were colonized by two distinct glacial lineages. Consequently, lakes harbouring only a single population could result from either the exclusion of a given ancestral population by the other or the colonization by a single lineage. In the latter case, it would be flawed to build ecological arguments, because the occurrence of a single population would only result from historical contingency. We therefore felt that a safer approach was to only compare lakes with sympatric pairs. Also, we realize that our study bears on the analyses of only six lakes which obviously is limiting from a statistical standpoint. Yet, we stress that these six lakes represent an exhaustive coverage of all lakes from this system still harbouring sympatric whitefish species pairs.

Higher differences in length between benthic and planktonic invertebrates in lakes with high phenotypic differentiation

In both the North American lake whitefish and the European whitefish (*Coregonus lavaretus*) dwarf (limnetic) whitefish consistently possess a higher number of gill rakers, relative to the benthic form(s) (Bernatchez, 2004; Østbye *et al.*, 2006; Kahilainen *et al.*, 2007). Gill raker numbers is a highly heritable trait (Rogers & Bernatchez, 2007) associated with the retention of smaller prey size (Robinson & Wilson, 1994; Sanderson *et al.*, 2001; Kahilainen & Østbye, 2006; Kahilainen *et al.*, 2007) that probably confers a fitness advantage for feeding on planktonic prey. Recently, Kahilainen *et al.* (2007) found a 'phenotype–environment correlation' for gill raker number (in the form of selected planktonic prey length in the stomach content vs. planktonic prey length availability in the environment) in lakes harbouring sympatric whitefish forms but not among whitefish from allopatric lakes harbouring a single population. Similarly, previous studies on lake whitefish revealed that overlap between gill raker number distributions of dwarf and normal whitefish (Bernatchez *et al.*, 1999; Lu & Bernatchez, 1999) was more pronounced in lakes where available planktonic invertebrate length distribution was broader (Landry *et al.*, 2007). Here, the benthic invertebrate communities showed a larger mean length in the lakes harbouring highly differentiated whitefish pairs (mean group A: 4.8325 mm, SD = 1.8846 mm, mean lake group B: 3.0189 mm, SD = 1.1740 mm), which translated into a significantly lower overlap between planktonic and benthic prey length distribution in these lakes as well, as revealed by an *a posteriori* evaluation of the overlap in range length between the planktonic (Landry *et al.*, 2007) and the benthic invertebrate communities sampled at the same time in each lake (overlap % in lake group A = 14.04, SD = 4.75; lake group B = 24.17, SD = 3.03; $t_4 = -3{,}598$, $P = 0.036$). Under the assumption that resources would be sufficiently limited to promote interspecific competition (Schluter, 2000), such dichotomy between two exploitable and available types of resources could impose divergent selective pressure sufficient to drive the evolution of phenotypes specializing for the efficient use of these alternative resources, as observed in the most differentiated lakes. In contrast, lakes with more pronounced overlap between planktonic and benthic community length could favour the maintenance of less specialized, more generalist, phenotypes characterized by more variation and overlap in gill raker number. These observations, along with previous results on stomach content analyses that suggested a functional link between morphological specialization and the potential for trophic niche partitioning throughout the ontogeny (Bernatchez *et al.*, 1999), as well as a correlation between the extent of adaptive phenotypic divergence and levels of gene flow (Lu & Bernatchez, 1999; Østbye *et al.*, 2005) bring further support to the hypothesis that the extent of phenotypic divergence between sympatric whitefish is driven by the strength of resource-based divergent natural selection operating in a given lake. This also adds to the previous demonstration of parallel phenotypic (including gene expression) evolution of dwarf (limnetic)/normal (benthic) whitefish, which provided indirect evidence for the role of natural selection in driving their phenotypic and genetic divergence (Pigeon *et al.*, 1997; Østbye *et al.*, 2005; Derome *et al.*, 2006; St-Cyr *et al.*, 2008; Jeukens *et al.*, 2009).

Patterns of benthic community assemblages differ between lakes with high and low phenotypic differentiation

Lakes harbouring the most divergent whitefish species pairs are characterized by more similar community assemblages than those from the other lake group. Studies in other taxonomic groups have also previously reported on the importance of community assemblages in driving phenotypic divergence. For instance, Edelaar & Benkman (2006) compared crossbill and pine cone morphology between island populations where squirrels are absent or present and mainland sites where squirrels are present. All comparisons supported an effect of squirrel absence on crossbill and cone morphology. Other studies also showed the role of interspecific interactions and habitat characteristics on the form of adaptation. Thus, Yonekura *et al.* (2007) examined whether functional diversification associated with morphological differences may be observed among the introduced populations of invasive bluegill sunfish *Lepomis macrochirus* in Japan. The results revealed that a population colonizing in a shallower lake, actually foraging on benthic invertebrates in the wild and experimentally had a greater impact on the benthic prey, whereas the other population colonizing in a deeper lake and actually foraging on crustacean zooplankton also experimentally consumed the pelagic prey more efficiently. Thus, although the introduced Japanese populations were recently derived from a common ancestor, the predation impacts on the native prey community varied because of morphological adaptations to different community of prey. These observations, along with the fact that different prey species have different length range, caloric and lipid content, life-history trait and behaviour (Cummins & Wuycheck, 1971; Arts *et al.*, 2009) suggests that different community structures may impose differential selective pressures, for instance by promoting particular feeding behaviour, feeding morphology and life-history traits resulting in a more or less pronounced level of divergence between sympatric dwarf and normal whitefish, depending on context.

More similarity within a given lake group also translated into a net significant difference in benthic community assemblages between lakes harbouring highly differentiated vs. those harbouring weakly differentiated whitefish pairs. Here, bivalvia and ostracoda taxa were more abundant in the latter lake group, whereas epibenthic copepoda taxa were more abundant in the former one. Previous studies showed that abundance of bivalve, ostracods and copepods may impact on feeding ecology of lake whitefish and possibly on their life-history strategy. For instance, Pothoven & Nalepa (2006) showed that smaller whitefish extract more energy from zooplankton, whereas larger whitefish obtained more energy from shelled invertebrates. These authors also concluded that zooplankton is digested more quickly than other prey which could increase its food value, especially in a tradeoff situation between foraging activity and predator escapement, which characterize the life style of dwarf (limnetic) whitefish. Conversely, shelled invertebrates, such as like bivalves and ostracods, are digested at a relatively slower rate and fish need to reach a minimum size before getting benefit from their exploitation (Pothoven & Nalepa, 2006; Fraser *et al.*, 2008). Although the functional link still needs to be established, these studies raise the hypothesis that a given invertebrate community assemblage may impose particular selective pressures that could directly or indirectly contribute to shape the pattern of phenotypic divergence observed between whitefish pairs inhabiting different lakes. Clearly, it would be highly relevant to quantify the energetic content of ingested prey relative to the feeding behaviour adopted of dwarf and normal whitefish in order to more rigorously test this hypothesis.

Higher seasonal fluctuation in benthic community assemblages of lakes with high differentiation between dwarf and normal whitefish

Given that data were collected during a single growing season, the following interpretations about the possible role of seasonal fluctuations in benthic community should be interpreted with caution. Yet, differential patterns observed between the two lake groups within a given year suggests that this could be an additional factor influencing the extent of phenotypic divergence between dwarf and normal whitefish in each lake. Thus, lakes also differed in terms of seasonal variation in benthic community assemblages, whereby a significantly more pronounced seasonal variation was observed in lakes harbouring highly differentiated whitefish pairs relative to those harbouring weakly differentiated ones. Previous studies indicated that temporal heterogeneity, as in the intensity of seasonality, could be responsible for increased disruptive selection or interspecific competition in some populations inhabiting environments with seasonal resource scarcity (Smith *et al.*, 1978; Grant & Grant, 2006; Svanbäck & Bolnick, 2007). Seasonal variation, and/or seasons with reduced selection, could also permit the maintenance of variation upon which selection could act more efficiently (Svanbäck & Bolnick, 2007). As mentioned previously, each taxa provides a particular amount of energy to fish and also has a particular turn over rate and thus seasonal productivity (see Benke *et al.*, 2001). Thus, it is not possible with our results to know if the seasonal variation in benthic invertebrate community assemblage could result in an increase, decrease or constant resource availability. However, in the hypothetical scenario of depleted of benthic invertebrate availability, benthic fish could reduce competition in lean time through diet specialization between fish related to their individual morphological characteristics. In turn, such periods could play a role in selecting for specific traits related to resource use (Smith *et al.*, 1978; Svanbäck & Bolnick, 2007).

Second, oxygen depletion in August in lakes harbouring highly differentiated pairs (Landry *et al.*, 2007) could reduce the availability to benthic prey in these lakes. However, the results of this study does not allow to tell apart whether seasonal change in benthic community assemblage is one of the causes of the observed degree of differentiation between whitefish pairs or whether it is because of the seasonal variation in oxygen availability that reduces habitat and access to resources in high differentiation lakes. On the other hand, both factors could interact whereby temporal differences in community assemblages could be driven by, or drive biochemical processes, and affect oxygen concentration. Clearly, as revealed by recent studies also, adaptive divergence may result from complex trophic, spatial and temporal interactions, resulting in particular food web dynamics, which can also be modulated by the level of ecotypic differentiation being reached (Harmon *et al.*, 2009; Losos, 2010).

Conclusion

In combination with Landry *et al.* (2007), this study brings further support to the general hypothesis that parallelism in the extent of phenotypic divergence among sympatric dwarf and normal whitefish is associated with parallelism in adaptive landscape defined by lake-specific limnological characteristics, as well as availability and structure of both the zooplanktonic and benthic prey communities. Thus, the highest differentiation between sympatric dwarf and normal whitefish occurs in lakes characterized by reduced limnetic habitat and zooplanktonic prey length availability that increase intra-specific competition for resources. These lakes are also characterized by less overlap in size distribution between limnetic and epibenthic prey, which could represent enhanced ecological opportunities for trophic specialization. Differences in actual community assemblages as well as inter-lake differences in seasonal variation of biotic and abiotic conditions may also play a role, but their possible effect on phenotypic evolution is unclear.

This study also adds to the mounting evidence which indicates that directional selection acting more strongly on dwarf whitefish (as opposed to divergent selection acting on both sympatric forms) may be the main force driving phenotypic divergence between dwarf and normal whitefish (Fenderson, 1964; Trudel *et al.*, 2001; Kahilainen & Lehtonen, 2002; Rogers *et al.*, 2002; Bernatchez, 2004; Rogers & Bernatchez, 2005; Derome *et al.*, 2006; St-Cyr *et al.*, 2008). There are more inter-lake differences in terms of prey size distribution and habitat availability used by dwarf relative to normal whitefish. Moreover, potential prey diversity in these lakes is lower in the limnetic than the epibenthic habitat (Landry *et al.*, 2007; this study), potentially translating into a more specialized diet of dwarf whitefish (Bernatchez *et al.*, 1999; see also Bodaly, 1979).

Studies of the type undertaken here and Landry *et al.* (2007) on the adaptive limnological landscape represent a first step towards bridging the gap between evolutionary (e.g. Schluter, 2000) and aquatic ecological theories (e.g. food web theory; Matthews *et al.*, 2010). A next logical and necessary step will be to not only explaining the ecological causes of evolutionary diversification, as exemplified by the phenotypic divergence of dwarf and normal whitefish, but also the effect of evolutionary diversification on ecosystems, as well as the 'eco-evo' dynamics between both. Such studies are still in their infancy, but recent work clearly shows that species pairs that evolved in post-glacial north temperate lakes are particularly prone to such innovative and integrative investigations (Harmon *et al.*, 2009).

Acknowledgments

We are grateful to David Basley, Derrick Cote and Frank O. Frost of the Department of Inland Fisheries and Wildlife (Maine), as well as R. Saint-Laurent, J. Roy and G. Côté for invaluable help in field sampling. We also thank I. Noël and J. Breton for assistance in the laboratory. We thank G. Winkler, S. McCairns, N.N. Brodeur, J. Landry, A. Drouin, M. Dionne, A. Nolte, J. St-Cyr, S.M. Rogers, M. Cusson, and P. Duchesne for their very constructive inputs. We are also grateful to Dr. R. Snook and two anonymous reviewers for their constructive input. Research was supported by grants from the Natural Sciences and Engineering Research Council of Canada, and the Canadian Research Chair in genomics and conservation of aquatic resources to L.B. L.L. was supported by Québec-Océan (Groupe interinstitutionnel de recherches océanographiques du Québec).

References

Abbott, I., Abbott, L. & Grant, P. 1977. Comparative ecology of galapagos ground finches (*Geospiza* Gould): evaluation of the importance of floristic diversity and interspecific competition. *Ecol. Monogr.* **47**: 151–184.

Abrams, P.A. 2000. The evolution of predator–prey interactions: theory and evidence. *Annu. Rev. Ecol. Syst.* **31**: 79–105.

Arts, M.T., Brett, M.T. & Kainz, M.J. 2009. *Lipids in Aquatic Ecosystems*. Springer, New York.

Benke, A.C., Wallace, J.B., Harrison, J.W. & Koebel, J.W. 2001. Food web quantification using secondary production analysis: predaceous invertebrates of the snag habitat in a subtropical river. *Freshw. Biol.* **46**: 329–346.

Bernatchez, L. 2004. Ecological theory of adaptive radiation: an empirical assessment from coregonine fishes (Salmoniformes). In: *Evolution illuminated: salmon and their relatives* (A.P. Hendry & S.C. Sterns, eds), pp. 175–207. Oxford University Press, New York.

Bernatchez, L., Chouinard, A. & Lu, G. 1999. Integrating molecular genetics and ecology in studies of adaptive radiation: whitefish, *Coregonus* sp., as a case study. *Biol. J. Linn. Soc.* **68**: 173–194.

Bernatchez, L., Renaut, S., Whiteley, A.R., Derome, N., Jeukens, J., Landry, L., Lu, G., Nolte, A.W., Østbye, K., Rogers, S.M. & St-Cyr, J. 2010. On the origin of species: insights from the ecological genomics of lake whitefish. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**: 1783–1800.

Bodaly, R.A. 1979. Morphological and ecological divergence within the lake whitefish (*Coregonus clupeaformis*) species complex in Yukon territory. *J. Fish. Res. Board. Can.* **36**: 1214–1222.

Bolnick, D.I. & Lau, O.L. 2008. Predictable patterns of disruptive selection in stickleback in postglacial lakes. *Am. Nat.* **172**: 1–11.

Carl, L.M. & McGuiness, F. 2006. Lake whitefish and lake herring population structure and niche in ten south-central Ontario lakes. *Environ. Biol. Fish* **75**: 315–323.

Chouinard, A. & Bernatchez, L. 1996. A study of trophic niche partitioning between larval populations of reproductively isolated whitefish (*Coregonus* sp.) ecotypes. *J. Fish Biol.* **53**: 1231–1242.

Clarke, K. 1993. Non-parametric multivariate analyses of changes in community structure. *Austral Ecol.* **18**: 117–143.

Cummins, K.W. & Wuycheck, J.C. 1971. *Caloric Equivalents for Investigation in Ecological Energetics*. International Association of Theoretical and Applied Limnology, Stuttgart.

Davis, B.M. & Todd, T.N. 1998. Competition between larval Lake herring (*Coregonus artedii*) and Lake whitefish (*Coregonus clupeaformis*) for zooplankton. *Can. J. Fish. Aquat. Sci.* **55**: 1140–1148.

Derome, N., Duchesne, P. & Bernatchez, L. 2006. Parallelism in gene transcription among sympatric lake whitefish (*Coregonus clupeaformis* Mitchill) ecotypes. *Mol. Ecol.* **15**: 1239–1249.

Edelaar, P. & Benkman, C.W. 2006. Replicated population divergence caused by localized coevolution? A test of three hypotheses in the red crossbill-lodgepole pine system. *J. Evol. Biol.* **19**: 1651–1659.

Fenderson, O. 1964. Evidence of subpopulations of lake whitefish, *Coregonus clupeaformis*, involving a dwarfed form. *Trans. Am. Fish. Soc.* **93**: 77–94.

Fraser, D., Huntingford, F. & Adams, C. 2008. Foraging specialisms, prey size and life-history patterns: a test of predictions using sympatric polymorphic arctic charr (*Salvelinus alpinus*). *Ecol. Freshw. Fish.* **17**: 1–9.

Grant, P. & Grant, B. 2006. Evolution of character displacement in Darwin's finches. *Science* **313**: 224–226.

Harmon, L.J., Matthews, B., Roches, S.D., Chase, J.M., Shurin, J.B. & Schluter, D. 2009. Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* **458**: 1167–1170.

Hendry, A.P., Bolnick, D.I., Berner, D. & Peichel, C.L. 2009. Along the speciation continuum in sticklebacks. *J. Fish Biol.* **75**: 2000–2036.

Hindar, K. & Jonsson, B. 1982. Habitat and food segregation of dwarf and normal arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. *Can. J. Fish. Aquat. Sci.* **39**: 1030–1045.

Jeukens, J., Bittner, D., Knudsen, R. & Bernatchez, L. 2009. Candidate genes and adaptive radiation: insights from transcriptional adaptation to the limnetic niche among coregonine fishes (*Coregonus* sp., Salmonidae). *Mol. Biol. Evol.* **26**: 155–166.

Johannesson, K., Panova, M., Kemppainen, P., Andre, C., Rolan-Alvarez, E. & Butlin, R.K. 2010. Repeated evolution of reproductive isolation in a marine snail: unveiling mechanisms of speciation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**: 1735–1747.

Kahilainen, K.K. & Lehtonen, H. 2002. Brown trout (*Salmo trutta* L.) and arctic charr (*Salvelinus alpinus* (L.)) as predators on three sympatric whitefish (*Coregonus lavaretus* (L.)) forms in the subarctic Lake Muddusjarvi. *Ecol. Freshw. Fish.* **11**: 158–167.

Kahilainen, K.K. & Østbye, K. 2006. Morphological differentiation and resource polymorphism in three sympatric whitefish *Coregonus lavaretus* (L.) forms in a subarctic lake. *J. Fish Biol.* **68**: 63–79.

Kahilainen, K.K., Lehtonen, H. & Kononen, K. 2003. Consequence of habitat segregation to growth rate of two sparsely rakered whitefish (*Coregonus lavaretus* (L.)) forms in a subarctic lake. *Ecol. Freshw. Fish.* **12**: 275–285.

Kahilainen, K.K., Malinen, T., Tuomaala, A., Alajarvi, E., Tolonen, A. & Lehtonen, H. 2007. Empirical evaluation of phenotype-environment correlation and trait utility with allopatric and sympatric whitefish, *Coregonus lavaretus* (L.), populations in subarctic lakes. *Biol. J. Linn. Soc.* **92**: 561–572.

Kassen, R., Llewellyn, M. & Rainey, P. 2004. Ecological constraints on diversification in a model adaptive radiation. *Nature* **431**: 984–988.

Landry, L., Vincent, W. & Bernatchez, L. 2007. Parallel evolution of lake whitefish dwarf ecotypes in association with limnological features of their adaptive landscape. *J. Evol. Biol.* **20**: 971.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D. & Schabenberger, O. 2004. *SAS for Mixed Models*, 2nd edn. SAS Institute Inc., Cary.

Losos, J.B. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. *Am. Nat.* **175**: 623–639.

Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K. & Rodriguez-Schettino, L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**: 2115–2118.

Lu, G. & Bernatchez, L. 1999. Correlated trophic specialization and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): support for the ecological speciation hypothesis. *Evolution* **53**: 1491–1505.

Matthews, B., Marchinko, K., Bolnick, D. & Mazumder, A. 2010. Specialization of trophic position and habitat use by sticklebacks in an adaptive radiation. *Ecology* **91**: 1025–1034.

McKinnon, J.S., Mori, S., Blackman, B.K., David, L., Kingsley, D.M., Jamieson, L., Chou, J. & Schluter, D. 2004. Evidence for ecology's role in speciation. *Nature* **429**: 294–298.

Moore, J.-S., Gow, J.L., Taylor, E.B. & Hendry, A.P. 2007. Quantifying the constraining influence of gene flow on adaptive divergence in the lake-stream threespine stickleback system. *Evolution* **61**: 2015–2026.

Nosil, P. & Reimchen, T.E. 2005. Ecological opportunity and levels of morphological variance within freshwater stickleback populations. *Biol. J. Linn. Soc.* **86**: 297–308.

Nosil, P., Crespi, B.J. & Sandoval, C.P. 2002. Host-plant adaptation drives the parallel evolution of reproductive isolation. *Nature* **417**: 440–443.

Østbye, K., Naesje, T.F., Bernatchez, L., Sandlund, O.T. & Hindar, K. 2005. Morphological divergence and origin of sympatric populations of European whitefish (*Coregonus lavaretus* L.) in Lake Femund, Norway. *J. Evol. Biol.* **18**: 683.

Østbye, K., Amundsen, P.A., Bernatchez, L., Klemetsen, A., Knudsen, R., Kristoffersen, R., Naesje, T.F. & Hindar, K. 2006. Parallel evolution of ecomorphological traits in the European whitefish *Coregonus lavaretus* (L.) species complex during postglacial times. *Mol. Ecol.* **15**: 3983–4001.

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

Pothoven, S.A. & Nalepa, T.F. 2006. Feeding ecology of lake whitefish in Lake Huron. *J. Great Lakes Res.* **32**: 489–501.

Rainey, P.B. & Travisano, M. 1998. Adaptive radiation in a heterogeneous environment. *Nature* **394**: 69–72.

Reimchen, T.E. & Nosil, P. 2002. Temporal variation in divergent selection on spine number in treespine stickleback. *Evolution* **56**: 2472–2483.

Robinson, B.W. & Wilson, D.S. 1994. Character release and displacement in fishes: a neglected literature. *Am. Nat.* **144**: 596–627.

Robinson, B.W., Wilson, D.S. & Margosian, A.S. 2000. A pluralistic analysis of character release in pumpkinseed sunfish (*Lepomis gibbosus*). *Ecology* **81**: 2799–2812.

Rogers, S.M. & Bernatchez, L. 2005. Integrating QTL mapping and genome scans towards the characterization of candidate loci under parallel selection in the lake whitefish (*Coregonus clupeaformis*). *Mol. Ecol.* **14**: 351–361.

Rogers, S.M. & Bernatchez, L. 2007. The genetic architecture of ecological speciation and the association with signatures of selection in natural lake whitefish (*Coregonus* sp. Salmonidae) species pairs. *Mol. Biol. Evol.* **24**: 1423–1438.

Rogers, S.M., Gagnon, V. & Bernatchez, L. 2002. Genetically based phenotype-environment association for swimming behavior in lake whitefish ecotypes (*Coregonus clupeaformis* Mitchill). *Evolution* **56**: 2322–2329.

Rolan-Alvarez, E., Carballo, M., Galindo, J., Moran, P., Fernandez, B., Caballero, A., Cruz, R., Boulding, E.G. & Johannesson, K. 2004. Nonallopatric and parallel origin of local reproductive barriers between two snail ecotypes. *Mol. Ecol.* **13**: 3415–3424.

Rundle, H.D., Vamosi, S.M. & Schluter, D. 2003. Experimental test of predation's effect on divergent selection during character displacement in sticklebacks. *Proc. Natl. Acad. Sci. USA* **100**: 14943–14948.

Sanderson, S.L., Cheer, A.Y., Goodrich, J.S., Graziano, J.D. & Callan, W.T. 2001. Crossflow filtration in suspension-feeding fishes. *Nature* **412**: 439–441.

Savolainen, V., Anstett, M.C., Lexer, C., Hutton, I., Clarkson, J.J., Norup, M.V., Powell, M.P., Springate, D., Salamin, N. & Baker, W.J. 2006. Sympatric speciation in palms on an oceanic island. *Nature* **441**: 210–213.

Schluter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, New York.

Simpson, G.G. 1953. *The major features of evolution*. Columbia University Press, New York.

Smith, J.N.M., Grant, P.R., Grant, B.R., Abbott, I.J. & Abbott, L.K. 1978. Seasonal variation in feeding habits of Darwin's ground finches. *Ecology* **59**: 1137–1150.

St-Cyr, J., Derome, N. & Bernatchez, L. 2008. The transcriptomics of life-history trade-offs in whitefish species pairs (*Coregonus* sp.). *Mol. Ecol.* **17**: 1850–1870.

Svanbäck, R. & Bolnick, D.I. 2007. Intraspecific competition drives increased resource use diversity within a natural population. *Proc. Biol. Sci.* **274**: 839.

Taylor, E.B. & McPhail, J.D. 2000. Historical contingency and ecological determinism interact to prime speciation in sticklebacks, *Gasterosteus*. *Proc. Biol. Sci.* **267**: 2375–2384.

Toju, H. 2007. Interpopulation variation in predator foraging behaviour promotes the evolutionary divergence of prey. *J. Evol. Biol.* **20**: 1544–1553.

Trudel, M., Tremblay, A., Schetagne, R. & Rasmussen, J.B. 2001. Why are dwarf fish so small? An energetic analysis of polymorphism in lake whitefish (*Coregonus clupeaformis*). *Can. J. Fish. Aquat. Sci.* **58**: 394–405.

Winkler, G., Sirois, P., Johnson, L.E. & Dodson, J.J. 2005. Invasion of an estuarine transition zone by *Dreissena polymorpha* veligers had no detectable effect on zooplankton community structure. *Can. J. Fish. Aquat. Sci.* **62**: 578–592.

Yonekura, R., Kohmatsu, Y. & Yuma, M. 2007. Difference in the predation impact enhanced by morphological divergence between introduced fish populations. *Biol. J. Linn. Soc. Lond.* **91**: 601–610.

Received 4 June 2010; revised 11 August 2010; accepted 19 August 2010