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Co-existence of a pair of pelagic planktivorous coregonid fishes

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ABSTRACT

Hypothesis: Ecological specialization facilitates co-existence of *Coregonus* spp. in Lake Stechlin. A difference in trophic ecology is the dominant means by which the species are ecologically segregated.

Background: Sympatric fish species pairs in post-glacial lakes often feed on different resources, segregating available trophic resources.

Organisms: Sympatric European winter-spawning *Coregonus albula* and the local endemic dwarf-sized spring-spawning *Coregonus fontanae*.

Time and place: March–December 2005, Lake Stechlin, North Germany.

Methods: By combining stomach content analyses and stable isotope analyses we compared consumption patterns of the two species at different depths over a 10-month period.

Results: Stable isotope analyses and stomach content analyses both showed little trophic difference between the two species, but a significant effect of capture depth and body size on individual diet.

Conclusions: The sympatric species pair in Lake Stechlin does not follow the expected pattern of niche segregation. Trophic divergence is not the dominant grounds for co-existence.

Keywords: δ^{13}C, δ^{15}N, niche overlap, reproductive isolation, resource competition, stable isotope analysis, stomach content analysis, sympatric species.

INTRODUCTION

Resource competition is a fundamental concept in ecology and classical competition theory predicts that sympatric species cannot have completely overlapping niches. The principle of competitive exclusion states that one competing species will always have an advantage that will lead either to extinction of the poorer competitor or to an evolutionary shift towards a

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different ecological niche (Hardin, 1960). Although the mechanisms for species diversity are highly debated (Kneitel and Chase, 2004), partitioning of resources is considered fundamental for the co-existence of species, particularly when they are closely related.

Resource partitioning in ecological communities is predominantly found along diet, time, and habitat niche axes (Schoener, 1974). Sympatric fish in post-glacial lakes frequently display resource polymorphism and segregate available niches, for example by habitat and diet (Robinson and Wilson, 1994; Lu and Bernatchez, 1999; Svanbäck and Eklöv, 2003; Knudsen *et al.*, 2006). Among the order Salmoniformes, the genus *Coregonus* shows a wide variety of sympatric populations, as recently reviewed by Hudson *et al.* (2007). Typically, co-existing species pairs follow two distinct strategies: smaller planktivorous species reside in pelagic habitats while larger benthivorous species live in littoral or profundal zones (e.g. Riget *et al.*, 2000; Parker *et al.*, 2001). Furthermore, morphological adaptations to different feeding types and habitats occur frequently, and traits related to foraging are the main diverging factors among European *Coregonus* spp. (Østbye *et al.*, 2005). Resource partitioning and morphology are closely coupled since many morphological traits, for example the structure of the gill-raker apparatus, show high heritabilities (Bernatchez *et al.*, 2004). Such ecological and morphological divergence of populations because of divergent or disruptive selection is believed to be an important process in speciation, since reproductive isolation may arise as a by-product (Dieckmann and Doebeli, 1999; Schluter, 2000; Doebeli *et al.*, 2007). However, in sympatry the development of reproductive isolation simultaneously requires the ability of the divergent populations to co-exist (Coyne and Orr, 2004). It is difficult to understand the co-existence of sympatric planktivorous fish that do not follow the benthic–pelagic pattern of segregation, since no resource partitioning is obvious and hence competition is expected to be extensive.

Two sympatric populations of small-bodied coregonid fish co-exist in the deep and stratified Lake Stechlin (northern Germany): *Coregonus albula* (vendace) and the dwarf-sized lake-endemic *C. fontanae* (Fontane cisco). These populations have separate spawning times, with *C. albula* spawning between December and January while *C. fontanae* spawns between March and July (Schulz and Freyhof, 2003). According to initial genetic analyses, it is suspected that the species pair may have evolved in sympatry since the last glaciation (Schulz *et al.*, 2006). Following frequent descriptions of resource polymorphism in *Coregonus* spp. (e.g. Lu and Bernatchez, 1999; Amundsen *et al.*, 2004; Kahilainen and Østbye, 2006), we predicted that ecological segregation along the habitat and diet axes also plays a decisive role in the co-existence of the Lake Stechlin coregonids. However, more detailed analyses revealed that *C. albula* and *C. fontanae* show few differences in morphology and habitat choice. The numbers of gill rakers largely overlap (*C. albula* 42–47, *C. fontanae* 40–46) and no difference in the structure of the gill rakers could be found, although the gill filament is shortened in *C. fontanae* (Schulz and Freyhof, 2003). The two species mature at the same age, but *C. fontanae* at a much smaller size (about 65 mm standard length) than sympatric *C. albula* (about 120 mm). Although, on average, *C. fontanae* remains in deeper and colder water than *C. albula* during hours of darkness (Helland *et al.*, 2007), both species are distributed throughout pelagic habitats (i.e. at all depths) and neither utilizes benthic habitats to any large extent. Moreover, both coregonid species perform regular diel vertical migrations by ascending from the deep water into shallower layers during dusk, and migrating back at dawn (Mehner, 2006; Mehner *et al.*, 2007). Since the two species appear to be relatively similar in terms of morphology and do not segregate their principal living habitats, we speculated that differences in diet should contribute substantially to ecological divergence and the avoidance of intense interspecific competition.

Accordingly, we investigated the diet composition of the two sympatric coregonid species in Lake Stechlin by combining stomach content analyses and stable isotope analyses of fish sampled at different depths over 10 months. Stomach content analysis reflects the seasonal variability of the diet composition, while stable isotope analysis reflects the long-term assimilated diet (Fry, 2006) and is a useful means of identifying trophic plasticity also within populations that appear to be homogeneous in their stomach content (Harrod *et al.*, 2005). Specifically, we compared the diet composition of the two species, between individuals caught at different depths, and for differently sized fish, to elucidate which of the factors most strongly contribute to ecological divergence of the two coregonids in Lake Stechlin.

MATERIALS AND METHODS

Study site and sampling

Lake Stechlin (53°10′N, 13°02′E; surface area 430 ha, mean depth 22.8 m, maximum depth 69 m) is a dimictic, oligotrophic lake situated approximately 120 km north of Berlin, Germany (for more details, see Koschel and Adams, 2003). Adults of the two coregonids studied here exclusively inhabit the pelagic area and together represent more than 95% of all pelagic fish in the lake. Other species including *Perca fluviatilis* (perch), *Rutilus rutilus* (roach), and *Alburnus alburnus* (bleak) are frequent in the littoral area and in epipelagic layers (Anwand *et al.*, 2003).

Between March and December 2005, we conducted monthly nocturnal midwater trawl hauls (mesh size 26 mm knot to knot in the frontal part, and 10 mm in the cod end, height of the trawl opening ~3 m, opening area ~10 m^2) and sampled the pelagic habitats of Lake Stechlin in four depth layers between 10 and 35 m (capture depths: 12.1 ± 0.8, 15.3 ± 1.4, 24.3 ± 1.7, and 31.6 ± 1.6 m; mean ± standard deviation) (see Helland *et al.*, 2007). Fish used for stomach content analyses were taken from two of the four depth layers (~15 m and 30 m) in each of the 10 months. Some individuals collected from deep-set (50 m) benthic multi-mesh gillnets (see below for details) fished separately during night and day in September 2005 were added to the data set. Individuals selected for stable isotope analysis were taken from the catch in each of the four trawl depths in September and December 2005, and from pelagic multi-mesh gillnets (type NORDEN, 30 m long, 3.0 m high, 12 mesh sizes from 5.0 to 55 mm) set at 35 m, 45 m, and 55 m in December 2005. Four *C. fontanae* caught by the midwater trawl in November 2005 were included in the stable isotope analyses. Fish were placed on ice and subsequently deep frozen before transportation to the laboratory for identification. After species identification and measurement of standard length (mm), the stomach was removed and stored in 4% formaldehyde. Stomach samples were subsequently transferred into ethanol, by gradually increasing the concentration from 25% to 50% and finally to 75% ethanol over a minimum of 10 days to avoid reduction of the tissue size in the samples. After thawing, fish muscle was excised from above the lateral line and macerated for stable isotope analysis. All muscle samples were oven-dried at 60°C for 24 h, homogenized using an agate pestle and mortar, and stored in a desiccator before weighing into tin cups for stable isotope analysis (typical mass = 0.55 mg).

Simultaneous with trawling, zooplankton were sampled with a conical closing plankton net (mesh size 90 μm, opening 0.02 m^2, length 1.2 m) at a fixed location near the deepest point of the lake (see Helland *et al.*, 2007). Triplicate hauls were taken from five water depths (0–10, 10–20, 20–30, 30–40, and 40 m to bottom). The three hauls per depth layer were subsequently pooled, fixed in sugar-formaldehyde, and species identified and enumerated in the laboratory from at least three smaller subsamples.

Stomach content analyses

In total, the stomach contents of 156 *C. albula* and 137 *C. fontanae* (Table 1) were analysed. Prey items in the stomach were identified and their relative importance examined by frequency of occurrence and total abundance. Prey biomasses were reconstructed based on length measurements of at least 20 individuals of the same prey group in each stomach (Mehner *et al.*, 1995). Recognizable fragments of prey were also counted and their biomass calculated based on average size of intact specimens of the same type.

Prey items included the zooplankton species *Acroperus harpae*, *Bosmina coregoni*, *Bosmina longirostris*, *Bythotrephes longimanus*, *Chydorus sphaericus*, *Ceriodaphnia quadrangula*, *Daphnia* spp., *Diaphanosoma brachyurum*, *Leptodora kindtii*, unidentified calanoid copepods, and unidentified cyclopoid copepods. Furthermore, fish eggs and some benthic organisms including ostracods, Hydrachnidia, chironomids (larvae and pupae), and unidentified parts of other insect larvae were found. Individuals with empty stomachs and all prey items that occurred in less than 15 stomachs were excluded from the statistical analyses. All adult copepods (nauplii and copepodit stages were not found) were grouped together as they were heavily digested, thus preventing species identification. The few fragmented and thus unidentified *Bosmina* spp. were also excluded to avoid confusion. The final data set therefore consisted of the diet of 120 *C. albula* and 101 *C. fontanae*, arranged into the six prey goups *Bosmina longirostris*, *B. coregoni*, *Leptodora kindtii*, copepods, chironomids, and miscellaneous. The contribution of the different prey items in the stomach content analyses was calculated from the index of relative importance (IRI) for each prey group using the formula

$$\mathrm{IRI} = \frac{(N_i\% + W_i\% + O_i\%)}{\sum_{i=1}^{s}(N_i\% + W_i\% + O_i\%)},$$

where N_i is the number of prey, W_i the prey biomass, and O_i the frequency of occurrence of prey (George and Hadley, 1979).

Stable isotopes analyses

Carbon and nitrogen stable isotope ratios were determined in 107 *C. albula* and 93 *C. fontanae* (Table 2) using a Eurovector elemental analyser (Eurovector, Milan, Italy) coupled to a Micromass Isoprime continuous flow mass spectrometer (Micromass, Manchester, UK). Stable isotope ratios are given using the δ notation expressed in units per millilitre as follows: $\delta\ (‰) = [(R_{\mathrm{sample}}/R_{\mathrm{standard}}) - 1] \times 1000$, and $R = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ or ${}^{15}\mathrm{N}/{}^{14}\mathrm{N}$. The reference materials used were secondary standards of known relation to the international standards of Vienna Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen. Repeated analysis of an internal fish standard (*Rutilus rutilus*, roach) revealed that precision for a single analysis was $\pm 0.1‰$ for $\delta^{13}C$ and $\pm 0.3‰$ for $\delta^{15}N$.

Lipids are depleted in ^{13}C (DeNiro and Epstein, 1977), hence variation in lipid concentrations between the two fish species considered here could influence comparisons of $\delta^{13}C$. Mean

Table 1. Number of individuals included in the stomach content analyses, classified by capture depth and month of sampling in 2005 in Lake Stechlin

		Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Total
15 m	*C. albula*	6	7	8	13	10	11	4	9	8	8	84
	C. fontanae	6	4	8		11	9	7	10	7		62
30 m	*C. albula*	10			6	4		9	10	10	6	55
	C. fontanae	5	4	9	3	8		8	10	10	8	65
50 m	*C. albula*							17				17
	C. fontanae							10				10
Total		27	15	25	22	33	20	55	39	35	22	293

Table 2. Number of individuals analysed for stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$), classified by capture depth and month of sampling in 2005 in Lake Stechlin

	12 m		15 m		25 m		30 m		35 m		45 m		55 m		
	A	F	A	F	A	F	A	F	A	F	A	F	A	F	Total
Sep					10	10									20
Nov		4													4
Dec	20	12	10	10	30	20	19	20	3	9	10		5	8	176
Total	20	16	10	10	40	30	19	20	3	9	10	0	5	8	200

Note: A = *C. albula*, F = *C. fontanae*.

C : N ratios (a correlate of lipid concentration) showed a small, but significantly lower ratio in *C. albula* (*t*-test: $t = -2.02$, d.f. = 112.6, $P < 0.05$), thus the $\delta^{13}C$ data were arithmetically lipid-normalized according to Kiljunen *et al.* (2006).

Statistical analyses

The stomach content analysis (SCA) data were standardized by percentage abundance and biomass contribution of the different food items in each individual and subsequently arcsine square root transformed to stabilize the variances. The individual SCA data (matrix dimension 221 specimens × 5 prey groups, the heterogeneous group of miscellaneous prey was excluded) were exposed to ordination by non-metric multidimensional scaling (NMS) to explore similarities in diet composition between the individuals. The NMS were calculated separately for the diet abundance and biomass matrices. The NMS were run with the Sørensen distance measure, going from 6 axes down to 1 axis, used 250 iterations and random starting coordinates, 0.20 step length, 50 runs with real data, 50 runs with randomized data, and an 0.001 stability criterion (McCune and Grace, 2002). To identify the prey groups that most strongly contributed to ordination, the Kendall tau correlation coefficients of prey groups to the significant ordination axes were calculated.

Multivariate group comparisons of SCA data were performed by multi-response permutation procedures (MRPP). The test statistic A in MRPP is the chance-corrected within-group agreement, and describes the homogeneity within a group compared with random expectation ($A = 0$ means that heterogeneity is equal to what is expected by chance, while $A = 1$ means that all individuals in a group are identical) (McCune and Grace, 2002). Individual diet data were grouped either by species or by month of catch. Furthermore, two size groups were compared using a threshold of 123 mm standard length for *C. albula* and 95 mm for *C. fontanae*. We used these size thresholds since body size is a major diverging character between the species, with little overlap in the data set (standard length: *C. albula* 120 ± 20 mm, *C. fontanae* 92 ± 14 mm; mean ± standard deviation) and any size-based comparisons could be influenced by these differences between the species. Finally, diet data were grouped by capture depth, based on fish caught either in intermediate (15 m) or deep (30–50 m) water layers. Individuals from 30 m and 50 m were grouped together, as there was a rather small number of individuals with non-empty stomachs caught at 50 m (9 *C. albula* and 8 *C. fontanae*), and because there was no significant difference in diet composition of fish caught at depths of either 30 or 50 m (MRPP on prey abundance data: $P = 0.060$, $A = 0.014$; on biomass data: $P = 0.070$, $A = 0.013$).

Since consumer tissue stable isotope ratios integrate consumption patterns over longer time periods, the data set becomes heterogeneous if fish groups are included that have performed a habitat shift during the preceding period. Since young-of-the-year coregonids remain in littoral habitats during their first weeks after hatching, their isotopic signature may be enriched in δ^{13}C. Accordingly, we excluded all *C. albula* <85 mm (31 individuals) and all *C. fontanae* <50 mm (6 individuals) from the main statistical analyses. To subsequently apply parametric tests, significant outliers in the data set [mean distance >3 standard deviations away from the grand mean distance (McCune and Grace, 2002)] were excluded (two *C. albula* and one *C. fontanae*). The final stable isotope analysis (SIA) data set consisted of 74 *C. albula* and 86 *C. fontanae*, which conformed to Shapiro-Wilks' test for normal distributions ($P > 0.05$). Although δ^{13}C ($P = 0.841$) but not δ^{15}N ($P = 0.020$) passed Levene's test for homoscedasticity, moderate heterogeneity of variances is not considered too serious for the overall test of significance (Sokal and Rohlf, 1995).

The SIA data were analysed by linear correlations (Pearsons' r) and analysis of covariance (ANCOVA). Analyses of covariance were performed separately on δ^{13}C and δ^{15}N with two fish species and three catch depths (12–15 m, 25–30 m, and 35–55 m) as the main effects and fish size as the covariate. Instead of using absolute fish lengths, individual size was relativized to the largest within-species length to facilitate interspecific comparisons of fishes of similar age. NMS and MRPP were performed in PC-ORD 5.01 (McCune and Mefford 1999), whereas all other tests were conducted using SPSS 14.0 (SPSS Inc., 2005, Chicago, IL, USA).

RESULTS

Stomach content analyses

There was no marked difference in the index of relative importance (IRI) between the two fish species (Fig. 1). *Bosmina coregoni* was by far the most frequently consumed prey by both species (62% of abundance in *C. albula* and 85% in *C. fontanae*). Other important prey items included copepods, *B. longirostris*, and *L. kindtii*. Other cladoceran species were

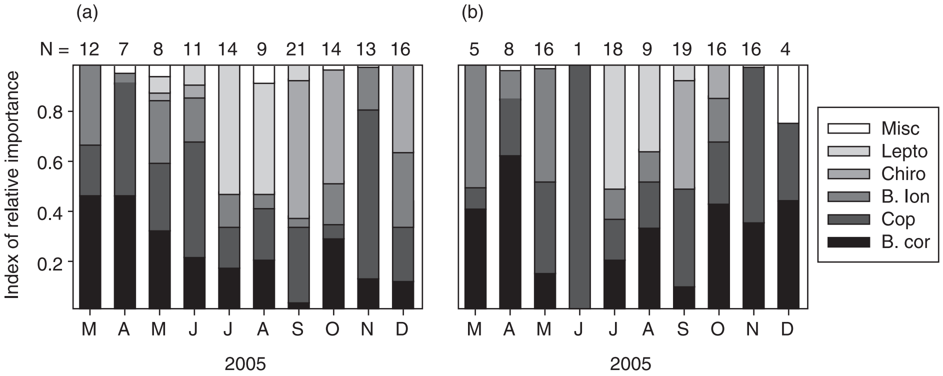


Fig. 1. Index of relative importance of the different prey groups – *B. coregoni* (B. cor), *B. longirostris* (B. lon), copepods (Cop), chironomids (Chiro), *L. kindtii* (Lepto), and miscellaneous (Misc) – found in the stomachs of *C. albula* (a) and *C. fontanae* (b) in Lake Stechlin from March to December 2005. Number of non-empty stomachs is noted above each of the bars.

found only in very small amounts in the stomachs. The biomass contribution for the remaining prey (i.e. ostracods, unidentified insect parts, and fish eggs) could not be calculated and was therefore excluded from the IRI, but this group contributed less than 2% of total prey individuals over the entire 10-month study period. *Leptodora kindtii* was the largest-bodied planktonic prey species and was only recorded during summer, peaking in July and August. Chironomids were quite frequently consumed in September, October, and December and contributed highly to the IRI during these months due to their large biomass. Based on the total amount of all measurable prey individuals in the stomachs, the size of the most important prey species did not differ between *C. albula* and *C. fontanae* (median tests, *B. coregoni*: $\chi^2 = 2.831$, $P = 0.102$; copepods: $\chi^2 = 1.692$, $P = 0.222$). However, there was a significant difference in the size of *B. longirostris* ($\chi^2 = 6.252$, $P = 0.017$), with *C. albula* consuming more large-bodied individuals.

Ordination by NMS found a three-dimensional solution for both prey abundance and biomass data. The final stress was 9.66 for prey abundance and 12.81 for prey biomass. For prey abundance, NMS explained 94% of total variance with axis 1 (35.1%) and axis 3 (30.5%) dominating (Table 3). For prey biomass, NMS explained 86% of total variance with axis 1 (41.1%) and axis 3 (24.5%) dominating. Kendall's correlation coefficients $> |0.5|$ of abundance prey groups to ordination axes were found for *B. coregoni* (−0.575) and chironomids (0.531) to axis 1, and for *B. coregoni* (0.775) to axis 3 (Table 3). For axis 3, copepods (−0.487) also had a high correlation coefficient. For the biomass data, strong correlations were found for chironomids (−0.505) and copepods (0.658) to axis 1, and *L. kindtii* (−0.518) to axis 3.

The NMS diagram of the dominant axes from the ordination of prey abundance data revealed little difference in diet composition between *C. albula* and *C. fontanae* (Fig. 2a). In contrast, a stronger segregation became apparent when the data were grouped according to capture depth (Fig. 2b). This pattern was confirmed by group comparisons by MRPP (Sørensen distance measure, rank transformed distance matrix). Significant differences in diet compositions were found between specimens caught at different depths (15 m vs. 30 + 50 m combined) and in different months, whereas species-specific differences were only weakly significant and size-specific differences were not at all significant (Table 4). In a

Table 3. Kendall correlation coefficients of the different prey groups to the significant ordination axes obtained by NMS, based on stomach analyses of *C. albula* and *C. fontanae*

	Abundance			Biomass		
% variance	Axis 1 (0.351)	Axis 2 (0.282)	Axis 3 (0.305)	Axis 1 (0.411)	Axis 2 (0.206)	Axis 3 (0.245)
B. coregoni	−0.575	0.005	0.775	0.000	0.808	−0.086
B. longirostris	0.005	0.498	−0.294	0.049	0.025	0.366
Chironomids	0.531	0.203	−0.064	−0.505	−0.432	0.340
Copepods	0.162	−0.622	−0.487	0.658	−0.329	−0.280
L. kindtii	−0.445	0.105	0.057	−0.352	−0.001	−0.518

Note: The values in parentheses below each axis are the proportions of explained variance between ordinated and original space.

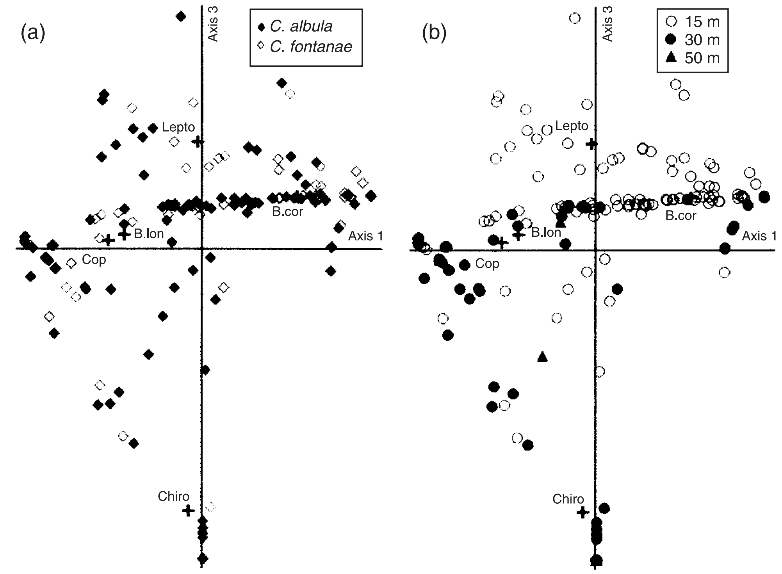


Fig. 2. Ordination diagram of the two axes describing most of the variance (axes 1 and 3) by non-metric multidimensional scaling of diet composition of *C. albula* and *C. fontanae* from stomach content analyses. The individuals are sorted by the two fish species (a), or by the three sampling depths 15 m, 30 m, and 50 m (b). The weighted average scores for the different prey groups – *B. coregoni* (B. cor), *B. longirostris* (B. lon), copepods (Cop), chironomids (Chiro), and *L. kindtii* (Lepto) – are included in the plots.

similar manner, prey biomass differed significantly between capture depths and months, but there were no significant differences between different size groups of fish or between the species (Table 4).

When the abundance or biomass proportions of the five prey groups were compared between species, size groups or capture depths, a similar pattern became obvious. Only capture depth decisively contributed to differences in the proportion of all prey groups

Table 4. Multivariate group comparisons by MRPP of diet composition by abundance or biomass between the two species *C. albula* and *C. fontanae*, two sampling depths (15 m vs. 30 + 50 m), two size classes (threshold *C. albula* SL 123 mm, *C. fontanae* 95 mm), and sampling time (once a month from March to December 2005)

	Abundance		Biomass	
	P	*A*	*P*	*A*
Species	0.028	0.008	0.073	0.005
Depth	<0.001	0.115	<0.001	0.097
Size	0.314	0.001	0.085	0.004
Month	<0.001	0.229	<0.001	0.273

Note: *A* is the chance-corrected within-group agreement, while *P* is the probability of a type I error. The tests are performed both on abundance of prey items and on their calculated biomass contribution, and are shown in separate columns. SL = standard length.

Table 5. Comparisons by Mann-Whitney *U*-test of the two species *C. albula* and *C. fontanae*, the two sampling depths (15 m vs. 30 + 50 m), and the two size classes (threshold *C. albula* SL 123 mm, *C. fontanae* 95 mm) for each of the five prey groups

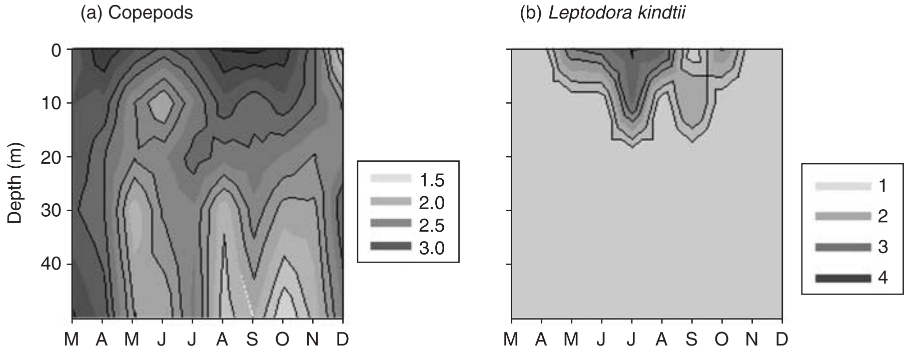
	Abundance			Biomass		
	Species	Size	Depth	Species	Size	Depth
B. coregoni	0.020	0.731	<0.001	0.056	0.847	<0.001
B. longirostris	0.065	0.338	<0.001	0.084	0.425	<0.001
Chironomids	0.023	0.898	<0.001	0.022	0.888	<0.001
L. kindtii	0.616	0.002	<0.001	0.716	0.003	<0.001
Copepods	0.941	0.326	0.069	0.884	0.312	0.118

Note: Values shown are *P*-values. The tests are performed both on abundance of prey items and on their calculated biomass contribution, and are shown in separate columns. SL = standard length.

except for copepods (Table 5). In contrast, differences between the fish species were weak or not significant, and differences between the size groups of fish were significant for *L. kindtii* only (Table 5).

Zooplankton

Of the main zooplankton groups recorded from stomachs of *C. albula* and *C. fontanae*, copepods dominated the zooplankton community in Lake Stechlin in 2005, occurring at all depths throughout the study (Fig. 3a). *Leptodora kindtii* was only present in summer (May to October) and never found below depths of 20 m (Fig. 3b). *Bosmina longirostris* was much more abundant than *B. coregoni* and occurred over the full season and at all depths, with a peak at intermediate water depths (10–30 m) in summer (June to September) (Fig. 3d).


(a) Copepods (b) *Leptodora kindtii*

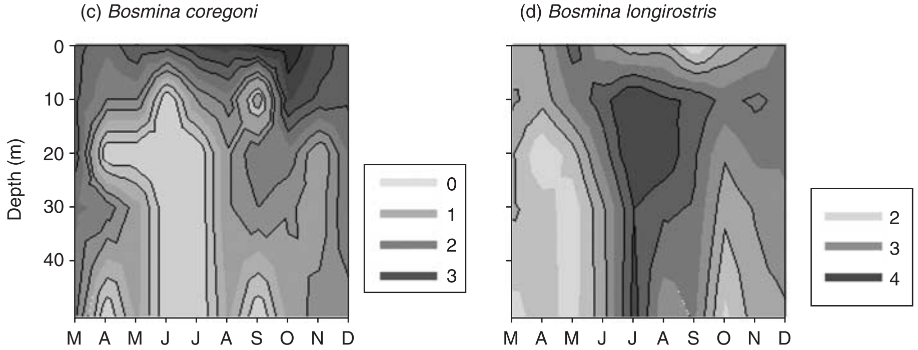

(c) *Bosmina coregoni* (d) *Bosmina longirostris*

Fig. 3. Abundance (individuals per m^3) of the main prey zooplankton – copepods (a), *L. kindtii* (b), *B. coregoni* (c) and *B. longirostris* (d) – over the water column in Lake Stechlin between March and December 2005. Note that the abundance is given on a logarithmic scale, and that the contour shades represent different abundances in the four plots.

In contrast, *B. coregoni* occurred in shallow layers (<15 m) from June to November, while it was present in deeper water in late autumn and winter (Fig. 3c).

Stable isotope analyses

The two species had almost identical mean (± standard deviation) $\delta^{13}C$ values (Fig. 4: *C. albula* $\delta^{13}C$ −24.8 ± 0.3‰, *C. fontanae* −24.8 ± 0.4‰). Individual body size was strongly related to $\delta^{13}C$ (ANCOVA, Table 6) with enriched values recorded from larger individuals of both species. However, the regression slopes between size and $\delta^{13}C$ were not homogenous between the species, and the effect of size was stronger in *C. fontanae* (Pearson's $r = 0.593$, $P < 0.001$) than *C. albula* ($r = 0.225$, $P = 0.054$). $\delta^{13}C$ was also significantly associated with capture depth even after controlling for fish size, as individuals caught in deeper water were depleted in $\delta^{13}C$ (Fig. 4a). $\delta^{13}C$ remained identical between the two species when fish size effects were controlled for (ANCOVA, Table 6).

Nitrogen stable isotope values showed minor but statistically significant variation (mean difference = 0.6‰) between the two species (Fig. 4), with mean (± standard deviation) $\delta^{15}N$-values being slightly enriched in *C. fontanae* (7.5 ± 0.9‰) relative to *C. albula* (6.9 ± 0.4‰). *Coregonus fontanae* captured in deep water (>30 m) were particularly enriched in ^{15}N

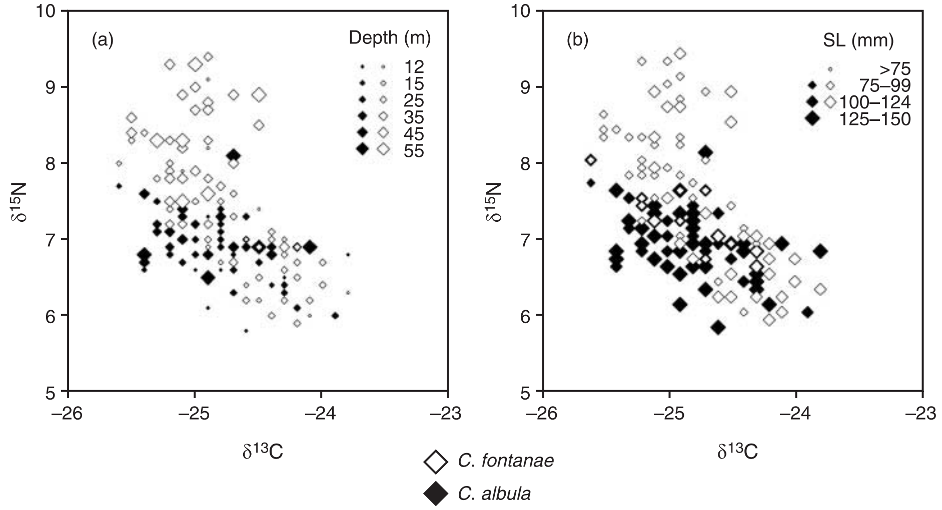


Fig. 4. Isotopic biplot comparing variation in $\delta^{13}C$ and $\delta^{15}N$ in *C. albula* (black) and *C. fontanae* (white). Note that marker size varies with the capture depth (a) and with fish size (b) to highlight the effect of these two factors. SL = standard length.

Table 6. Comparisons (ANCOVA) of trophic signatures ($\delta^{13}C$ and $\delta^{15}N$) between *C. albula* and *C. fontanae* and between different depths (12–15 m, 25–30 m, 35–55 m), with size (relative standard length) as the covariate

	$\delta^{13}C$				$\delta^{15}N$			
	Sum of squares	d.f.	*F*	*P*	Sum of squares	d.f.	*F*	*P*
Size	4.923	1	38.786	<0.001	12.020	1	28.608	<0.001
Depth	1.284	2	5.059	0.007	7.389	2	8.794	<0.001
Species	0.321	1	2.530	0.114	6.984	1	16.623	<0.001
Species * Depth	0.002	2	0.086	0.918	0.624	2	0.746	0.477
Error	19.420	153			64.283	153		
Total	98456.434	160			8594.182	160		
Corrected total	25.459	159			100.142	159		

(Fig. 4a, significant depth effect in ANCOVA, Table 6). However, fish size explained most of the variation in the data set (Table 6) and smaller individuals of both species showed enriched $\delta^{15}N$-values. After controlling for variation in fish size, the two coregonid species differed significantly in $\delta^{15}N$ (Table 6).

DISCUSSION

There was no marked difference in stomach contents between *C. albula* and *C. fontanae*, and the diet composition only varied slightly for a few sub-dominant prey groups. Similar to other studies (Schulz *et al.*, 2003; Kahilainen *et al.*, 2005; Northcote and Hammar, 2006), *B. coregoni* was by far the most frequently consumed prey in both fish species despite its low abundance in comparison with other edible prey in Lake Stechlin. Copepods were the second most frequent prey group. They were more heavily digested than the other prey groups, probably because they lack a compact carapace as found in the cladocerans. As copepods were not readily distinguishable they were grouped together in our analyses. However, such a broad level of taxonomic resolution was probably unsuitable and may have contributed to our inability to demonstrate dietary differences in these closely related fish. There was also no apparent difference in size-selectivity for the main prey species between the two coregonids.

Stable isotope ratios also overlapped between the coregonids. δ^{13}C was particularly close, indicating that both assimilate energy from a similar basal source. Although a difference was found in mean δ^{15}N between the two species, the magnitude of difference was extremely small (0.6‰) and well within the variation typically associated with consumers feeding at similar trophic levels (Post *et al.*, 2000). Compared with mean stable isotope data from other co-existing fish populations (Table 7), the difference in isotopic signature between the Lake Stechlin coregonids is small and probably biologically insignificant. Nevertheless, *C. albula* appears to be more specialized than *C. fontanae*, showing less variation along the δ^{15}N-axis (Fig. 4). Furthermore, both capture depth and fish size were strongly associated with variation in isotopic values, and there seems to be a complex relationship between these factors, while the species-specific difference was less apparent. Lake ecosystems typically show a pattern of relative enrichment in consumer δ^{15}N and depletion in consumer δ^{13}C with increasing depth (Vander Zanden and Rasmussen, 1999). Accordingly, much of the isotopic variation shown in our study is likely attributable to the fact that fish were foraging at different depths. Individuals of *C. fontanae* captured in deeper water showed enriched δ^{15}N and depleted δ^{13}C signatures, although differences in fish size also contributed to the variability of the δ^{13}C signature. Water depth had less influence on isotopic variation in *C. albula*, but both δ^{13}C and δ^{15}N values of this species were significantly correlated to body size. Our δ^{13}C data were corrected for lipid variation (Kiljunen *et al.*, 2006), indicating that these relationships have an ecological rather than a physiological basis. Hence, the variance in isotopic signatures might reflect an ecological difference in form of species-specific differences in depth distribution, growth rate or age (Overman and Parrish, 2001), even if the coregonids in Lake Stechlin do not differ in their prey choice.

The fact that *C. fontanae* from deeper (> 30 m) waters were enriched in δ^{15}N relative to all *C. albula* and the *C. fontanae* caught in shallower water suggests that they fed at a higher trophic level. Enrichment of δ^{15}N may be due to a greater contribution of copepods to the diet of deepwater *C. fontanae*, since some copepod species are zooplanktivorous and are therefore functionally second-level consumers (Santer *et al.*, 2006). A strong effect of capture depth on the individual diet was also revealed by the stomach content analysis of both fish species. However, the stomach contents showed no evidence that the differences were attributable to the proportion of copepods, as there was no significant depth effect for this prey group. Nevertheless, we do not know whether benthic species of copepods (e.g. *Megacyclops* sp.) were among the unclassified copepods grouped together in our analyses and if these benthic copepods may have contributed differently to the diet of the two species. Also earlier diet analyses of coregonids from Lake Stechlin have shown that fish caught by bottom gillnets differed in their diet composition from those caught in pelagic areas (Schulz *et al.*, 2003). In the present study, a distinction between benthic and pelagic food sources was not achievable, since discrimination between planktonic and benthic copepods was not possible and since it is unclear whether consumption of chironomids took place at the lake bottom

Table 7. Comparison of the difference in mean δ^{15}N and δ^{13}C between *C. albula* and *C. fontanae* in Lake Stechlin with the difference in trophic signatures of other co-existing freshwater fish populations found in the literature

Species	Area	Co-existing populations	δ^{15}N	δ^{13}C	Conclusion	Reference
Coregonus spp. (Vendace)	Lake Stechlin, Germany	*C. albula*	6.9 (0.4)	−24.8 (0.3)	Overlap	Present study
		C. fontanae	7.5 (0.9)	−24.8 (0.4)		
Salvelinus spp. *Oncorhynchus* spp. (Trout)	Pender Oreille Lake, Idaho, USA	Large bull trout	12.9	−30.7	Overlap	Clarke *et al.* (2005)
		Large lake trout	12.7	−30.4		
		Small rainbow trout	8.7	−26.2		
		Small cutthroat trout	8.2	−26.1		
Coregonus lavaretus (Whitefish)	Finland (Average of four lakes)	Densly rakered	8.5 (0.23)	−28.3 (0.23)	Different feeding modes	Harrod *et al.* (in prep.)
		Small sparsely rakered	10.1 (0.27)	−28.5 (0.26)		
		Large sparsely rakered	7.3 (0.54)	−25.5 (0.52)		
Lepomis macrochirus (Bluegill sunfish)	Lake Biwa, Japan	Herbivorous	*	*	Different feeding modes	Uchii *et al.* (2007)
		Planktivorous	15.3	*		
		Benthivorous	13.6	*		
Salvelinus alpinus (Arctic charr)	Gander Lake, Newfoundland, Canada	Dark form, large	15.6 (0.2)	−25.6 (0.3)	Different feeding modes	Power *et al.* (2005)
		Dark form, small	12.7 (0.2)	−26.4 (0.1)		
		Pale form, deep	13.2 (0.1)	−29.9 (0.2)		
		Pale form, shallow	10.9 (0.2)	−28.1 (0.1)		
Perca fluviatilis *Rutilus rutilus* (Perch, roach)	Lake Jyväsjärvi, Finland	2003: Roach	13.3	−27.9	Expanded niches after bio-manipulation	Syväranta and Jones (2008)
		Perch	15.0	−29.9		
		2006: Roach	14.5	−31.1		
		Perch	16.7	−32.0		

Note: Standard deviations (present study; Power *et al.*, 2005) or standard errors (Harrod *et al.*, in preparation) are given in parentheses where available.

* Mean values not given when differences were non-significant.

or while the larvae were swimming in the water column (Oliver, 1971; Grey, 2002). However, it is clear that at least an occasional uptake of prey from the bottom takes place, because developing fish eggs have been found in *Coregonus* spp. stomachs. Nevertheless, the contribution of benthic sources to total energy uptake of both coregonids in Lake Stechlin remains unknown.

It can be difficult to assign fish to either pelagic or benthic food webs in deep stratified lakes, as many fish move between the littoral and benthic zones and utilize resources from both habitats (Harrod and Grey, 2006). For coregonids, defining habitat use and diet sources is even more complex, since both coregonid species in Lake Stechlin perform regular diel vertical migration at dusk and dawn (Mehner, 2006; Mehner *et al.*, 2007). Whereas both species are found in deep hypolimnetic areas and close to the bottom during daytime, a slight difference in vertical habitat use has been documented for the night-time period. On average, *C. fontanae* were found in deeper water than *C. albula* (Helland *et al.*, 2007), but neither of them is characterized by a strictly benthic occurrence. However, the spatial segregation along the vertical habitat dimension may support avoidance of intense interspecific competition, and this is reflected by the depth-related differences in diet in the present study. Unfortunately, we did not perform stable isotope analysis of chironomids and other benthos, which, with values from zooplankton, would have allowed us to estimate the proportion of energy assimilated from these different putative food sources. However, our aim in using stable isotope analysis was simply to examine the levels of isotopic differentiation between the species, rather than providing an absolute description of their dietary patterns. Future work should detail and compare spatial and temporal variation in the coregonids, the zooplankton, and benthic invertebrate communities.

The most striking difference between the coregonids in Lake Stechlin is that *C. albula* and *C. fontanae* reproduce during distinct times of the year, and such temporal isolation in breeding reduces gene flow (Hendry and Day, 2005). Thus, segregation of the populations can be maintained without any specialization in feeding ecology or habitat use. There are many examples of assortative mating among sympatric freshwater fish (Hendry *et al.*, 2000; Rundle *et al.*, 2000; Olafsdottir *et al.*, 2006), and it is believed that ecological specialization in combination with assortative mating can lead to reproductive isolation and speciation. Many sympatric populations of coregonids have temporal or spatial divergence in spawning (Steinmann, 1950; Sandlund, 1992; Kottelat and Freyhof, 2007), and body size is one of the major traits for assortative mating (Schliewen *et al.*, 2001; McKinnon *et al.*, 2004). Adams *et al.* (2006) reported an example of sympatric polymorphic populations of *Salvelinus alpinus* (Arctic charr) where population structure probably is maintained by a high level of site fidelity during spawning. Furthermore, sympatric speciation by temporal breeding separation has recently been demonstrated in a seabird (Friesen *et al.*, 2007).

However, the development of reproductive isolation is not enough to avoid competitive exclusion since the ability to co-exist is based on ecological divergence (Coyne and Orr, 2004), and we found surprisingly large diet overlap between *C. albula* and *C. fontanae*. Hence, it is difficult to understand just how two highly specialized pelagic zooplanktivores can co-exist in sympatry with so little ecological divergence. Evidence for competition in the field can be hard to prove (Schoener, 1983), but the slow growth rate in the Lake Stechlin coregonids compared with other *C. albula* populations could be an indication of food limitation. Ecologically similar species should experience intensive competition and it is expected therefore that they can co-exist only by resource partitioning (Dayan and Simberloff, 2005). Bøhn and Amundsen (2001) found evidence of a compressed realized niche of *Coregonus lavaretus*

(European whitefish) after invasion of the closely related *C. albula*, where high competition from the new specialized zooplanktivore caused a diet shift in the *C. lavaretus* population towards more benthic feeding. A similar diet shift is found for *C. clupeaformis* (North American lake whitefish) in the presence of *C. artedii* (lake herring) (Carl and McGuiness, 2006). Several other studies have also demonstrated food partitioning when fish are exposed to high intraspecific (Svanbäck and Bolnick, 2007) or interspecific competition (Haugen and Rygg, 1996; Mookerji *et al.*, 2004; Gray *et al.*, 2005). However, some examples of other co-existing planktivores with low diet niche partitioning are also known, such as *C. albula* and *Osmerus eperlanus* (smelt) in Lake Mälaren, Sweden (Northcote and Hammar, 2006) and some of the coregonid populations in Lake Superior, North America (Johnson *et al.*, 2004a, 2004b; Mason *et al.*, 2005).

In summary, we have shown that ecological segregation between adult *C. albula* and *C. fontanae* is low and this was therefore probably of minor importance for the divergence and the evolution of reproductive differences in Lake Stechlin. Since no substantial diet segregation is apparent between the two coregonid species, other processes may have initiated and maintained the reproductive isolation between them.

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