Is ecological segregation in a pair of sympatric coregonines supported by divergent feeding efficiencies?

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Abstract: Some of the sympatric species pairs commonly described in temperate freshwater fishes provide evidence for ecological specialization driven by competition for food resources as a potential prerequisite of subsequent sympatric speciation. In the postglacial Lake Stechlin (Germany), two sympatric coregonines coexist, common vendace (*Coregonus albula*) and endemic dwarf-sized Fontane cisco (*Coregonus fontanae*). The species segregate vertically along the light intensity and prey density gradients of their pelagic environment. Accordingly, we hypothesized that the species might show differences in their foraging efficiency associated with these environmental gradients. We investigated the feeding behaviour by measuring the functional response of both species to *Daphnia magna* at various prey densities (0.25–8 individuals·L^{-1}) and light intensities (0.005–5 lx) at a deep blue light spectrum to simulate their natural habitat. Decreasing light intensity and prey density significantly depressed consumption rates in both species. Overall, we observed only weak differences in feeding behaviour, which indicates that the species are functionally similar, coexisting planktivores.

Résumé : Quelques-unes des paires d'espèces sympatriques couramment décrites chez les poissons d'eau douce des régions tempérées montrent des signes de spécialisation écologique reliée à la compétition pour les ressources alimentaires, ce qui est potentiellement une condition préalable pour une spéciation sympatrique subséquente. Dans le lac Stechlin (Allemagne), un lac post-glaciaire, coexistent deux corégoninés sympatriques, le corégone blanc (*Coregonus albula*) et le corégone de Fontane (*Coregonus fontanae*), une espèce endémique naine. Il y a ségrégation verticale des espèces le long des gradients d'intensité lumineuse et de densité de proies dans leur milieu pélagique. C'est pourquoi, nous formulons l'hypothèse selon laquelle les espèces devraient montrer des différences d'efficacité de recherche de nourriture en relation avec ces gradients environnementaux. Nous avons étudié leur comportement alimentaire en mesurant la réponse fonctionnelle des deux espèces à *Daphnia magna* à diverses densités de proies (0,25–8 individuals·L^{-1}) et sous différentes intensités lumineuses (0,005–5 lx) dans un spectre de lumière bleu foncé afin de simuler leur habitat naturel. Une intensité lumineuse et une densité de proies décroissantes réduisent les taux de consommation chez les deux espèces. Globalement, nous n'observons que de légères différences de comportement alimentaire, ce qui indique que les espèces sont des planctonophages qui coexistent tout en affichant un fonctionnement similaire.

[Traduit par la Rédaction]

Introduction

Sympatric species pairs have been most commonly described in several families of teleost fishes in temperate postglacial lakes, basically in sticklebacks, smelts, and salmonids, including the coregonines (Taylor 1999). Many of these species pairs show clear ecological segregation (Schluter 1996, 2000), wherefore much of the recent research in this field has focused on the role of ecological specialization in driving and maintaining divergence in sympatry. There is ample evidence that the process is often driven by competition for food resources (Robinson and Wilson 1994; Smith and Skúlason 1996), and evidence for the process of sympatric speciation has been provided for

some of these species pairs (e.g., Gislason et al. 1999; Knudsen et al. 2006).

Sympatrically living species are common among coregonines (whitefishes and ciscoes; see Hudson et al. 2007). Many of them exhibit profound differences in feeding strategies and habitat preferences (e.g., Lu and Bernatchez 1999; Amundsen et al. 2004). However, species pairs that do not display a divergence in diet or habitat also co-occur, for instance in the North American Lake Superior (Smith and Todd 1984; Turgeon et al. 1999). In these cases, alternative segregating strategies that contribute to the coexistence of the species have not been described so far. Since many environmental factors such as temperature, turbidity, and especially the light regime influence the feeding behaviour of

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planktivorous fish (Matthews 1998; Wootton 1998), diverse feeding efficiencies of sympatric planktivorous species might be expected if the species segregate along environmental gradients.

It is generally assumed that fish vision is well adapted to the light characteristics of the environment (Lythgoe 1979), and spectral adaptations have been described in many deepwater marine fishes (Lythgoe 1988). Planktivorous coregonines, like most other fish species (Guthrie and Muntz 1993), are particulate feeders depending on vision to catch their prey (Janssen 1978; Dabrowski and Jewson 1984), and light intensity is considered to be an important factor controlling their feeding activity (Aksnes and Giske 1993). Fish feeding under sufficient light conditions benefit from better visibility of prey as well as higher reactive volume (Townsend and Risebrow 1982; Ryer et al. 2002; Pekcan-Hekim and Horppila 2007). However, most of our understanding of fish feeding ecology is based on studies conducted under moderate to high light levels, and foraging models for planktivores assume negligible feeding rates at extremely low light intensity (Giske and Salvanes 1995; Hölker and Breckling 2001). Moreover, most studies employ a light spectrum commonly used for room illumination, although the spectrum of the light changes considerably with increasing water depth towards predominantly blue wavelengths (Jerlov 1976; Gerking 1994). It is known that the spectral composition influences the consumption rate of zooplanktivorous fish, because reaction distance is reduced as the wavelength of light decreases from red to blue (Dabrowski and Jewson 1984; Henderson and Northcote 1985).

In the deep and oligotrophic Lake Stechlin (Germany), vendace (*Coregonus albula*) is the dominant pelagic fish species living in sympatry with the endemic dwarf-sized Fontanae cisco (*Coregonus fontanae*; Schulz and Freyhof 2003). The species are easily distinguished by spawning time, with vendace spawning in winter and Fontanae cisco spawning from spring to summer. The species have been described distinct by morphological characteristics (Schulz and Freyhof 2003), and it has been suggested from mtDNA and microsatellite analyses that this species pair evolved via sympatric speciation (Schulz et al. 2006). Both species are planktivores inhabiting the pelagic habitat where they perform diel vertical migrations by ascending from their deepwater daytime habitat into shallower water layers during nighttime (Helland et al. 2007; Mehner et al. 2007). No species-specific difference in diet composition has been observed (Schulz et al. 2003; Helland et al. 2008), and this contrasts the commonly observed divergence along the limnetic–benthic axes found in many other sympatric species in temperate freshwater systems (Lu and Bernatchez 1999; McKinnon and Rundle 2002; Knudsen et al. 2006). Habitat segregation between the Lake Stechlin coregonines has only been observed with respect to vertical distribution within the pelagic habitat (Helland et al. 2007) with Fontane cisco occurring on average in deeper waters than vendace. Zooplankton density, besides light intensity and temperature, also declines continuously with depth in Lake Stechlin (Mehner et al. 2005). Moreover, owing to the weak ecological segregation, high exploitative competition between the species can be assumed. Hence, segregating strategies for reducing interspecific competition were ex-

pected according to the competition exclusion principle (see Pianka 2000).

Accordingly, we hypothesized that the species would show a divergence in their efficiency to consume zooplankton. Such a divergence would suggest heritable trait differences, since the fish were hatched and raised under the same laboratory conditions. We investigated the influence of light intensity and prey density on the functional response curves of both species. We hypothesized that Fontane cisco is more efficient at those low light levels and low prey densities, which are typical for the deepwater areas, whereas vendace should be superior at the brighter light and higher prey densities found in lower water depths, where this species is commonly found.

Materials and methods

Study species

Fontane cisco and vendace were caught by gillnetting (15 mm mesh size) during their respective spawning times in Lake Stechlin (53°10′N, 13°02′E), Germany. Ripe adults were striped and propagated artificially, and both species were raised under identical laboratory conditions. Larvae were hatched in glass aquaria and subsequently raised in circular basins (80 L). They were fed with brine shrimp, rotifers, and commercially available dry food for fish larvae. Juveniles were maintained in 500 L basins and fed with salmon dry food and *Daphnia magna* to habituate to this prey type. The fish were held at the experimental temperature of 8 °C for at least 2 weeks before experiments started. The prey species *Daphnia magna* was held in circular basins fed with *Desmodesmus subspicatus* algae.

Experimental design

Functional response tests were carried out in six 110 L cubic glass aquaria (48 cm × 48 cm × 48 cm) that were placed in a climatic chamber. The aquaria were filled with 80 L aerated fresh water up to a fill level of 35 cm. The climatic chamber was darkened with light-impermeable curtains inside and outside the entrance. Another row of dark curtains was installed as blinds in front of the aquaria with small peepholes for observation of the feeding activity. Small plastic reservoirs above each of the aquaria served as holding units for *Daphnia* for the feeding experiments. The outlets of these reservoirs were equipped with a valve that opened a tube for the introduction of the *Daphnia* into the aquaria approximately 10 cm below the water surface, which resulted in a homogeneous distribution of the *Daphnia* throughout the entire arena within a short time period. The valves were connected via a stick to a hand gear outside the blinds to introduce the prey without disturbing the fish. Luminaries equipped with 60 W halogen lamps were installed above each of the aquaria. The lamps were connected to a six-channel digital–analogue dimmer (Eurolight LD6230, Behringer, Germany) to allow fine-tuning of the light intensity at very low levels. The intensity of the light was set on a percent scale according to an exponential transmission characteristic of the dimmer. The color temperature of the flashlights (2.800 kelvin (K)) was converted to approximately 20.000 K using tungsten conversion filters (E-Colour+, Rosco, UK). It was adjusted to this value by

Fig. 1. Capture rates (mean and standard error) of Fontane cisco (*Coregonus fontanae*, black bars) and vendace (*Coregonus albula*, grey bars) at 5, 0.5, and 0.05 lx for all prey densities (individuals·L^{-1}): (*a*) 0.25; (*b*) 0.5; (*c*) 1; (*d*) 2; (*e*) 4; (*f*) 8. Differences between light intensities were significant between 0.5 and 0.05 lx at all prey densities in both species, but only partly significant between 5 and 0.5 lx. The only significant difference between species was found at 8 individuals·L^{-1} at 5 lx, as indicated by an asterisk.
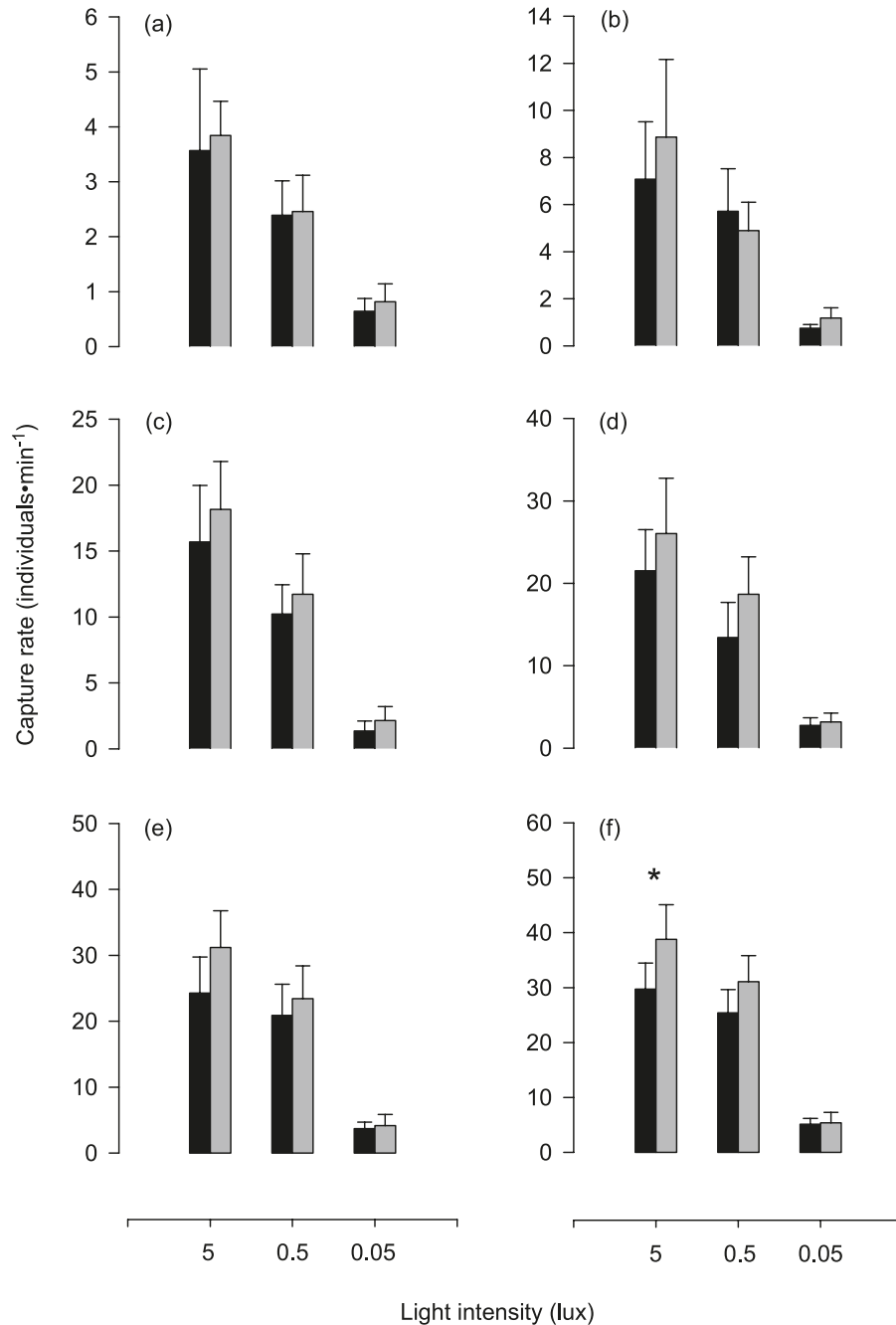
placing two conversion filters (Double and Quarter C.T. Blue) on top of each other in front of the lamps behind a framed glass. Color temperature varied from 17.000 to 23.000 K depending on the light intensity used for the respective experiment. The conversion was done to simulate the blue spectrum of the natural habitat, since these fish usually feed in depths of more than 15 m during crepuscular to dark light periods and more than 35 m during daytime according to average year-round population depths (Helland et al. 2007; Mehner et al. 2007). Color temperature was meas-

ured with a color analyzer (TF5, Thoma, Germany). Light intensity was measured at mean depth in the aquaria using a light detector (SUD033/Y/W) connected to a research radiometer (IL 1700, International Light Technologies, Massachusetts, USA). The light detector had a measurement range of 400–700 nm and a dynamic range of 8×10^{-4} to 8×10^{5} lx.

Infrared lamps (880 nm, 60 W, WRL-I/LED06, Videor Technical, Germany) were installed above each of the aquaria to allow the observation of feeding activity at very low

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Table 1. *P* values of the analysis of variance (ANOVA) Tukey's test for differences between light intensities at all prey densities.

Prey·L^{-1}	*Coregonus albula*		*Coregonus fontanae*	
	5 vs. 0.5 lx	0.5 vs. 0.05 lx	5 vs. 0.5 lx	0.5 vs. 0.05 lx
0.25	0.056	0.022	0.141	0.013
0.5	0.022	0.036	0.842	0.004
1	0.014	<0.001	0.026	<0.001
2	0.110	<0.001	0.063	0.008
4	0.044	<0.001	0.751	<0.001
8	0.071	<0.001	0.645	<0.001

Note: In both species, differences between 5 and 0.5 lx were partly significant, whereas differences between 0.5 and 0.05 lx were entirely significant.

Table 2. *P* values of the analysis of variance (ANOVA) Tukey's test for differences between species at all prey densities and light intensities.

Prey·L^{-1}	5 lx	0.5 lx	0.05 lx
0.25	0.990	0.999	0.999
0.5	0.640	0.978	0.999
1	0.696	0.949	0.997
2	0.570	0.409	0.999
4	0.092	0.908	0.999
8	0.016	0.404	0.999

Note: The only significant difference in consumption rate was found at the highest light intensity (5 lx) and prey density (8 individuals·L^{-1}) combination.

light intensities. This was done using night-vision glasses (D-2MV PRO, Hupra, Germany), which allowed the observation of the fish as well as the *Daphnia* during the experiments. Hence, it was possible to track an individual fish and its consumption of *Daphnia* through the peepholes of the aquaria without disturbing it.

Experimental protocol

Functional response experiments were performed at a water temperature of 8 °C at four different light intensities (0.005 ± 0.001, 0.05 ± 0.005, 0.5 ± 0.02, and 5 ± 0.01 lx). Six prey densities of 0.25, 0.5, 1, 2, 4, and 8 *Daphnia*·L^{-1} were used at each of the four light intensities. These prey densities were the mean densities over a feeding trail where each fish was allowed to eat six *Daphnia*. Accordingly, the total number of *Daphnia* introduced into the 80 L aquaria was 23, 43, 83, 163, 323, and 643 individuals for the six densities, respectively. Since the experiments were terminated after six *Daphnia* were captured, prey depletion was 26.1%, 14.0%, 7.2%, 3.7%, 1.9%, and 0.9% for the increasing prey densities, respectively. We therefore assume that the modest ratios of prey depletion did not substantially bias the results.

One fish was placed in each of the six aquaria, which thereby served as replicates for the specific light intensity and prey density combinations. The subsequent acclimation to experimental conditions was allowed overnight at the light intensity of the upcoming experiment. Individuals were randomly selected from a 500 L tank holding all potential experimental fish. Specimens used for this study were all juveniles and measured 6–11 cm (mean ± standard deviation, SD: 8.3 ± 1.3 cm) and 6–13 cm (mean ± SD: 9.7 ± 1.7 cm) total length for Fontane cisco and vendace, respectively. On the next day, prior to the experiments, *Daphnia* of 1.5–3 mm in size were sieved out of their holding tanks, counted, and poured into the small plastic reservoirs above the aquaria. After another 3 h, trails started with the introduction of the prey into one aquarium at a time. The time from the beginning of the feeding activity until the fish had eaten six *Daphnia* was measured using a stopwatch with an intermediate memory function. Typically, at the beginning of an experiment the fish stayed near the bottom. After perceiving the first *Daphnia*, the fish started to swim more actively, thereby searching for prey. At that time the *Daphnia* were already quite evenly distributed throughout the arena. The fish usually used the entire arena to forage continuously. After all six trails were counted, the fish were removed from the aquaria. Subsequently, the water was sieved to remove the remaining *Daphnia* and to prepare for the next experiment.

Data analysis

Three types of functional responses are distinguished: (*i*) the linear type I response with consumption rate increasing linearly with prey density until a satiation value is reached, with $N = \alpha P$, where N is the consumption rate (individuals·L^{-1}), P is prey density (individuals·L^{-1}), and α is the slope of the consumption rate; (*ii*) the cyrtoid type II response with consumption rate increasing with prey density at a decreasing rate until satiation is reached, with $N = \beta_1 P(\beta_2 + P)^{-1}$, where β_1 is the maximum consumption rate, and β_2 is the prey density at which the consumption rate reaches half of its maximum (Holling 1959; Arditi and Ginzburg 1989); and (*iii*) the sigmoid type III response with consumption rate accelerating first with increasing prey density and thereafter decelerating towards satiation, with $N = \beta_1 P^2(\beta_2 + P^2)^{-1}$, We used linear and nonlinear regression analyses to fit these functional response curves.

A method based on information criterion was used to determine the regression model for the functional response that best described the experimental data. We used the Schwarz–Bayesian information criterion (S–BIC, Schwarz 1978). It is a restrictive criterion on increasing parameter numbers: S–BIC $= k \ln(n) + n \ln(RSS \cdot n^{-1})$, where k is the given number of parameters, n is the number of observations, and RSS is the residual sum of squares. The model associated with smallest value of S–BIC is the most appropriate.

Statistics

Functional response data were compared for significant differences using the following tests based on a significance level of $P < 0.05$. Analysis of variance (ANOVA, Tukey's test) was used to compare the mean values between species and light intensities at a particular prey density. To evaluate the influence of fish length, an analysis of covariance (ANCOVA) was performed. Further, we linearized the functional response data by taking the $\log_{10}$ of

Table 3. Statistical results and selection criterion for the best-fit models of the functional response according to types I, II, and III curves for both species at all three light intensities.

Model	*Coregonus albula*			*Coregonus fontanae*		
	Type I	Type II	Type III	Type I	Type II	Type III
5 lx						
k	1	2	2	1	2	2
n	33	33	33	33	33	33
df	32	31	31	32	31	31
RSS	3369.92	786.78	1000.82	3226.95	1062.13	1097.19
S–BIC	156.16	111.65	119.59	154.73	121.55	122.63
0.5 lx						
k	1	2	2	1	2	2
n	31	31	31	33	33	33
df	30	29	29	32	31	31
RSS	1732.65	646.66	728.51	1333.18	347.62	432.05
S–BIC	128.16	101.04	104.74	125.56	84.70	91.87
0.05 lx						
k	1	2	2	1	2	2
n	30	30	30	29	29	29
df	29	28	28	28	27	27
RSS	70.20	35.85	44.53	37.67	27.10	32.38
S–BIC	28.90	12.15	18.65	10.95	4.76	9.93

Note: The model associated with the lowest values in S–BIC was selected as the most appropriate. Abbreviations are as follows: k, number of parameters used; n, total number; df, degrees of freedom; RSS, residual sum of squares; S–BIC, Schwarz–Bayesian information criterion

prey density and compared the capture rate with prey density relationship between the species by ANCOVA. ANOVA and ANCOVA tests were performed using SPSS 14.0 (SPSS Inc., Chicago, Illinois). The estimated mean values for β_1 and β_2 were tested for significance using a t test.

Results

Capture rates in both species generally increased with prey density. Mean capture rates for both species at all prey densities and light intensities are shown (Fig. 1). No feeding activity was observed at 0.005 lx. In both species, differences between light intensities were all significant when 0.5 and 0.05 lx were compared, but only partly significant when 5 and 0.5 lx were compared (ANOVA, Tukey's test, Table 1). Significant differences between the species were found at the highest light intensity and prey density combination (5 lx and 8 individuals·L^{-1}). All other 17 interspecies comparisons were not significant. The differences between the species generally tend to increase with increasing light intensity and prey density (ANOVA, Tukey's test, Table 2). Fish size, measured as total body length, did not significantly affect capture rates (ANCOVA, $P > 0.1$ at all prey densities).
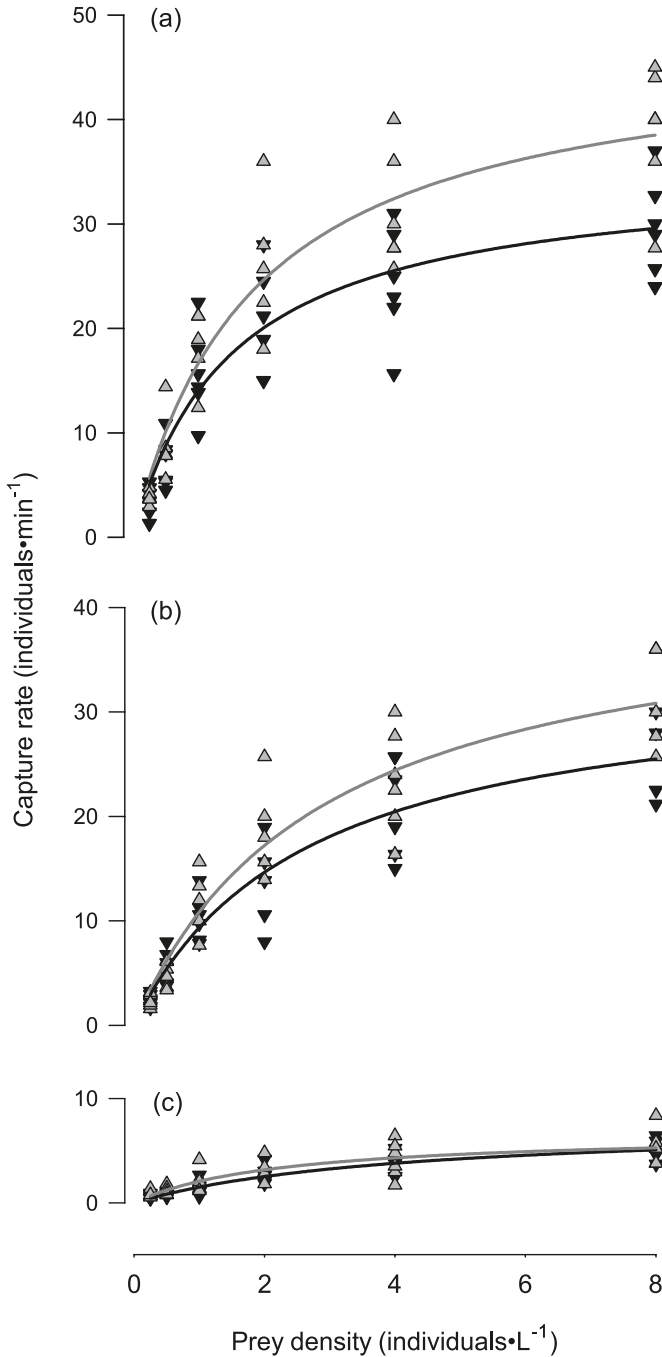
According to the S–BIC, the functional response type II gave the best fits to the data sets at all light intensities (5, 0.5, and 0.05 lx) in both species. However, the type III function gave comparably good fits in some cases (Table 3). The increase in capture rate with prey density at all light intensities is shown (Fig. 2). Capture success was depressed with decreasing light intensity in both species. After log-transforming prey density, ANCOVA showed a significant difference between the species at 5 lx ($P = 0.003$), but no significant difference at 0.5 lx ($P = 0.051$) and 0.05 lx ($P = 0.129$). The estimated parameters of the functional response type II fits are presented (Fig. 3, Table 4). According to the t test, maximum feeding rates were significantly higher in vendace compared with Fontane cisco at 5 lx (df = 10, $P = 2.839$), but there was no significant difference between species at 0.5 lx (df = 10, $P = 1.568$) and 0.05 lx (df = 10, $P = 0.563$). Differences between light intensities were not significant between 5 and 0.5 lx, but were significant between 0.5 and 0.05 lx in both species. Prey densities of half maximum feeding rate were not significantly different between species at all light intensities (5 lx: df = 10, $P = 0.699$; 0.5 lx: df = 10, $P = 0.284$; 0.05 lx: df = 8, $P = 1.151$).

Discussion

The consumption rate of Fontane cisco and vendace feeding on *Daphnia magna* increased with increasing prey density at a decreasing rate until satiation was reached. It thus followed a type II functional response. This type of response has been reported for other coregonines, for instance bloater (*Coregonus hoyi*; Miller et al. 1992), and was found in a recent study on a Swedish vendace population (U. Beier, Swedish Board of Fisheries, Drottningholm, Sweden, unpublished data). Some studies have reported a linear type I or a sigmoid type III functional response for planktivores (e.g., Winkler and Orellana 1992; Ryer et al. 2002), and a shift from type II to another response at low light intensity has also been described (Townsend and Risebrow 1982;

Fig. 2. Capture rates as a function of prey density of Fontane cisco (*Coregonus fontanae*, black triangles and black lines) and vendace (*Coregonus albula*, grey triangles and grey lines) at (*a*) 5 lx, (*b*) 0.5 lx, and (*c*) 0.05 lx. Shown are all individual data and a curve fitted according to a Holling type II functional response, which was determined as the best-fit model. Capture rate increases with increasing prey density at all light intensities in both species. Fontane cisco showed a significantly lower functional response compared with vendace at 5 lx (*P* = 0.003), but not at 0.5 lx (*P* = 0.051) and 0.05 lx (*P* = 0.129).

Fig. 3. (*a*) Maximum feeding rates and (*b*) prey densities of half maximum feeding rates of Fontane cisco (*Coregonus fontanae*, black bars) and vendace (*Coregonus albula*, grey bars) at 5, 0.5, and 0.05 lx. Shown are parameter estimates of the functional response type II fits and their standard errors. Maximum feeding rate significantly increases between 0.05 and 0.5 lx, whereas differences in prey density of half maximum feeding rate are not significant. Interspecies differences are significant only for the maximum feeding rate at 5 lx, as indicated by an asterisk.
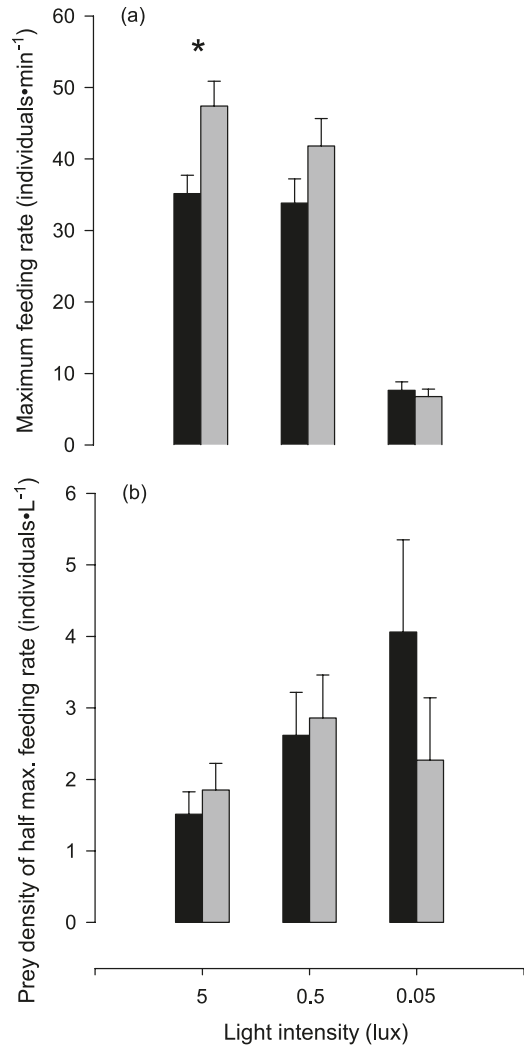
proaches for analyzing functional response data have been proposed (see Juliano 2001).

The two planktivorous coregonines of Lake Stechlin showed a marginal divergence in their feeding behaviour. Significant differences in functional response were only found at the highest light intensity and when associated with high food density. At all other light and food conditions investigated in this study, the species showed no difference in functional response. The combination of high food abundance and relatively high light intensity seems to represent a rather extreme condition. We re-examined field data based on zooplankton samplings from Lake Stechlin (Helland et al. 2007) and computed a mean zooplankton density for the most relevant prey species of the coregonines, including daphnids, small cladocerans, and copepods

Koski and Johnson 2002). However, the type II function is most frequently observed in planktivorous fishes (Jeschke et al. 2004). It has to be mentioned that different ap-

Table 4. Estimates and standard errors for parameters of the type II functional responses for both species at all three light intensities.

	Coregonus albula			*Coregonus fontanae*			Comparison	
	n	Estimate	SE	n	Estimate	SE	df	P
5 lx								
β_1	6	47.43	3.47	6	35.16	2.58	10	2.839
β_2	6	1.85	0.37	6	1.51	0.32	10	0.699
0.5 lx								
β_1	6	41.85	3.82	6	33.84	3.38	10	1.568
β_2	6	2.86	0.60	6	2.62	0.60	10	0.284
0.05 lx								
β_1	5	6.77	1.05	5	7.66	1.18	8	0.563
β_2	5	2.27	0.87	5	4.06	1.29	8	1.151

Note: The only significant difference between the species was found for β_1 at 5 lx. β_1, maximum consumption rate (individuals·min^{-1}); β_2, prey density of half maximum consumption rate; n, total number; SE, standard error; df, degrees of freedom.

of about 2.5 individuals·L^{-1} below 10 m depth. High food abundances of 8 individuals·L^{-1} or more in these depths are found only for some weeks during summer. Further, hydroacoustic surveys in the lake suggest that the fish feed in depths where light intensity is seldom at a level of 5 lx or above. The species stay below 35 m depth during day and migrate to lower depth during crepuscular light and at nighttime, so that foraging is generally associated with lower light intensities (S. Busch and T. Mehner, unpublished data). Thus, because of the migration pattern, a combination of high light intensity and high food density can be assumed to be very unlikely (i.e., for the most relevant environmental conditions found in situ, the species do not differ considerably with respect to their feeding efficiency). However, vendace feeding was slightly more efficient than that of the deeper living Fontane cisco at the combination of the highest light intensity and the highest food level, suggesting a beginning or ongoing segregation in their functional response along the light gradient.

Light intensity had a major influence on the feeding behaviour in both species, with declining efficiency down to a threshold between 0.05 and 0.005 lx. Generally, it is in accordance with many other studies on fish feeding behaviour that capture success is reduced as light intensity decreases. However, ongoing feeding activity of fishes that usually use vision for prey capture has been reported under light conditions approaching darkness in some species (e.g., Janssen 1978; Townsend and Risebrow 1982; Pekcan-Hekim and Horppila 2007). Hence, fishes might rely on nonvisual senses, for example the mechanosensory lateral line system, to locate and attack prey under light conditions where vision is ineffective (Janssen and Corcoran 1993; Hölker and Thiel 1998; Liang et al. 1998). The lack of feeding activity at the lowest light intensity (0.005 lx) investigated in this study suggests that the coregonines are unable to feed when light intensity approaches zero. However, we have to note that an effect of light spectrum on foraging behaviour cannot be completely ruled out. Hence, the described influence of light intensity on the feeding efficiency may possibly be confounded by an effect of color spectrum. This is contrasted by the fact that the change of color temperature during the

experiments was associated with relatively minor changes in transmitted wavelength, since the color filter we used had a transmission characteristic of 50%–65% at 400–500 nm wavelengths but only 5%–10% in the 550–700 nm range, leaving mainly the blue and violet wavelengths just like clear water in depths of 15 m and more. Moreover, feeding activity of coregonines is generally discussed to be strongly influenced by light intensity and its diel and seasonal patterns. Dabrowski and Jewson (1984) showed that the feeding activity of Irish pollan larvae (*Coregonus pollan*) was strongly determined by light intensity and Gjelland et al. (2004) reported that feeding activity of pelagic common whitefish (*Coregonus lavaretus*) and vendace was more strongly correlated to light intensity than to circadian rhythms.

The diel vertical migration of the Lake Stechlin coregonines may be explained by the bioenergetics efficiency, the feeding opportunity, or the predator avoidance hypotheses (Scheuerell and Schindler 2003). If the latter applies, this would emphasize the importance of feeding at low light intensities to avoid predation, since yellow perch (*Perca flavescens*) as the most abundant predator species in the lake usually forage in shallow water at moderate to high light levels. However, hydroacoustic surveys from Lake Stechlin suggest that the seasonal variation of depth distribution of both species is more strongly correlated to temperature than to water transparency, and thus the migration patterns of these coregonines are only weakly related to the light regime and the occurrence of the most important food resources and potential predatory fish (Mehner et al. 2007). Hence, there is only little support for the predator avoidance as well as the feeding opportunity hypotheses, favoring the bioenergetics efficiency hypothesis to explain diel vertical migrations and putting forward temperature as the ultimate abiotic factor driving species' vertical orientation.

Our results clearly demonstrate a significant influence of food density and light intensity on capture rates in both species. Since they show an ecological segregation with respect to their vertical distribution within the pelagic habitat (Helland et al. 2007), where light intensity and food density decline continuously with depth (Mehner et al. 2005), these gradients induce severe species-specific consequences with respect to energy budgeting. The difference in average population depth imposes energetic disadvantages on the deeper-living Fontane cisco, because this species encounters lower food abundances under less favorable light conditions compared with sympatric vendace without showing any compensatory mechanism via enhanced feeding efficiency. This conclusion is supported by growth analysis (Schulz and Freyhof 2003) showing that individuals of Fontane cisco have a lower growth rate compared with vendace. That raises the question how this species is able to sustain a life-supporting energy budget under such unfavorable conditions and high exploitative competition with vendace.

The cooler temperatures at greater depths reduce the metabolic requirements considerably. An average temperature difference of only 1 °C means 7%–10% less metabolic costs for Fontane cisco. Furthermore, it appears that this species has adapted to the unfavorable conditions by reducing its standard metabolic rate. We found substantially lower standard costs in Fontane cisco compared with vendace over the

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whole range of environmental temperatures (Ohlberger et al. 2008). Although the relative amount of energy for metabolism of dwarf fish could be higher (Trudel et al. 2001), dwarfism per se might also be an adaptive strategy to living in deeper waters, instead of being its consequence, since smaller body size means on average less total energy expenditure for maintenance. Svärdson (1979) argued that in a situation of reduced food ration due to competition between pelagically living sympatric forms, the "dominated", inferior population could have a better energy budget if it withdraws to deeper and cooler waters. Further, the lower energy costs of smaller fish inspired Hamrin and Persson (1986) to base their hypothesis about the oscillation cycles in single vendace populations on a principle of competition between age classes. They argued that small vendace experience a competitive advantage compared with larger fish during periods of low food abundance because of their lower metabolic requirements.

In summary, in contrast with our hypothesis, the ecological segregation between the co-occurring species is not facilitated by differences in feeding efficiency, since their functional response curves barely differed within the natural range of environmental conditions. Instead, together with a study on the species' feeding preference, our data suggest that these coregonines are functionally similar, coexisting planktivores that only use slightly different feeding niches within their pelagic environment. We conclude that species' coexistence may be facilitated by alternative energetic strategies and recommend this as a promising field for future research.

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