

Diet overlap between young-of-the-year perch, *Perca fluviatilis* L., and burbot, *Lota lota* (L.), during early life-history stages

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Abstract – The diet overlap between young-of-the-year (YOY) perch and burbot in the pelagic zone of Lake Constance during spring and summer was investigated in relation to gape size limitation. Because perch were larger and grew faster than burbot during their early life history, perch overcame gape size limitation for various zooplankton taxa earlier than burbot. The interspecific diet overlap between perch and burbot decreased continuously until June, but increased slightly, when burbot became able to feed on large daphnids by the beginning of July. All zooplankton taxa could be found within perch stomachs by the middle of June, when perch overcame gape size limitation for large cladocerans. However, there was an increasing tendency for individual diet specialisation of perch, as the similarity between individual perch stomach contents decreased. In contrast, the similarity between individual burbot stomach contents remained at almost 50% until the end of August, indicating that all burbot rely on cyclopoid copepods during their entire pelagic life-history stage. Because by July YOY perch are more abundant by one order of magnitude in the pelagic zone than burbot, YOY perch may be more affected by intraspecific competition than by interspecific competition with burbot. Burbot, on the other hand, may evade strong competition with YOY perch by performing diel vertical migrations, thus being restricted to feed on migrating zooplankton prey.

Key words: feeding; competition; larvae; juvenile; stomach; multivariate statistics

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Introduction

The re-oligotrophication of many prealpine lakes such as Lake Constance has caused a decline in crustacean zooplankton abundance (Bürgi et al. 2006). As a consequence the food resources for larval and juvenile fish may have become limited (Eckmann et al. 2006; Schleuter & Eckmann 2007) and the potential for competition between two members of the pelagic fish community of Lake Constance perch, *Perca fluviatilis* L., and burbot, *Lota lota* (L.), may have increased. While preferences for similar zooplankton prey taxa by perch and

burbot are described (Hartmann 1983, 1986; Wang & Appenzeller 1998), no attempt has been made to quantify the potential for exploitive competition between both species during their pelagic stage. For this endeavour, the analysis of diet overlap provides an approach to quantify the common resource use of different species or individuals (Schoener 1971; Bowen 1996; Schleuter & Eckmann 2007).

During their earliest life-history stages, young-of-the-year (YOY) perch and burbot co-exist in the pelagic zone of Lake Constance (Wang & Appenzeller 1998; Miler & Fischer 2004). Whereas perch larvae migrate from the littoral towards the pelagic

zone within a few days after hatch (Wang & Eckmann 1994), burbot larvae migrate from the lake profundal towards the surface waters (Fischer 1999). Both species can be found in the pelagic zone between May and July. From the beginning of June burbot start to perform diel vertical migrations (DVM) and by July achieve considerable amplitudes of more than 50 m (Miler & Fischer 2004; Probst & Eckmann 2009). Contrary to burbot, YOY perch always remain in epilimnetic waters and are rarely found below 10 m depth (Wang & Appenzeller 1998). Perch perform an ontogenetic niche shift as juveniles, when they migrate towards the littoral zone in July (Wang & Eckmann 1994). The feeding periodicities of both species indicate that perch feed during the day and crepuscular hours (Wang 1994a,b), whereas burbot seem to feed mainly around dusk. Due to the DVM of burbot, the spatial overlap between YOY perch and burbot during feeding hours, which is a prerequisite for interference competition, is confined to daylight hours in May and early June. However, both species may exploit the same zooplankton resources.

During the ontogeny of both species, it is reasonable to expect that the magnitude of diet overlap will decrease, because both species will overcome the gape size limitation for large zooplankton taxa and thus become able to diversify their diet. A more diverse spectrum of ingestible prey increases the potential for individual specialisation, which may reduce intra- as well as interspecific competition (Bolnick et al. 2003; Svanbäck & Eklov 2003). However, because of their faster growth perch overcome gape size limitation for each taxon earlier than burbot (Wang & Appenzeller 1998). As a consequence, the diet overlap should decrease when perch overcome gape size limitation for taxa, which burbot cannot yet ingest and increase, when burbot becomes able to feed on the same resource as perch.

The aim of this study was to assess the diet overlap between perch and burbot during their larval and early juvenile life-history stages and to capture the temporal dynamics of diet overlap under various constellations of gape size limitation. We expected to find periods of higher and lower diet overlap according to the gape size limitations of both species. Furthermore, the intraspecific diet overlap of both species was assumed to decrease as their diet spectrum increased. The multivariate methods applied in this study also allow the analysis of intraspecific diet overlap within both species, which especially for YOY perch may be of major importance, as in the middle of the summer perch are the most abundant species in many parts of the pelagic zone of Lake Constance (Wang & Appenzeller 1998).

Materials and methods

Study site

Lake Constance is the second largest prealpine lake in Central Europe. It has a total surface area of 536 km² and a maximum depth of 254 m (IGKB 2008a,b). Since the 1950s the loading of total phosphorous had increased from <10 µg·l⁻¹ to more than 80 µg·l⁻¹ in the mid-1980s (Mürle et al. 2004). To overcome the problem of eutrophication in Lake Constance, nutrient loadings were reduced since the 1970s by lake-wide installations of sewage plants and the introduction of phosphorous-free detergents. Consequently, the content of total phosphorous has decreased to about 8 µg·l⁻¹ since the mid-1980s (IGKB 2008a,b). The reduction of nutrient loading has been demonstrated to affect lake whitefish growth (Thomas & Eckmann 2007), and may have caused a decline of invasive ruffe (Schleuter 2007), but the influence on zooplankton dynamics remains uncertain. While Gaedke (1998) did not find any significant changes in zooplankton crustacean biomass by 1998, Bürgi et al. (2006) report the declines of zooplankton biomass during spring and summer since the 1990s.

The pelagic fish community of Lake Constance is dominated by lake whitefish, *Coregonus lavaretus* L., which is also the commercially most important fish species (Thomas & Eckmann 2007). However, besides whitefish, perch and burbot are the only two fish species, which utilise the pelagic zone as a nursery habitat as larvae and juveniles (Wang & Appenzeller 1998). While perch is the second most important species for commercial fishing, burbot is caught in low quantities of <5 t per year (Klein 2002).

Fish sampling and diet analysis

Fish larvae and juveniles were caught every second to third week between May and August on five occasions in 2006 and on seven occasions in 2007. During each occasion, sampling was conducted at day (around noon) and night (around midnight). For detailed description of catch methods, see Probst & Eckmann (2009) and Probst et al. (2009).

To catch YOY perch and burbot, two different net types were used: (i) Three-meter long ichthyoplankton nets with a circular opening of 1.4 m diameter were used to catch larvae and early juveniles of both species. Mesh sizes of the two nets were 1200/800 and 1600/1200 µm in the front and the rear end respectively. The ichthyoplankton nets were attached to a 160-m-long tow line of 10 mm diameter. (ii) A fry-net of 8 m length with 6 mm mesh size in the front and 4 mm mesh size at the cod end was used to catch perch juveniles in July/August 2006 and July 2007. In

2006, all nets were fitted with a flow meter to calculate the sampled volume of the water body. Unfortunately no flow meter was used in 2007 and thus quantitative data on perch and burbot abundance are lacking from this year. To adjust the trawl depth (from surface to 25 m depth), appropriate weights were attached. For towing depths > 10 m, a hydrodynamic V-fin with 15 kg weight (HYDROBIOS, Kiel, Germany) was used. Information on trawl depth was derived from an ultrasonic depth transponder attached to the bridle of the nets. The depth transponder measured the trawl depth to the nearest meter.

Depending on the time of the year and weather conditions, the nets were trawled between the surface and 35 m depth with a speed of 2.5–5.5 km·h⁻¹. The speed was adjusted to maintain a consistent depth, but was held as fast as possible. Fish samples were killed in trichloromethyl-propanol (2 g·l⁻¹) directly after catch and subsequently preserved in 4% formalin or put on ice. Within 6 h, all fish that had been put on ice were stored in a freezer at 18 °C until they were further processed.

Total length (TL) of larvae and juveniles (only frozen individuals) were recorded in the laboratory to the nearest millimetre. Fish were dissected under a stereo microscope and stomach contents were counted and classified according to the traditional classification system of zooplankton within the working group ‘Fish ecology’ from the Limnological Institute of Konstanz University into the following taxa: *Daphnia* sp. < 1.6 mm carapace length (CP), *Daphnia* sp. > 1.6 mm CP, *Daphnia galeata* < 1.6 mm CP, *D. galeata* > 1.6 CP, cyclopoid copepods < 0.8 mm CP and cyclopoid copepods > 0.8 mm CP, calanoid copepods < 0.8 mm CP, calanoid copepods > 0.8 mm CP, *Leptodora kindtii*, *Bythotrephes longimanus*, *Bosmina* sp. and copepod nauplii (Table 1). The numerical abundance of prey taxa, was converted into biomass by using mean lengths and wet weights from the literature (Becker 1992; Mehner et al. 1995; Eckmann et al. 2002). Only stomach contents from individuals containing at least two food items were included into the data set.

Table 1. Five periods of different gape size limitations of perch and burbot.

Period (DOY)	Perch			Burbot		
	Taxa	No. _{pred}	No. _{obs}	Taxa	No. _{pred}	No. _{obs}
<138	NAUP CYC < 0.8	3	1	NAUP* CYC < 0.8	3	2
138–147	CAL < 0.8 NAUP CYC < 0.8; CYC > 0.8 CAL < 0.8* ; CAL > 0.8* DS < 1.6 DG < 1.6* BOS*	8	6	CAL < 0.8 NAUP* CYC < 0.8; (CYC > 0.8) CAL < 0.8*	3	4
147–167	NAUP CYC < 0.8; CYC > 0.8 CAL < 0.8* ; CAL > 0.8* DS < 1.6; (DS > 1.6)* DG < 1.6* BOS*	8	8	NAUP CYC < 0.8; CYC > 0.8 CAL < 0.8* ; CAL > 0.8* DS < 1.6* ; (DS > 1.6)* DG < 1.6 BOS*	8	6
167–178	NAUP CYC < 0.8* ; CYC > 0.8* CAL < 0.8* ; CAL > 0.8* DS < 1.6; DS > 1.6 DG < 1.6; DG > 1.6 BOS* BYT LEPT	12	11	NAUP CYC < 0.8; CYC > 0.8 CAL < 0.8* ; CAL > 0.8* DS < 1.6* ; DS > 1.6 DG < 1.6; DG > 1.6 BOS* BYT LEPT	12	6
>178	NAUP CYC < 0.8; CYC > 0.8 CAL < 0.8* ; CAL > 0.8* DS < 1.6; DS > 1.6 DG < 1.6* ; DG > 1.6 BOS BYT* LEPT	12	11	NAUP CYC < 0.8* ; CYC > 0.8 CAL < 0.8; CAL > 0.8 DS < 1.6* ; DS > 1.6 DG < 1.6; DG > 1.6* BOS BYT* LEPT*	12	7

DOY, day of year counted continuously from 1st of January; No., the taxa which can be ingested by perch and burbot according to the gape size models (pred.) and actually observed (obs.); CYC, cyclopoid copepods; NAUP, nauplii; DS, *Daphnia* sp.; DG, *Daphnia galeata*; BOS, *Bosmina* sp. Numbers behind taxa abbreviations indicate size class. Taxa printed in bold indicate taxa which were observed to be ingested, taxa in brackets are taxa which were observed to be ingested, but not predicted to be consumable according to gape size models. Asterisks denote taxa which contributed <5% to the mean stomach content biomass.

Gape size calculation

At the time of first catches in the middle of May, burbot and perch had similar TL (6.0–7.0 mm), but in August, perch had grown to more than twice the size of YOY burbot (Fig. 1). From the regression between the day of the year (DOY) and TL ($TL = aDOY^b$ with a and b as estimated regression coefficients), a predicted TL at a given DOY was calculated and used to compute the gape size of both species at the according DOY.

The gape size (GS) of perch and burbot were calculated using the following equations:

$$GS_{\text{Perch}} = 0.2152 + 0.0781 * TL(\text{mm})$$

(Guma'a 1978)

$$GS_{\text{Burbot}} = -0.36 + 0.15 * TL(\text{mm})$$

(Ghan & Sprules 1993)

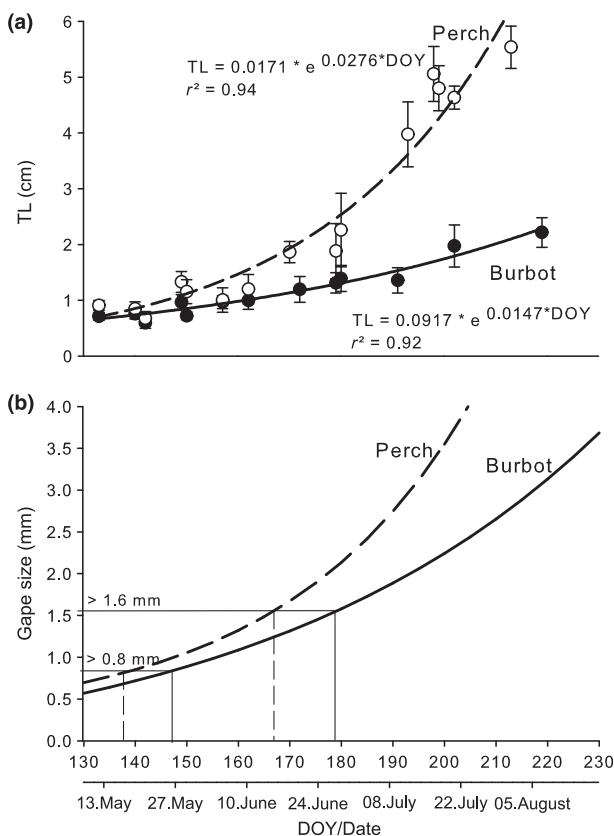


Fig. 1. The growth of YOY perch and burbot during spring and summer in Lake Constance. (a) The relationship between day of the year (DOY) and total length (TL). Both regressions were highly significant ($P < 0.001$). (b) Changes of both species' gape size during spring and summer. Black lines indicate the estimated time for the overcoming of gape size limitation for large copepods (>0.8 mm carapace length) and large daphnids (>1.6 mm carapace length) for perch (hatched line) and burbot (straight line).

According to the regression between DOY and gape size, five periods of various diet-overlap scenarios were assigned as following: Before DOY 138, both perch and burbot were assumed to be gape size limited for all taxa except small cyclopoid and calanoid copepods with a CP < 0.8 mm and copepod nauplii (Table 1). Between DOY 138 and DOY 147, perch should be able to ingest larger copepods (>0.8 mm CP) and small daphnids, but burbot were still gape size limited for these taxa. Between DOY 148 and DOY 167, perch and burbot should be able to ingest large copepods but still be gape size limited for large daphnids and predatory cladocerans (>1.6 mm CP), and between DOY 167 and 178 only perch should overcome this limitation. After DOY 178, perch as well as burbot should ingest all prey taxa. Because the gape size limitations are similar for perch and burbot between DOY 147 and DOY 167 and after DOY 178, during these periods higher rates of diet similarity/overlap were expected.

Statistics

The regression between DOY and mean TL was analysed with STATEasy (Lozan & Kausch 1998). Within STATEasy, the data for the regression analysis are tested for normality and autocorrelation of the residuals. Neither the regression between DOY and mean TL of burbot nor perch violated any of these assumptions.

The difference in growth between the years 2006 and 2007 was analysed by a general linear model (GLM) implemented with STATISTICA 6.0 (Stat Soft, Tulsa, USA). The year of catch and the species were entered as categorical factors, DOY as continuous covariate and log(mean TL) as dependent variable into the GLM. The total GLM R^2 was 0.90, $P < 0.001$. The univariate statistics from the model were as follows: influence of species (on mean TL): $F = 37.403$, $P < 0.001$; influence of year on mean TL: $F = 1.168$, $P = 0.290$; influence of DOY on mean TL: $F = 155.387$, $P < 0.001$. Furthermore, no differences in diet composition between 2006 and 2007 were found for either perch or burbot in nonmetric multi-dimensional scaling (nMDS) plots produced by Primer-E (Clarke & Gorley 2006). In nMDS plots, the distances of the Bray-Curtis similarities are projected onto a two-dimensional plane and result in groups (in this case categorised by years), which are clustered according to their similarity. In our case, if all stomach content data are aggregated within a single group, there is no visual evidence for differences in the stomach contents.

Because no significant differences in growth or diet composition were observed, the stomach content data of both years were pooled. This approach increased

the sample size within the five periods of various gape size limitations and was assumed to result in a better statistical resolution of stomach content differences or similarities.

For all analyses of stomach contents, biomass data were used. The stomach contents by wet weight were compared between perch and burbot with similarity percentage analysis (SIMPER) using Primer-E 6.0 (Clarke & Warwick 2001; Clarke & Gorley 2006). The SIMPER-analysis allows to investigate the similarity of stomach contents between individual perch and burbot. SIMPER also identifies the dissimilarity between perch and burbot stomach contents and allocates the relative contribution of the ingested zooplankton taxa to the observed similarity or dissimilarity. Prior to the SIMPER-analysis, the absolute biomass data of stomach contents were standardised to relative amount of biomass per stomach.

The diet overlap (C) between perch and burbot for the five periods was calculated after Schoener (1971):

$$C = 100 * \left(1 - 0.5 * \sum |p_{bi} - p_{pi}| \right),$$

where p_{bi} is the mean proportion of prey item i in the stomach of burbot and p_{pi} is the mean proportion of food item i in the stomach of perch.

Results

Catches

The pelagic fish catches from 2006 and 2007 consisted exclusively of YOY perch and burbot. From the total of 657 perch and 236 burbot caught in both years, 548 perch and 223 burbot stomachs were analysed. This amounted to 83% and 94% of analysed perch and burbot stomachs, respectively. In 2006, perch catches peaked in the middle of June, sharply declined by the middle of July and became absent by the beginning of August (Fig. 2). Burbot catches were highest in early May and continuously declined until August. Perch were always more abundant than burbot, the maximum abundance dominance occurred by the middle of June, when perch were 36 times more abundant than burbot (Fig. 2).

Stomach contents composition

The predictions of gape size limitation matched the observed taxa ingested by perch (Table 1, Fig. 3). As perch grew and their gape size increased during summer, their diet spectrum diversified, and after DOY 167 all prey taxa except for copepod nauplii could be found within the perch stomachs. Before DOY 138, larval YOY perch fed exclusively on small cyclopoid copepods. From DOY 138 onwards, daph-

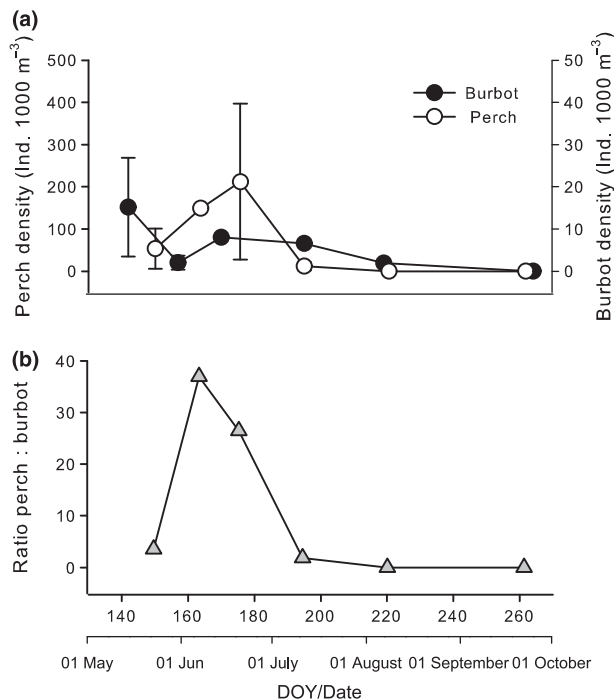


Fig. 2. Trends in seasonal abundance of YOY perch and burbot in the pelagic zone of Lake Constance in 2006. (a) Abundance of perch and burbot at a given date (\pm SE on dates were replicate hauls were conducted). (b) Ratio of perch versus burbot abundance. DOY, day of year counted from the 1st of January 2006. Different scales for perch and burbot abundance are shown in this figure.

nids became increasingly abundant in perch stomach contents until after DOY 167 even larger daphnids were ingested and daphnids accounted for more than 66% of all consumed biomass. After DOY 167 also large cladocerans (*Bythotrephes longimanus* and *Leptodora kindtii*) as well as *Bosmina* sp. contributed to about 10% of perch diet, whereas copepods became less dominant: before DOY 167 copepods contributed about 66% to the consumed biomass, but after perch overcame the gape size limitation for large daphnids, copepods contributed <33% to perch stomach content biomass.

Similar to perch, the diet of burbot became more diverse as they grew, however, not as many different prey taxa were consumed (Fig. 3, perch = 11 prey taxa, burbot = 7 prey taxa after DOY 178, Table 1). Burbot fed mainly on small cyclopoid copepods before DOY 147, but to a small extent also consumed nauplii during this time (Fig. 3). From DOY 147 onwards, large cyclopoid copepods constituted at least 40% of the diet, which matched the predicted ending of gape size limitation for this taxon. The regression model between TL and gape size predicted a gape size of >1.6 mm at DOY 180, and in accordance, large daphnids were not found before DOY 179. However, small daphnids (<1.6 mm CP) were only consumed in minimal proportions during the entire summer. After

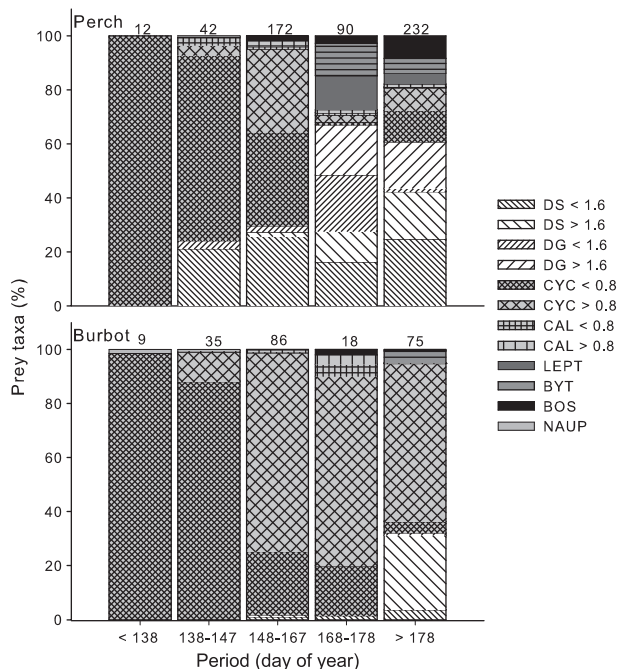


Fig. 3. Relative composition of stomach content biomass of perch and burbot during the five investigation periods with different gape size limitations. DOY indicates the first and last day of the year for the according period. Numbers of analysed stomachs are indicated above each column. Zooplankton taxa are abbreviated as: DS, *Daphnia* sp.; DG, *Daphnia galeata*; CYC, cyclopoid copepods; CAL, calanoid copepods; LEPT, *Leptodora kindtii*; BYT, *Bythotrephes longimanus*; BOS, *Bosmina* sp. Numbers behind abbreviations refer to carapace length in millimetre.

DOY 178, also a small number of *Bythotrephes longimanus* was consumed, indicating that burbot overcame gape size limitation for even the largest taxon of crustacean zooplankton.

Diet overlap

The stomach content dissimilarities between perch and burbot increased until DOY 178, but decreased in the last period after DOY 178 (Table 2). Until DOY 147,

Table 2. Results of SIMPER-analysis on square-root transformed, standardised biomass data of perch and burbot stomach contents.

Period (DOY)	Similarity perch (%)	Similarity burbot (%)	Dissimilarity (%)
<138	100.0	98.1	1.1
138-147	55.4	80.2	36.3
147-167	40.4	53.0	57.3
167-179	22.9	44.7	95.4
>179	22.9	46.4	79.8

Similarity refers to the arithmetic mean similarity between perch and burbot samples respectively. Dissimilarity refers to the mean dissimilarity between perch and burbot stomach contents of the according period. Mean similarities and dissimilarities are based on Bray-Curtis distances calculated for pair-wise comparison samples within the according period based, which is DOY = day of year counted from the 1st of January.

the interspecific differences in stomach content composition were mostly attributable to copepod nauplii, small cyclopoid copepods and small *Daphnia* sp. (Table 3). After DOY 147, however, the stomach contents of both species also differed as a result of different amounts of consumed large cyclopoid copepods accounting for about 27% of the observed dissimilarity.

Comparing the trajectories of Schoener's C and SIMPER dissimilarity during the periods of varying gape size limitations between perch and burbot, the observed values of both methods indicate similar trends in diet overlap (Fig. 4). Interspecific diet overlap decreased continuously until the last period (>DOY 178), when burbot began to consume large daphnids and thus their diet spectrum approached a similar width as the diet spectrum of perch.

The intraspecific similarity of perch stomach contents decreased until DOY 178 and remained at 23% (Table 2). The ingested prey taxa, which accounted most often for the similarity of perch stomach contents, were small cyclopoid copepods until DOY 167 and small daphnids after DOY 167 (Table 4). The contributions to similarity of single taxa decreased constantly over time, reaching <10% of the total similarity after DOY 168 and thus reflecting the diversification of perch diet.

The intraspecific similarity between burbot stomach contents decreased during the summer (Table 2) and was caused exclusively by cyclopoid copepods, which always contributed more than 50% to the calculated total similarity (Table 4).

Discussion

The earliest catches of perch and burbot in this study occurred in the middle of May, which correspond well to the first presence of both species within the pelagic zone of Lake Constance as found by Wang & Appenzeller (1998). However, perch and burbot are well known to commence exogenous feeding on green algae and rotifers (Guma'a 1978; Ryder & Pesendorfer 1992; Ghan & Sprules 1993; Wang 1994a,b), which in this study were not found in any stomach. Hence, the earliest stages of exogenous feeding must have been missed by the present sampling scheme. Despite this shortcoming, this study gathered data before the diets of perch and burbot diverged as indicated by the high diet similarity before DOY 138 (Fig. 2).

Hartmann (1986) described that larval perch and burbot are mostly limited in prey type selection by their gape size. The present results generally confirm this pattern during the larval stage, but as juveniles the feeding strategies of perch and burbot diverge. Whereas only a total of seven different prey taxa were found in all burbot stomachs after DOY 178,

Table 3. Main taxa responsible for interspecific dissimilarities between perch and burbot stomach contents during the five periods of various gape size limitations.

Period (DOY)	Prey taxa	Av.Abund. perch	Av.Abund. burbot	Av.Diss. (%)	Diss./SD	Contrib. (%)	Cum. (%)
<138	CYC < 0.8	100.0	98.9	0.5	0.5	50.0	50.0
	NAUP	0.0	1.1	0.5	0.5	50.0	100.0
138–147	CYC < 0.8	70.5	89.3	16.4	0.9	45.1	45.1
	DS < 1.6	17.5	0.0	8.7	0.6	24.1	69.2
148–167	CYC < 0.8	55.8	51.7	23.0	1.3	40.2	40.2
	CYC > 0.8	21.8	45.7	22.0	1.2	38.5	78.7
168–178	CYC > 0.8	3.3	55.8	27.5	1.3	28.8	28.8
	CYC < 0.8	2.0	36.2	18.0	0.9	18.8	47.7
	DG < 1.6	22.3	0.0	11.1	0.8	11.7	59.3
>178	CYC > 0.8	14.3	60.6	27.5	1.5	34.4	34.4
	DS > 1.6	21.9	19.4	15.1	0.9	18.9	53.4

Av. Abund., average relative abundance of prey taxon in stomach content data; Av. Diss., average dissimilarity between pair-wise comparisons of perch and burbot stomach content data; Diss./SD, average dissimilarity/standard deviation of pair-wise comparisons; Contrib., relative contribution to dissimilarity value of Table 2; Cum., cumulative contribution; CYC, cyclopoid copepods; NAUP, nauplii; DS, *Daphnia* sp.; DG, *Daphnia galeata*; BOS, *Bosmina* sp. Numbers behind taxa abbreviations indicate size class. The list of contributing prey taxa was cut off, when the cumulative contribution was >50%.

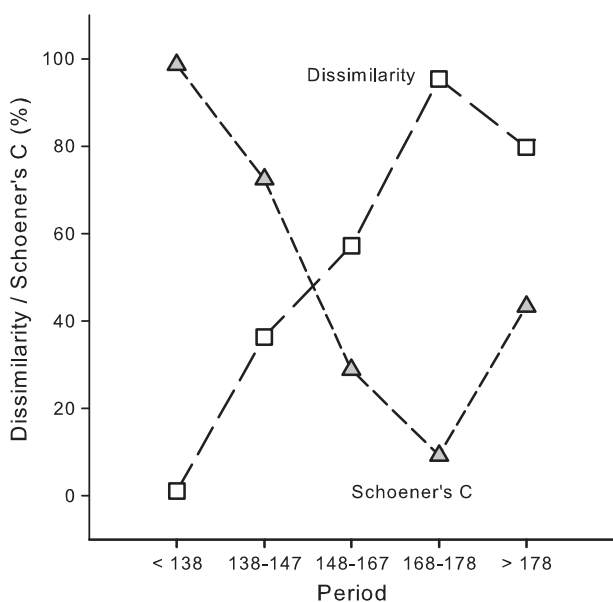


Fig. 4. The trajectories of observed diet overlap (Schoener's C and SIMPER dissimilarity) between perch and burbot during the five periods of various gape size limitations.

perch consumed all classified taxa except for nauplii ($N = 11$, Table 1).

During their ontogeny, the diet of burbot was not exclusively restricted by gape size, because between DOY 148 and DOY 167 small daphnids (<1.6 mm CP) should have become edible for burbot, but this taxon was never a considerable part of burbot diet. The reason for this diet limitation may be found in the lack of spatial overlap with small daphnids or the dependence on copepods as an essential part of burbot diet during their ontogeny. The spatial overlap between small daphnids and burbot may have been limited due to the DVM of burbot (Probst & Eckmann 2009).

Throughout the diel cycle, the amplitude of DVM in daphnids is size dependent (Lampert & Sommer 1999). Thus, during daytime, small daphnids may be higher in the water column than burbot. As described Probst & Eckmann (2009) and Hartmann (1983), burbot seem to feed mainly around dusk when they are still below or within the thermocline. Hence, burbot may be confined to migrating zooplankton taxa, which they meet in a crepuscular light window and thus the spatial overlap between burbot and small daphnids may be limited.

Alternatively, the restriction of burbot to cyclopoid copepods may be explained by nutritional demands. Marine copepods are considered to contain essential nutrients for the survival, development and growth of many fish larvae (Olsen et al. 1991; Koven 2003; Malzahn et al. 2007) and strong dependencies on food quality have also been found in freshwater systems (Coutteau & Sorgeloos 1997; Kolkovski et al. 2000). The consistent presence of copepods in the diet of burbot may thus reflect the nutritional dependency of burbot on fatty acids or phospholipids contained in their copepod diet. Also the capture rates and handling times of planktivorous fish can vary for different zooplankton taxa (Werner & Hall 1974). Thus, due to specific foraging behaviour and preferences, burbot may forage more efficiently on copepods than on daphnids during late larval and early juvenile stages.

When YOY perch and burbot simultaneously inhabit the pelagic zone of Lake Constance, perch can be more abundant by one or two orders of magnitude (Wang & Appenzeller 1998). Because of their numerical dominance and the sooner overcoming of various gape size limitations, perch can be assumed to be the superior competitor exerting competitive pressure on burbot. Perch are well known to feed on many prey types (Guma'a 1978; Schleuter & Eckmann

Table 4. Main taxa accounting for at least 50% of intraspecific similarities (Sim.) of perch and burbot stomach content during five time periods of differing gape size limitations.

Sim. between:	Period (DOY)	Prey taxa	Av. Abund. (%)	Av. Sim. (%)	Sim./SD	Contrib. (%)	Cum. (%)
Perch	<138	CYC < 0.8	100.00	100.00		100.00	100.00
	138–147	CYC < 0.8	70.53	51.08	1.35	92.16	92.16
	148–167	CYC < 0.8	55.80	32.45	0.86	80.42	80.42
	168–178	DG < 1.6	22.25	7.97	0.55	34.85	34.85
		DS < 1.6	19.87	6.75	0.53	29.48	64.33
	>178	DS > 1.6	21.88	6.12	0.37	26.71	26.71
		CYC < 0.8	16.93	5.32	0.47	23.25	49.96
		DS < 1.6	14.57	4.98	0.52	21.73	71.69
		CYC < 0.8	98.94	97.99	39.29	99.89	99.89
	Burbot	<138	CYC < 0.8	98.94	97.99	39.29	99.89
138–147		CYC < 0.8	89.29	79.69	2.29	99.35	99.35
148–167		CYC < 0.8	51.73	29.25	0.90	55.21	55.21
168–178		CYC > 0.8	55.83	31.22	0.80	69.80	69.80
>178		CYC > 0.8	60.64	39.34	1.09	84.85	84.85

Av. Abund., relative abundance of prey taxon in stomach content data; Av. Sim., average similarity based on pair-wise comparisons between individual stomach content data; Sim./SD, average similarity/standard deviation of pair-wise comparisons; Contrib., relative contribution to similarity value of Table 2; Cum., cumulative contribution; CYC, cyclopoid copepods; DS, *Daphnia* sp.; DG, *Daphnia galeata*. Numbers behind taxa abbreviations indicate size class. The list of contributing prey taxa was cut off when the cumulative contribution was >50%.

2007) and due to their faster growth could utilise all zooplankton resources by the middle of June. Because of the dominant abundance and wider diet spectrum of perch, DVM may help burbot to reduce the interspecific interference competition with perch.

The evidence for resource limitations for planktivorous fish is scarce (Mehner & Thiel 1999; Persson et al. 2000). Gaedke (1998) found no evidence, that the re-oligotrophication of Lake Constance has caused a decline in lake whitefish by the end of the millennium. Consequently, there is no reason to assume food limitation for other planktivorous fish. However, while Eckmann et al. (2002) found no evidence for a top-down control of daphnids by lake whitefish, *Coregonus lavaretus* L., whitefish were estimated to affect significantly the mortality rate of *Bythotrephes longimanus* Leydig 1860. Furthermore, during the eutrophication from 1915 until 1970, the fisheries' yields of perch and burbot have increased (Nümann 1973). Therefore, lower densities of zooplankton in oligotrophic lakes may generally lead to increased competition between YOY fish (Guillard et al. 2006). The re-oligotrophication of Lake Constance may increase mortality rates during the common pelagic stage of perch and burbot due to increased inter- and intraspecific competition.

The relative compositions of stomach content biomass indicate that the potential for exploitive competition between both species exists mainly until DOY 147, which was the time when the interspecific dissimilarities between stomach contents of perch and burbot were <50% (Table 2). Because of their dependency on small cyclopoid copepods during their early life history, both perch and burbot can be expected to react sensitive to absolute changes in abundance of

cyclopoid copepods. However, due to extended dependency of burbot on cyclopoid copepods, their year-class strength should be particularly affected by this zooplankton taxon. Contrary, changes in the abundance and population dynamics of a single prey taxon should have less impact on the survival and growth of YOY perch. Hence, the changes in zooplankton community as a result of re-oligotrophication may affect the ontogeny of YOY perch and burbot differently. When copepods densities remain at similar levels, but cladocerans decrease in abundance, re-oligotrophication may have stronger impacts on the population of Lake Constance perch than burbot. Contrary, a total decline in copepods abundance may affect burbot more severely than perch, because they rely longer on this zooplankton taxon and do not seem to be able to utilise other prey taxa as flexible as perch. Time series of the Lake Constance zooplankton community indicates that the total abundance of zooplankton as well as the ratio of daphnid:copepod abundance is decreasing (Bürgi et al. 2006). Therefore, the reoligotrophication of Lake Constance may be expected to have less impacts on the feeding of burbot, but is increasing the competition between perch for zooplankton resources. After their ontogenetic habitat shift to the littoral zone in July, juvenile perch are currently found to consume increasing proportions of benthic invertebrates (Schleuter & Eckmann 2007). This observation provides evidence for the limited zooplankton availability for juvenile perch during summer, which fed exclusively on zooplankton during this season in years of eutrophication (Schleuter 2007).

The intraspecific total similarity between perch stomach contents decreased to <25%, but remained

at almost 50% in burbot (Table 2). Thus, perch seem to become individual specialists, whereas burbot continue to feed on a common resource, i.e., cyclopoid copepods.

By the middle of June, the abundance of burbot decreases to such low numbers, that perch may rather be subject to intraspecific competition than to interspecific competition with burbot (Fig. 2). The similarity in stomach contents of perch decreased continuously until DOY 178, with total similarities remaining at 23% during the last period of their pelagic stage (Table 2). While overcoming gape size limitations for various zooplankton prey taxa, the decreasing intraspecific similarity values suggest that individual perch specialised on a limited number of prey taxa and thereby reduce intraspecific competition (Bolnick et al. 2003). The intraspecific similarity values of perch decreased most markedly after the gape size limitation for large copepods and large daphnids were overcome by DOY 147 and DOY 167 respectively. Before DOY 167, more than 50% of taxon-related similarity resulted from small cyclopoid copepods, whereas after DOY 168 values of taxon-related similarities were small (<10%, Table 4) and only attributable to daphnids and cyclopoid copepods. During the last two periods (from DOY 168 onwards), the similarity of perch stomach contents remained at 23% (Table 2). The inability to further reduce intraspecific competition in combination with declining zooplankton abundances in July may induce the ontogenetic habitat shift towards the littoral zone frequently observed in juvenile perch populations (Treasurer 1988; Wu & Culver 1992; Wang & Eckmann 1994; Urho 1996).

The intraspecific diet overlap of burbot remained high even after the overcoming of gape size limitation for large daphnids (Table 2). However, considering the low densities of YOY burbot in Lake Constance in summer (Fig. 2), intraspecific competition for zooplankton resources may affect burbot growth or survival only during spring. However, the diet overlap of juvenile burbot, which have settled to the lake bottom, remains to be quantified to assess the full potential for intraspecific competition between burbot during their first year of life.

In meso- and oligotrophic lakes, the fish community is usually dominated by percids and salmonids (Persson et al. 1991). Mehner et al. (2005) further identify two types of fish communities depending rather on water depth and temperature than on trophic status: In warm, shallow lakes the fish community is dominated by cyprinids, whereas in deep, cold lakes salmonids and percids are proportionally most abundant. Accordingly, perch is the dominant fish in the littoral zone, while burbot abundance is fourfold lower (Reyjol et al. 2005). The study by Mehner et al.

(2005) revealed that deep lakes with cool, oxygen rich water are also a preferred habitat of burbot. Because perch and burbot have been native members of the Lake Constance fish community prior to the eutrophication, they can be expected to remain present in the lake throughout the ongoing process of re-oligotrophication (Nümann 1973; Hartmann & Nümann 1977).

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