Not to be cited without prior reference to the author – CM 2006/J:28

The diet of large eels (*Anguilla anguilla*) in relation to food availability

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Key words: *Anguilla*, piscivory, predation, stable isotopes, macroinvertebrates, zoobenthos

Abstract

The aim of the present study was to analyse and compare the feeding behaviour of large eels *Anguilla anguilla* (> 30 cm total length) in two lakes of different environmental state and corresponding differences in food availability. Investigations were conducted in Lake Großer Vätersee, Germany (clear water, mesotrophic, submerged macrophytes present) and in Lake Vallum, Denmark (turbid, eutrophic, no submerged macrophytes). Fish were sampled regularly by electrofishing. We focused our study on diet patterns. The availability of macrozoobenthos was higher in Lake Vallum (3,500 ind. m^{-2}) than in Lake Großer Vätersee (1,500 ind. m^{-2}), which was due to a high density of insect larvae in Lake Vallum (2,700 ind. m^{-2}) compared to Lake Großer Vätersee (680 ind. m^{-2}). Both, the abundance of eels and small prey fish (40-99 mm TL) were higher in Lake Vallum. Despite the latter, fish was unimportant as prey for eels in Lake Vallum which instead fed on macroinvertebrates and in particular chironomid larvae. In contrast, in Lake Großer Vätersee where availability of insect larvae was low eels used fish as the main food component. Based on these results as well as similar observations for smaller eels, we suggest that piscivory among eels to a wide extent is generally controlled by the availability of insect larvae. Stable isotope analyses confirmed the dietary results. The estimated mean trophic positions of eels in Lake Großer Vätersee (3.74 ± 0.2) was one level higher than those of eels in Lake Vallum (2.71 ± 0.2). Stable isotopes provided an estimate of 82% benthic reliance in the carbon signature of eels in Lake Vallum and 37% in Lake Großer Vätersee, indicating that eels may act as integrators between benthic and pelagic food webs when availability of insect larvae is low.

Introduction

Together with other species such as pike *Esox lucius*, pikeperch *Sander lucioperca* and perch *Perca fluviatilis* eel *Anguilla anguilla* is a member of the piscivorous fish community in many European lakes, but is generally considered less important, than the others as a predator . Eels are night-active hunters (Tesch, 1999), seeking their prey close to the bottom rather, than in open water (Barak & Mason, 1992). Recent studies indicate that large eels may play a more vital role in controlling the abundance of age 0 fish than has been assumed hitherto (Radke & Eckmann, 1996; Dörner & Benndorf, 2003). In contrast, eels are also described as opportunistic feeders using all food components available (Lammens et al., 1985; Schulze et al., 2004). As the main result of an intensive investigation of resource partitioning and niche shifts of eel and bream in Lake Tjeukemeer, The Netherlands, Lammens et al. (1985) demonstrated that diet shifts in eels were caused by changes in availability of larval chironomids which were, in turn, caused by diet shifts in bream *Abramis brama*. At low chironomid abundance eels shifted to smelt (*Osmerus eperlanus*) as prey but, because eels above 40 cm TL were seldom in Lake Tjeukemeer (Lammens & Visser, 1989), their study was restricted to eels ranging in size from 17.5 to 37.5 cm TL (Lammens et al., 1985). Large eels have also been described as preying on macozoobenthos and fish (Moriarty, 1972, 1973; De Nie, 1987). The question if their feeding behaviours and tactics are also precipitated by differences in the availability of prey resources remains nearly unknown. The aim of the present study, therefore, was to compare diet patterns of large eels in two lakes of very different environmental characteristics in order to recognize if differences in macroinvertebrate and small fish abundance could determine their feeding behaviour.

Material and methods

Study sites

Lake Vallum is a small (11 ha), shallow, non-stratified lake situated in Jutland, Denmark (56°23'N; 10°31'E, 67 m a.s.l.). The lake is eutrophic (Table 1) and no submerged macrophytes are present. The lake has a maximum depth of 3.2 m, a mean depth of 2.1 m and its volume is *circa* 230,000 m^3. The fish population in 2001 was dominated by small sized roach (*Rutilus rutilus*). Pike and perch were, together with eel, the main fish predators. The eel population in Lake Vallum is the result of natural immigration of elvers.

Lake Großer Vätersee (area 12 ha, maximum depth 11.5 m, mean depth 5.2 m, volume 633,000 m^3) is a mesotrophic, to slightly eutrophic lake, in the Baltic lake region of north-eastern Germany (53°00'N; 13°33'E, 60 m a.s.l.). Details of its hydrography, trophic characteristics, submerged macrophytes, and preliminary characteristics of the pelagic food web structure are provided in Kasprzak et al. (2000). In 2002, roach and perch were the dominant fish species in terms of number as well as biomass (Schulze et al., in press). The abundances of perch and roach of between 6 and 150 mm TL, and thus within the potential predation window of large eels, were 1,775 and 2,161 ind. ha^{-1}, respectively (Hölker et al, submitted). Pike, pikeperch and perch (≥ 150 mm total length) were the top predators (Schulze et al., in press). The lake was stocked with eel between 1993 and 1995 (K. Anwand, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany, pers. com.). More information on the two study sites is given in Table 1.

Macroinvertebrate sampling

Macrozoobenthos was sampled monthly with Ekman grabs (15 x 15 cm) in both lakes at three sites, at water depths of 0.5 and 2 m, from June until October in Lake Großer Vätersee and in August and October in Lake Vallum. The samples were sieved through 0.5 mm mesh. Larvae from Lake

Vallum were preserved in alcohol before further processing; larvae from Lake Großer Vätersee were identified, counted and measured immediately after sampling. For each lake, mean densities were calculated. The benthic samples from both lakes were analysed by the same person.

Fish sampling

Fish in Lake Vallum and Lake Großer Vätersee were caught monthly from June to the end of September (Lake Großer Vätersee) and early October (Lake Vallum) in 2002. On each occasion, a minimum of 50 randomly chosen locations in the littoral zone were selected by 'point abundance sampling'. Electro-fishing methods were then used to sample the Piscean community (PASE) (Lake Großer Vätersee: EFG/400: 4 kW, 200-610 V, DC, Lake Vallum, Electracatch WFC12, 800 hz, ¾ pulse width, 300 v with a variable duty cycle of 0-50%). At each location the anodes were fixed at 20s (see Skov & Berg, 1999 for details on the PASE procedure). All fish narcotised by the electric current were counted and their total lengths (TL) measured to the nearest 1 mm. Potential eel prey fish were separated into two size groups, 40-99 mm TL and 100-150 mm TL, irrespective of their species. A maximum number of 30 eels was killed immediately after capture by sectioning the vertebral column to avoid regurgitation and placed on ice. If the number of eels caught during the regular sampling program was not sufficient for diet analysis, additional electrofishing took place in further randomly selected sections of the littoral zone. Stomachs were dissected and deep frozen until further processing could take place in the laboratory.

Stomach content analyses

Eel stomach contents were analysed by counting and measuring prey organisms using a combination of binocular and light microscopes. The biomass of invertebrate prey organisms was calculated using length-weight regressions (Mehner et al., 1995). Prey fish biomass was calculated from length-weight regressions determined for young fish caught by electrofishing. To calculate possible preferences for perch and roach as prey species of eel, the index of selectivity by Strauss (1979) was modified as follows: $L = r_i - p_i$, where L = linear index of selectivity, r_i = proportion on perch or roach on fish prey i (0 to 1) and p_i = proportion of perch or roach abundance i on perch and roach abundance (0 to 1). Values for the index of selectivity can range from –1 to +1. A positive value indicates preference for a certain prey species, a negative value avoidance.

Abiotic parameters

During the period from May to mid September water temperature (at 1 m depth in the littoral zone) was determined every 1 h by using T-loggers in both lakes (Lake Großer Vätersee: ONSET, Optic StowAway® temperature logger; Lake Vallum: TidbiT temperature logger). Secchi depth was determined regularly at six dates from May to October in Lake Vallum. Secchi depth and epilimnetic (0-6 m depth) chlorophyll-*a* concentrations were determined at biweekly intervals in Lake Großer Vätersee.

Trophic position calculation based on stable isotopes

The stomach content analyses in 2002 indicated that the large eels were highly specialist feeders: only 1.9 % of the eels showed a mixed diet. In order to prove whether the stomach content analysis really mirrored the eels' general feeding behaviour, additional samplings for stable isotope analyses were done in September (Lake Großer Vätersee) and October (Lake Vallum) 2004. The samples covered the whole benthic food web including eels, potential prey fish (perch, roach, tench (*Tinca tinca*), crucian carp (*Carassius carassius*), rudd (*Scardinius erythrophthalmus*) and ruffe (*Gymnocephalus cernuus*)), crayfish (*Orconectes limosus*), snails, mussels (*Anodonta* spec., *Sphaerium* spec.), trichopterans (*Molannidae*, *Limnephilidae*), chironomid larvae, *Asellus* *aquaticus*, tubifex larvae, macrophytes (*Chara* spec., *Ceratphyllum* spec.), filamentous green algae, reed (*Phragmites australis*), water lilies (*Nymphaea alba*) to detritus. Thirty six eels were sampled in Lake Großer Vätersee (Mean sizes ± S.D.: 46.1 ± 11.2 cm TL, size range: 30.0 – 88.0 cm) and 12 in Lake Vallum (Mean sizes ± S.D.: 40.8 ± 6.2 cm TL, size range: 30.6 – 57.2 cm).

Eel muscle samples and other potential food items were dried for 48 h at 70 ^{0} C, and ground to a fine powder using a mortar, pestle and liquid nitrogen. Only muscle tissue was used because of its slow turnover rate, resulting in a history of food assimilation over periods of months, thereby excluding short-term variability (Gearing 1991). Nitrogen stable isotope compositions were measured with a Carlo Erba NA 1500 elemental analyser with an interface (Conflo III) connected to a ThermoFinnigan DeltaPlus mass spectrometer. Nitrogen isotope rations are expressed in the delta notation (δ^{15}N) relative to Vienna PDB and atmospheric nitrogen. Average reproducibilities based on replicate measurements of standards for stable isotopes were about 0.15 ‰. As a standard for ^{15}N, ammonium sulphate IAEA-N-2 (=20.3) was used.

The N isotope values of the eel samples from the study lakes alone do not represent trophic position and cannot be directly compared. δ^{15}N of primary producers has been shown to be highly variable within lakes over time and among lakes (e.g. Kling et al., 1992; Toda & Wada, 1990; Cabana & Rasmussen, 1996). The eel's isotopic signature has to be measured relative to lake-specific "baseline" δ^{15}N signatures. Since unionid mussels are relatively large and long-lived primary consumers integrating temporal variability in primary producer δ^{15}N Cabana & Rasmussen (1996) interpreted fish δ^{15}N relative to unionid mussels representing the baseline δ^{15}N signature. Unionid mussel δ^{15}N values were measured for both study lakes. According to Vander Zanden et al. (1997), measures of trophic positions were calculated for both eel populations using the formula:

$$\text{Trophic position} = [(\text{fish } \delta^{15}\text{N} - \text{mussel } \delta^{15}\text{N})/3.4] + 2$$

where 3.4 represents a 1.0 trophic level increment in δ^{15}N .

Since the $\delta^{15}N$ value measured for mussels in Lake Großer Vätersee was extremely low indicating a strong use of bacteria as food, the lake specific "baseline" ^{15}N signature was estimated using the isotopic value of detritus using the formula:

Trophic position = [(fish $\delta^{15}N$ – detritus $\delta^{15}N$)/3.4] + 1

Littoral and pelagic isotopic end-member pathways were derived from the empiric isotopic signature of detritus and snails (Lake Großer Vätersee) and of mussels and snails (Lake Vallum), incorporating community-level enrichment values between trophic levels of +3.4‰ for $\delta^{15}N$ and =0.47‰ for $\delta^{13}C$ (Vander Zanden & Rasmussen , 2001).

A two-end-member mixing model was used to test for the importance of resource origin for the estimates of the eel's trophic position. To estimate the contribution of benthic and prey fish production to consumer population the following formula was used based (modified after Vander Zanden & Vadeboncoeur, 2002):

Percentage benthic contribution = $(\delta^{13}C_e - \delta^{13}C_{fp})/(\delta^{13}C_b - \delta^{13}C_{fp})$

where $\delta^{13}C_{e,}$ $\delta^{13}C_{fp,}$ and $\delta^{13}C_b$ are the mean $\delta^{13}C$ of the eels, fish prey, and benthic prey (chironomids), respectively. The model estimates the contribution of pelagic *tertiary* (fish prey) and benthic *secondary* (benthic prey) production.

Trophic position calculation based on dietary data

Estimates of the "trophic positions" of prey organisms were required to calculate the trophic positions of the eel populations in the study lakes. Calculations done in this study follow the procedure described by Vander Zanden et al. (1997). Primary producers are defined as trophic level "1", primary consumers as trophic level "2", etc.. Trophic interactions among invertebrates remain poorly understood (Vander Zanden et al., 1997), thus the simplest possible assumptions concerning the eel prey were used (Table 2) based on the littoral and pelagic end-member pathways estimated for both lakes. The trophic position of eel was calculated following Winemiller (1990) and Vander Zanden & Rasmussen (1996) (described in Vander Zanden et al., 1997). Dietary data of eels and the trophic position estimates for prey items were used to calculate the trophic positions for both eel populations using the formula:

$$T_a = \sum(V_i * T_i) + 1$$

where T_a = mean trophic position of the *a*th eel population, V_i = weight contribution of the *i*th prey item, T_i = and trophic position of the *i*th food item.

Statistics

Differences in fish abundance between the two lakes were analysed using Mann-Whitney U-tests. The proportions of empty stomachs and diet components were analysed by x^2 test. Differences in macrozoobenthos abundance between the two lakes were analysed by using Student's *t*-test. Significance level for all tests was set to $p < 0.05$. Freeware R statistical environment was used for all analyses (R Development Core Team, 2005).

Results

Macroinvertebrate density

No difference in the abundance of molluscs was observed between the two lakes (Table 1, Mann-Whitney U-test: $p = 0.615$), whereas the abundance of non-gastropod invertebrates was four times higher in Lake Vallum (Table 1, Mann-Whitney U-test: $p = 0.046$). The most important taxa within the non-gastropod invertebrates were chironomid larvae which made up more than 50% in both lakes, followed by Oligochaeta (23%) in Lake Vallum and Ephemeroptera in Lake Großer Vätersee (17%).

Prey fish density

Abundance of eel was 6 to 7 times higher in Lake Vallum (0.59 ± 1.52 ind. $PASE^{-1}$) than in Lake Großer Vätersee (0.09 ± 0.29 ind. $PASE^{-1}$, Mann-Whitney U-test: $p < 0.001$). The abundance of small prey fish (40-99mm TL) was significantly higher in Lake Vallum over the whole investigation period, but no difference in the abundance of larger (100-150 mm TL) fish was observed (Table 3) between the two lakes. Roach and perch made up 62% (total catch, $n = 477$) of the small and 57% (total catch, $n = 192$) of the larger sized group in Lake Großer Vätersee and were, with values of 90% (small) and 98% (large), also the dominant species within both groups in Lake Vallum (small group, $n = 703$; large group, $n = 170$). Other species, occasionally caught in both lakes, were rudd, pike, and bream, whereas tench, crucian carp, ruffe and bleak *Alburnus alburnus* were only caught in Lake Großer Vätersee.

Eel diet

A total of 225 eel stomachs were analysed during the investigation. Mean sizes (± S.D.) of eels analysed were 41.1 ± 10.4 cm TL for Lake Großer Vätersee ($n = 101$, size range: 30.0 – 77.0 cm) and 42.4 ± 6.4 cm TL for Lake Vallum ($n = 118$, size range: 30.0 – 72.5 cm). The proportions of eels with empty stomachs were not different between the lakes with 54 % empty in Lake Großer Vätersee and 49 % empty in Lake Vallum (x^2 test, $p = 0.624$). Only 1 out of 118 (0.8%) stomachs from Lake Vallum contained fish, whereas this proportion was 17.8% in Lake Großer Vätersee, which was significantly higher (x^2 test, $p < 0.001$). Only 2 eels out of 104 filled stomachs had a mixed diet of fish and invertebrates: one of these individuals was feeding on chironomids and fish, and the other on crayfish and fish. The size of piscivorous eels ranged from 32.5 to 77.0cm TL (mean ± S.D.: 43.8 ± 10.4). The average length (TL) of the piscivorous eels did not differ from the average length of all the eels analysed (paired *t*-test: $p = 0.367$). The length (TL) of eel prey fish ranged from 30 to 134 mm (mean ± S.D.: 66 ± 31 mm TL, $n = 19$).

During the study period, fish dominated the stomach contents by weight of eels in Lake Großer Vätersee, followed by the crayfish, larval chironomids and Gastropoda (Fig. 1a). Perch was the most important prey fish species (53% of the prey fish abundance in the eel diet), followed by ruffe, roach, bream, tench, crucian carp and pike. The eels in Lake Großer Vätersee showed a strong preference for perch as prey (*L* ± S:D.: 0.46 ± 0.02) and avoided roach (L ± S:D.: -0.46 ± 0.10) (Fig. 2). By pooling the data from June to October percent composition of the diet weight was 40% perch, 34% roach, 17% crayfish, 8% insect larvae, and 2% Gastropoda resulting in diet-based estimated trophic position of 4.14. The eels in Lake Vallum were found to feed almost exclusively on macroinvertebrates (Fig 1b). The dominant macroinvertebrate prey and prey item by number of eels in both lakes were chironomid larvae. Pooled eel diet data (June to October) revealed 93% insect larvae, 4% Gastropoda and 3% fish. The estimated trophic position for eels in Lake Vallum was with 3.13 one trophic level lower than those for the eels in Lake Großer Vätersee.

Isotopic analyses

The isotopic composition showed clear separation of the study lakes (Fig. 3, 4). Whereas Lake Lake Vallum appeared to be $\delta^{13}C$- depleted relative to Lake Großer Vätersee, $\delta^{15}N$ values were higher in Lake Großer Vätersee. It was possible to separate the invertebrates into trophic levels according to their $\delta^{15}N$ values in most cases but not all. For example, chironomids in Lake Großer Vätersee were positioned above mussels and snails whilst in Lake Vallum chironomids occupied a position between them. In both lakes fish were placed on top of the food web ($\delta^{15}N$ values) but the position of eels differed between the two lakes (Fig. 3, 4). In Lake Vallum all investigated fish species (perch, roach and ruffe) but not rudd were more ^{15}N-enriched than the eels. Eels in Lake Großer

Vätersee were most ^{15}N-enriched sharing this position with roach and the invertebrate predator *Chaoborus flavicans*.

The mean trophic position (based on δ^{15}N values) of eels in Lake Großer Vätersee was significantly higher (ANOVA, $p < 0.001$) than those estimated for eels in Lake Vallum (Table 4). Individual trophic positions of eels in Lake Vallum were at all TLs lower than those in Lake Großer Vätersee (Fig. 5). The estimates of the mean contributions of benthic (chironomid) carbon, as estimated using a δ^{13}C mixing model, resulted in 82% for eels in Lake Vallum and 37% for eels in Lake Großer Vätersee (Table 4) but were not significantly different (Wilcoxon signed-rank test, p = 0.28).

Discussion

The objective of the present study was to test whether relative availability of insect larvae and small sized fish between two lakes had an effect on the feeding habits of large eels. In the two selected lakes, feeding conditions differed quite markedly with respect to food abundance: density of both insect larvae and small fish being much higher in Lake Vallum than in Lake Großer Vätersee.

The most important prey items in terms of stomach content weight for large eels in the two lakes were larval insects (especially chironomids) in Lake Vallum, and fish in Lake Grosser Vätersee. Chironomid larvae were the most important invertebrate prey of eels in Lake Grosser Vätersee. The dominance of chironomids, and also the appearance of trichopterans and ephemeropterans as eel prey, has been observed in several other studies (Frost, 1946; Sina & Jones, 1967; Moriarty, 1979; De Nie, 1987). Although abundant in both lakes, molluscs were of minor importance as eel prey. Molluscs are known to be important prey of benthivores such as large roach and bream (Schiemer & Wieser, 1992, Hölker & Breckling 2001), but seem not to be targeted by eels. This might be explained by the fact that eels lack a feeding apparatus, cf. the pharyngeal bones of cyprinid fish, which might be used to crush the hard shells of molluscs.

Consumption of fish by eels has been found in several studies (Moriarty, 1972, 1973; Biro, 1974, Lammens et al., 1985). Fish clearly dominated the food of large eels in Lake Großer Vätersee, and small perch were the preferred species (Fig. 2). This finding is in accordance with findings of other studies (Radke & Eckmann, 1996; Dörner & Benndorf, 2003; Schulze et al., 2004). Juvenile perch are vulnerable to eel predation because they generally settle inactively on the bottom at night (Wang & Eckmann, 1994). This behaviour could be even more pronounced for small perch in Lake Großer Vätersee, where an introduction of pikeperch has led to a reduction of small perch activity at night (Hölker et al., submitted). In contrast to other studies (Schultz et al., 2004), the importance of fish as prey did not increase with increasing eel size.

Eels in Lake Vallum were found to feed almost exclusively on macroinvertebrates, although the availability of potential prey fish was high. We believe that the differences in diet composition between the two eel populations were caused by the difference in availability of larval chironomids. This contrasts with the feeding behaviour of large perch, which has also been described as an opportunistic feeder (Craig, 1987), consuming macroinvertebrates and fish. In a comparative study on the feeding patterns of large perch (25.5 to 37.5 cm TL) in two lakes of different environmental characteristics by Dörner *et al*. (2003), it was shown that prey fish and not macroinvertebrate availability determined diet composition. The contrary seems to be the case for large eels which can be explained by different daily activity patterns, foraging and hunting behaviours. Large perch are day-active hunters (Jacobsen et al., 2002), seeking their prey over relatively large areas, in open water. In contrast the eel is night-active, hugs the bottom , and has a daily foraging range that seldom extends over more than c. 40 m^2 (Baras et al., 1998).

Relatively low insect larvae abundance in Lake Großer Vätersee was linked to a high degree of piscivory by large eels. The high macroinvertebrate abundance in Lake Vallum, on the other hand, corresponded with its almost exclusive use as a food resource, irrespective of the fact that there was a highly abundant source of potential prey fish. A negligible percentage of the eels showed a mixed diet. This is in strong accordance with the studies of Lammens et al. (1985) and De Nie (1987) on feeding of eels < 35 cm TL in Lake Tjeukemeer. Eels there only switched to fish as prey when chironomid biomass was low and the need for resource partitioning with benthivorous bream high.

Trophic positions derived form dietary and stable isotope mixed end-member models showed the same pattern with higher trophic positions of eels in Lake Großer Vätersee. The dietary approach resulted in trophic positions being approx. 0.4 trophic levels higher than the mean $\delta^{15}N$ trophic position estimates. A possible explanation could that diet and isotope samples were not taken in the same period. More important, limitations of the dietary approach such as the requirement for assumptions of the trophic positions of prey items could be a possible error source. The different ways the two methods integrate variation in trophic position was also mentioned to be problematic in previous studies (Vander Zanden et al., 1997). Whereas $\delta^{15}N$ is considered to be a time-integrated measure also accounting for variation in feeding at lower levels, dietary data provide snapshots and the variability within the trophic position of prey items may not be not reflected in a predator’s trophic position based on a dietary estimation (Vander Zanden et al., 1997). Since the present study focuses on an omnivorous predator feeding on omnivorous prey items a high degree of variability is certainly given. However, detailed stomach content data for a large number of eels in both study lakes have been sampled throughout a year, and the dietary estimates were in close correspondence to the maximum $\delta^{15}N$ trophic positions indicating that the observed patterns estimated with both methods are robust.

The $\delta^{15}N$ trophic position of eel in Lake Vallum was lower than those of its potential prey fish reflecting its almost exclusive benthivorous feeding. A comparably trophic position of eel in an eutrophic shallow lake in Norfolk, U.K., has also been shown by Jones & Waldron (2003). In Contrast, eel in Lake Großer Vätersee exhibited a higher $\delta^{15}N$ trophic level than small perch its preferred prey fish. The eel's dietary based trophic position was even higher than those of > 20 cm TL perch (4.09) and only 0.2 trophic levels below those of pike (4.34) and pikeperch (4.36) (diet data taken from Schulze et al., in press) showing the eel being a member of the piscivorous guild and thus may be able to influence top-down processes in the pelagic food web. This was also reflected in the comparably low (37%) of benthic ^{13}C reliance in the eel's isotope signature. The percentage reliance of benthic ^{13}C accounted only for direct consumption. The eels fed on zoobenthos-supported small perch and roach (40% of small perch diet (Haertel et al., 2002); 10% of small roach diet (Hölker et al., 2002), thus total benthic contribution to the eel's signature was probably between 50 and 60%. Since both prey species were predominantly planktivorous (Haertel et al., 2002; Hölker et al., 2002) indirect planktivory of eel must have acoounted for a significant contribution to the eel's isotopic signature indicating a pelagic-benthic pathway with an energy flow from pelagic to benthic. Eel were thus able to couple pelagic and benthic food webs under the circumstance of low insect larvae density.

No significant difference between the benthic ^{13}C reliance in the eel's isotope signature of both lakes was observed likely caused by a wide variation in $\delta^{13}C$ values. A possible explanation could be heterogeneity in the high lipid content of their tissues (DeNiro & Epstein, 1997; cited in Jones & Waldron, 2003). The wide variation in $\delta^{13}C$ values can, however, also be interpreted as a reflection of omnivory on population level, and varied diet of the individual eels thus indicating for specialist feeding on either fish or invertebrate prey. This would also be in close correspondence to the nonmixed eel diet found in this study a phenomenon which has also been observed in previous studies (Lammens et al., 1985; De Nie, 1987).

In summary, the present study suggests that the availability of insect larvae strongly influences the feeding behaviour of large eels. As a result, piscivory of eels is negligible if macroinvertebrate (insects) availability is high. This can be the case even if the abundance of potential prey fish is high. Under circumstances of low insect larvae availability eels can be predominantly piscivorous and thus couple benthic and pelagic food webs.

Acknowledgements

The study was financed by the German Research Council (DFG; project numbers ME 1681/4-2) and the Danish Ministry of Food, Agriculture and Fisheries. We wish to thank C. Helms, M. Gramkow, M. Böhm and T. Eichhorn for technical support. We thank F. Hölker for very useful comments on a previous version of this paper.

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Table 1: Overview on variables measured in Lake Großer Vätersee and Lake Vallum. Data are combined from [1]Kasprzak et al. (2000), [2]Skovgaard (2002) and this investigation.

Variable	Lake Großer Vätersee	Lake Vallum
Mean depth (m)	5.2 (1)	2.1 (2)
Chlorophyll (µg l^{-1})	2.5 – 8.2 (Epilimnion)	12-110 (2)
Summer Secchi depth (m)	3 – 5	0.5-1.5 (2)
Mean summer Temperature (°C) in the littoral zone (1 m depth)	20.8	19.6
Young fish community	Roach and perch dominating	
Macrophyte cover (%)	ca. 21 (1)	0 (2)
Macrozoobenthos:		
Abundance excluding molluscs (Mean ± SD; ind. m^{-2})	678 ± 418	2,711 ± 1,089
Molluscs (Mean ± SD; ind. m^{-2})	800 ± 500	719 ± 555

Table 2. Estimated trophic positions values for prey items used in dietary calculations of trophic position in Lake Großer Vätersee (GV) and Lake Vallum (V).

Prey category	Estimated trophic position GV / V	Includes
Fish	3.3	Perch
	3.5 / 3.3	Roach
Omnivorous zoobenthos	2.1	Chironomids, other unidentified insect larvae
Molluscs	2.0	Gastropoda
Crayfish	2.5	Decapoda (*Orconectes limosus*)
Detritus	1.0	Detritus, plants, mud

Table 3. Comparison of the mean numbers ± S.D. of small (40-99 mm TL) and large (100-150 mm TL) potential prey fish per PASE point in Lake Großer Vätersee and Lake Vallum in 2002 (*n* = number of points, + = significant higher in Lake Vallum, -- = significant lower in Lake Vallum, n.s.: not significant, *: $p < 0.05$, **: $p < 0.01$, *** $p < 0.001$).

Month	Lake Großer Vätersee		Lake Vallum		
	mean ± S.D.	*n*	mean ± S.D.	*n*	*p*
Small prey fish (40-99 mm TL):					
June	2.3 ± 8.9	50	1.0 ± 4.4	79	n.s.
July	0.6 ± 1.3	80	4.1 ± 6.2	73	+ ***
August	1.1 ± 3.6	160	1.8 ± 2.7	88	+ ***
Sep./Oct.	1.6 ± 5.2	80	2.0 ± 5.2	85	+ *
whole period	1.3 ± 4.8	370	2.2 ± 4.8	325	+ ***
Large prey fish (100-150 mm TL):					
June	0.2 ± 0.5	50	0.3 ± 0.7	79	n.s.
July	0.5 ± 1.2	80	0.9 ± 1.8	73	n.s.
August	0.6 ± 4.1	160	0.2 ± 0.4	88	n.s.
Sep./Oct.	0.5 ± 1.4	80	0.7 ± 2.2	85	n.s.
whole period	0.5 ± 2.8	370	0.5 ± 1.5	325	n.s.

Table 4. Summary of mean stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) and mixing model results for the eels Lake Großer Vätersee (GV) and Lake Vallum (V). TP_s, trophic position (mean ± SD) based on $\delta^{15}N$ values; BC, percentage of benthic reliance into the isotopic signature; TP_d, trophic position based on dietary data; *n*, number of individuals.

	Lake	$\delta^{13}C$	$\delta^{15}N$	TP_s	Range TP_s	BR (%)	TP_d	*n*
Eels	V	-31.14 ± 0.7	11.25 ± 0.7	2.71 ± 0.2	2.44 – 3.08	82	3.13	12
Eels	GV	-22.55 ± 0.7	7.37 ± 0.9	3.74 ± 0.2	3.21 – 4.03	37	4.14	36

Figure captions

Figure 1: Diet composition of eel from (a) Lake Großer Vätersee and (b) Lake Vallum from June to September 2002. Numbers of stomachs analysed are indicated above the bars.

Figure 2: Index of selectivity ± SD (Strauss, 1979) for small perch and roach in the diet of eel in Lake Großer Vätersee in 2002.

Figure 3: Results of stable isotope analyses showing mean (±1SD) of $\delta^{13}C$ and $\delta^{15}N$ (%) for primary producers, invertebrates and fish in Lake Vallum.

Figure 4: Results of stable isotope analyses showing mean (±1SD) of $\delta^{13}C$ and $\delta^{15}N$ (%) for primary producers, invertebrates and fish in Lake Großer Vätersee .

Figure 5: Trophic positions in relation to TL of eels from Lake Großer Vätersee (bullets) and Lake Vallum (triangles) calculated using $\delta^{15}N$ methods. Data were fitted in a non-parametric smooth function according to Friedman (1984).

Figure 1

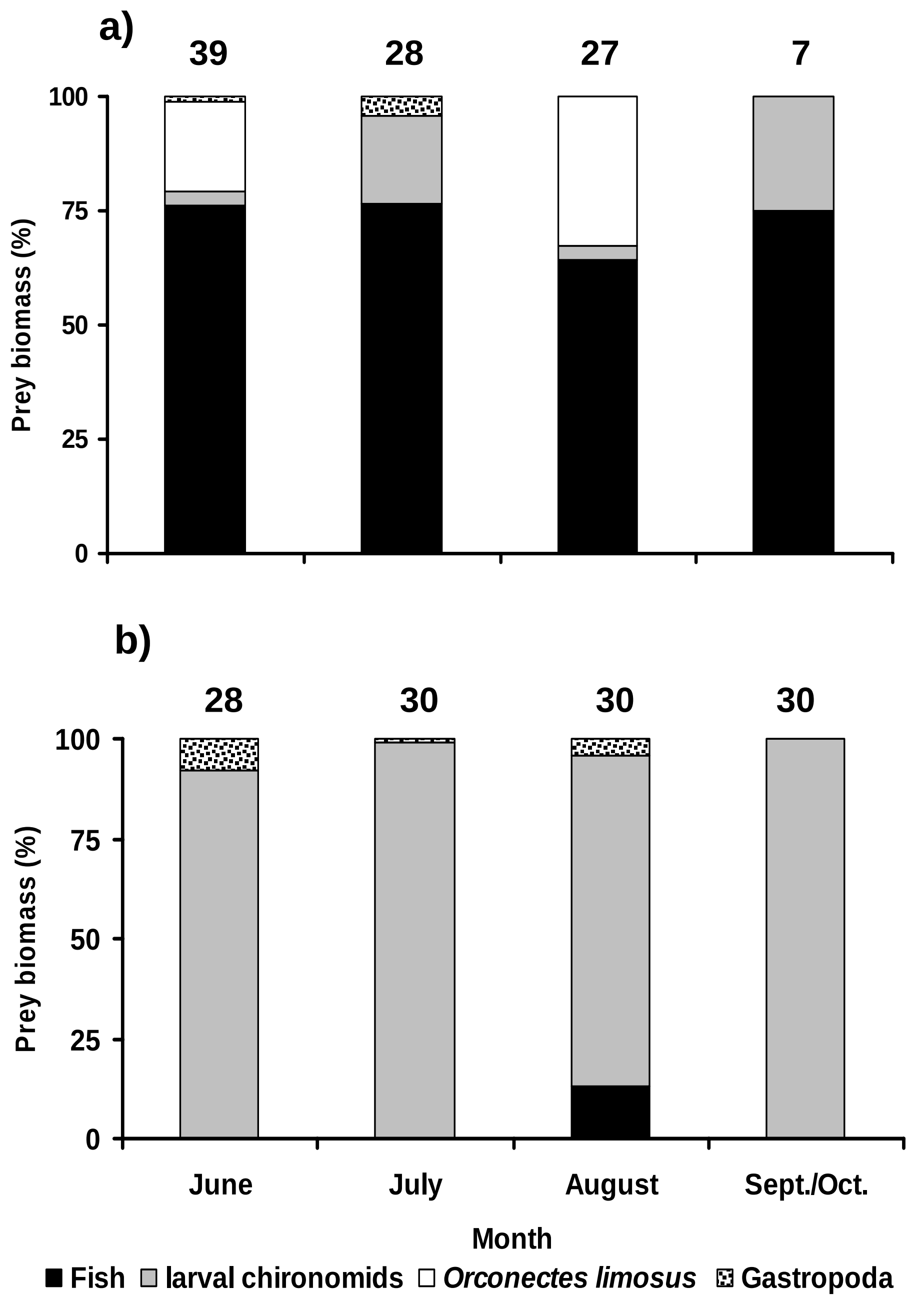

a)
39
28
27
7
100
75
50
25
0
Prey biomass (%)
b)
28
30
30
30
100
75
50
25
0
Prey biomass (%)
June
July
August
Sept./Oct.
Month
Fish
larval chironomids
Orconectes limosus
Gastropoda

Figure 2

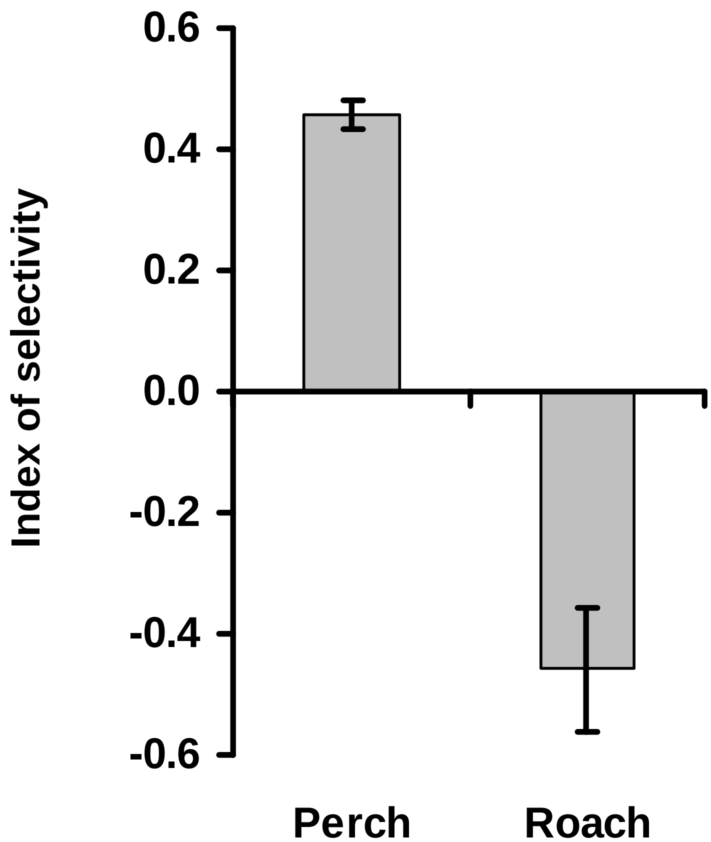
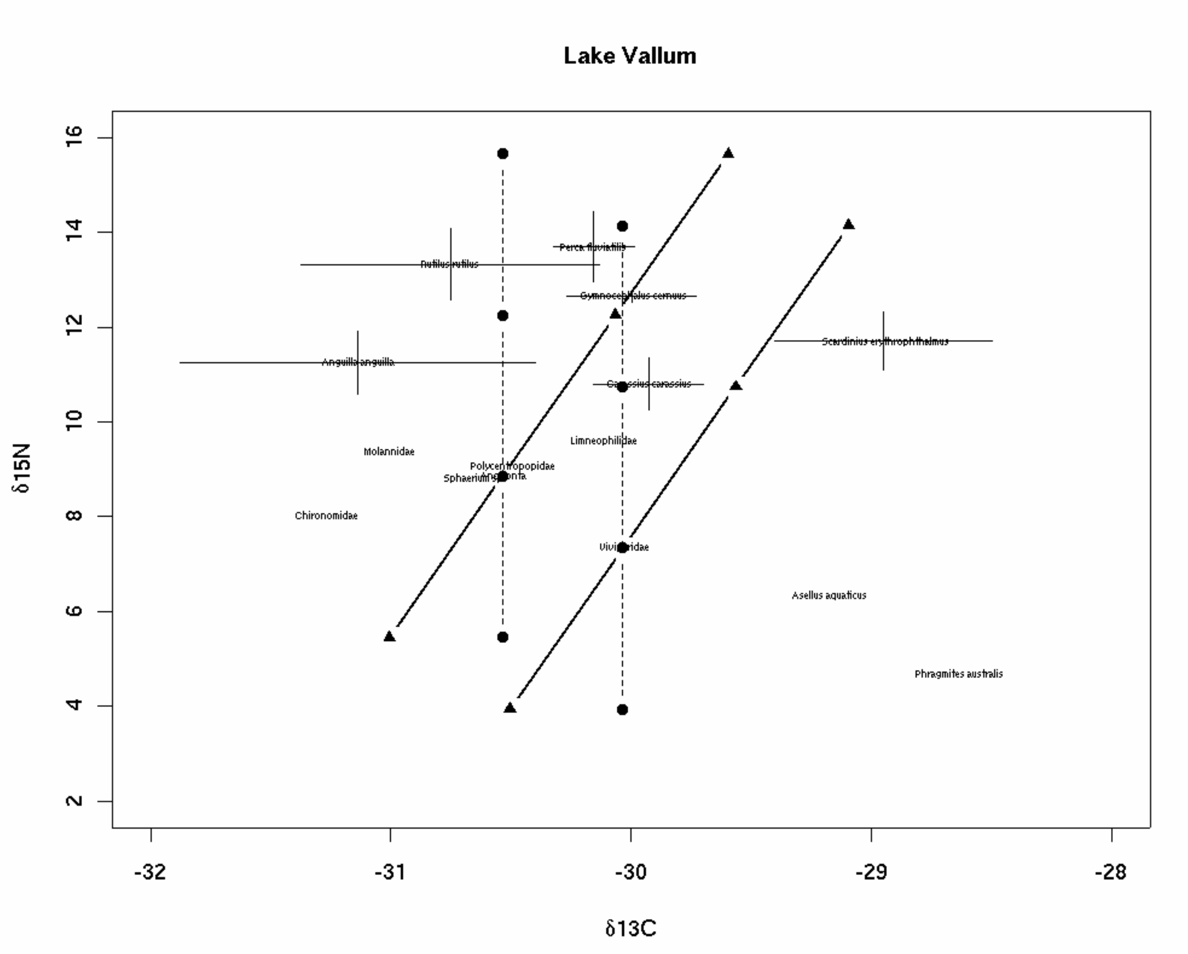


Figure 3



Lake Vallum
δ15N
δ13C
16
14
12
10
8
6
4
2
-32
-31
-30
-29
-28
Rutilus rutilus
Perca fluviatilis
Gymnocephalus cernuus
Scardinius erythrophthalmus
Anguilla anguilla
Carassius carassius
Limnephilidae
Molannidae
Polycentropodidae
Chironomidae
Viviparidae
Asellus aquaticus
Phragmites australis

Figure 4

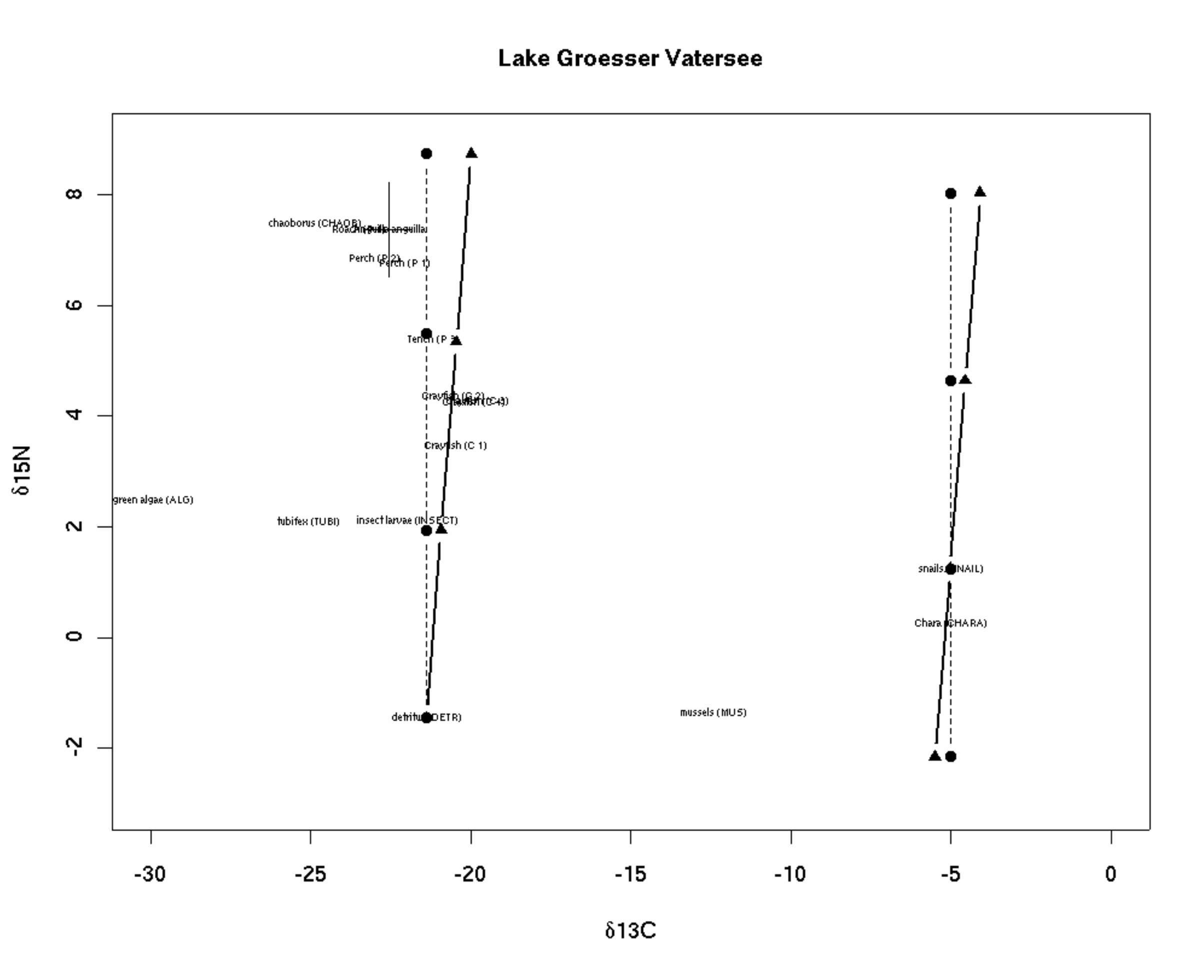
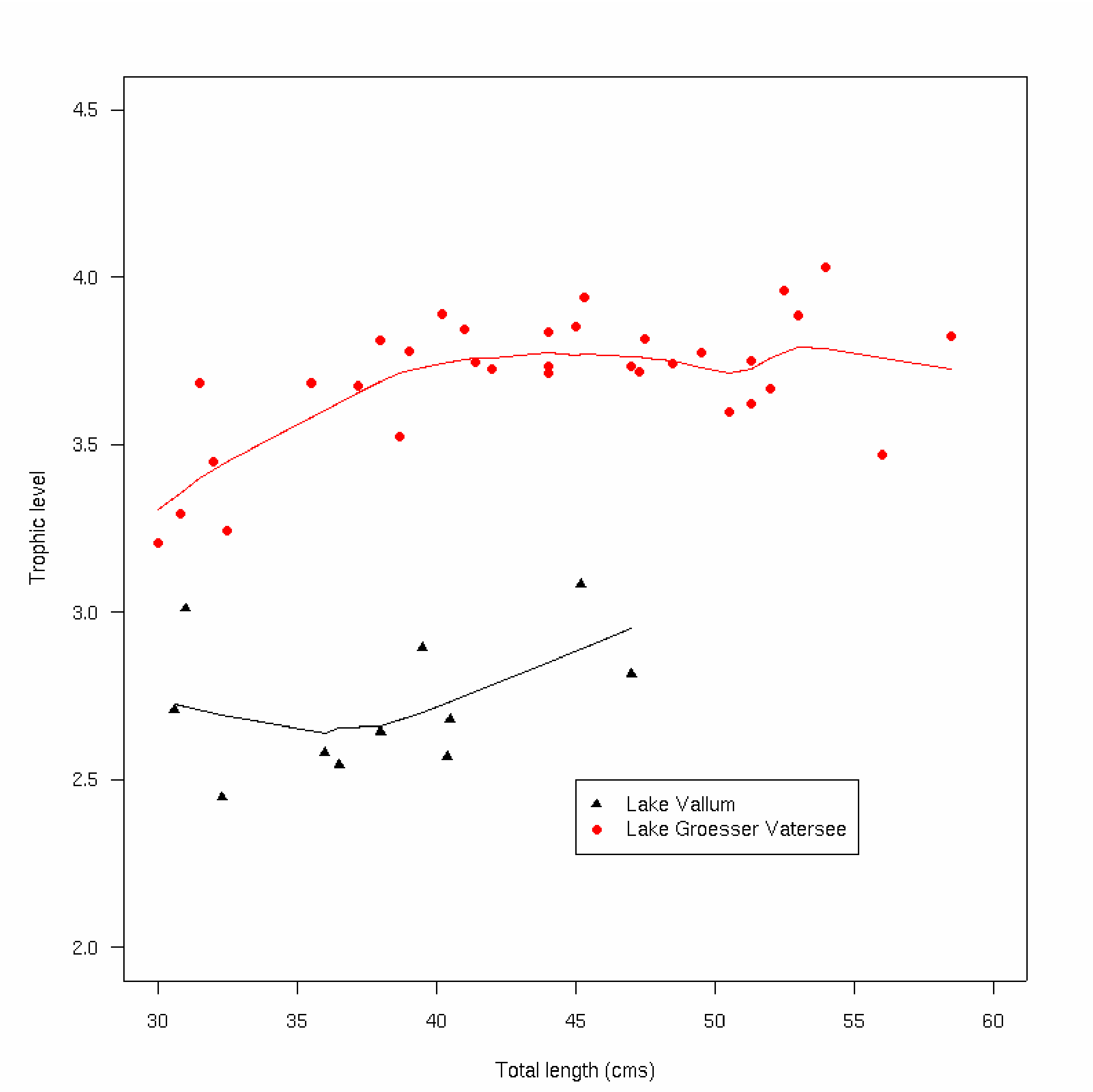

Lake Groesser Vatersee
chaoborus (CHAOB)
Perch (P 2)
Perch (P 1)
Tench (P 3)
Crayfish (C 2)
Crayfish (C 1)
green algae (ALG)
tubifex (TUBI)
insect larvae (INSECT)
snails (SNAIL)
Chara (CHARA)
mussels (MUS)
δ15N
δ13C
8
6
4
2
0
-2
-30
-25
-20
-15
-10
-5
0

Figure 5



4.5
4.0
3.5
3.0
2.5
2.0
Trophic level
30
35
40
45
50
55
60
Total length (cms)
Lake Vallum
Lake Groesser Vatersee