Arch. Hydrobiol. **167** 1–4 281–299 Stuttgart, September 2006

# Isotopic variation complicates analysis of trophic relations within the fish community of Plußsee: a small, deep, stratifying lake

**Chris Harrod**[1] and **Jonathan Grey**[1,2]

With 3 figures and 3 tables

**Abstract:** Analysis of carbon and nitrogen stable isotopes has allowed freshwater ecologists to examine lake food webs in increasing detail. Many such studies have highlighted the existence of separate within-lake pelagic and benthic-littoral food webs but are typically conducted on large ($>10\,km^2$) lakes, whereas the majority of lakes are actually relatively small. We used stable isotope analysis ($\delta^{13}C$ & $\delta^{15}N$) to examine trophic interactions between fish and their prey in Plußsee, as an example of a small, stratifying lake, and to determine whether separate pelagic/benthic-littoral food webs could be distinguished in such systems. Our results indicate that the Plußsee food web was complicated, and due to extensive intra-annual isotopic variation in zooplankton (e. g. cladoceran $\delta^{13}C$ annual range = 25.6 ‰), it may be impossible to definitively assign consumers from small, eutrophic stratified lakes to pelagic or benthic-littoral food webs. We present evidence that some components of the Plußsee food web (large bream) may be subsidised by carbon of methanogenic origin.

**Key words:** $\delta^{13}C$, $\delta^{15}N$, stable isotope analysis, food web, lake size, pelagic, benthic-littoral.

## Introduction

Over the past two decades, stable isotope analysis (SIA) has become increasingly used as a means of characterising food webs and trophic relationships between consumers and their energy sources in a range of ecosystems (McConnaughey & McRoy 1979, Rau et al. 1983, Tieszen & Boutton 1988, van Dover & Fry 1989, Eggers & Jones 2000). Much of our under-

[1] **Authors' addresses:** Department of Physiological Ecology, Max Planck Institute for Limnology, Postfach 165, 24302 Plön, Germany;
E-mail: harrod@mpil-ploen.mpg.de

[2] School of Biological Sciences, Queen Mary, University of London, London, E1 4NS, UK; E-mail: j.grey@qmul.ac.uk

DOI: 10.1127/0003-9136/2006/0167-0281 0003-9136/06/0167-0281 $ 4.75

standing of how consumer stable isotopes relate to patterns of consumption and predation has been produced from studies of large (e. g. $> 10\,km^2$) lake ecosystems (Estep & Vigg 1985, Yoshioka et al. 1994, Gu et al. 1996, Keough et al. 1996, Fry et al. 1999, Vander Zanden & Rasmussen 1999, Yoshii et al. 1999, Grey et al. 2001). Although large lakes are undoubtedly important globally due to their biological and hydrological functions and the ecosystem goods and services they provide to human populations (Wetzel 2001), their ecology may not be representative of the smaller lake systems that dominate the earth (Wetzel 1990, Lewis 2000, Vadeboncoeur et al. 2002). Although some studies have used stable isotopes to examine trophic relationships in small shallow lakes (e. g. Beaudoin et al. 2001, Jones & Waldron 2003) or along a gradient of lake area (Hecky & Hesslein 1995, Post 2002), these are comparatively rare and there is a definite need for further detailed studies of food webs of lakes that are more representative of the systems that are typically managed and utilised by humans (Wetzel 2001).

Wetzel (1990) noted that of the tens of millions of lakes on the earth, the majority have a surface area less than $10\,km^2$ and millions are smaller than $1\,km^2$. As an example of the dominance of smaller lake systems in some areas, in a recent survey of lakes in Great Britain, Hughes et al. (2004) reported that 95 % of lakes were smaller than $0.1\,km^2$. Apart from being small, most lakes (~ 90 %) are situated in temperate regions (Lewis 2000), and if conditions allow (e. g. depth, exposure to wind or inflowing water) are likely to undergo stratification during summer months (Hutchinson & Löffler 1956, Lewis 1983). Stratification has significant consequences for lake food webs – not least by modifying the availability of nutrients to primary producers, but also that hypolimnetic deoxygenation can restrict consumers to certain habitats (e. g. fish with elevated requirements for dissolved oxygen will be constrained to the epilimnetic zone).

Vadeboncoeur et al. (2002) suggested that the majority of lake ecologists wrongly focus on the importance of pelagic rather than benthic energy pathways to lake food webs. However, the use of stable isotope analysis to estimate the relative contribution of pelagic and benthic-littoral energy sources to lake food webs is growing (Hecky & Hesslein 1995, Vander Zanden & Vadeboncoeur 2002). These studies have exploited the apparent isotopic distinction between the two lake zones; benthic-littoral primary producers and their consumers tend to be enriched in $^{13}C$ relative to those from pelagic habitats by ca. 7‰ (Post 2002), a pattern that extends along a gradient of lake surface area and depth. However, it is unclear if the patterns shown by Post (2002) and others (France 1995, Hecky & Hesslein 1995) extend to all small lake systems. Using stable isotope analysis, we detail the food web of Plußsee, a small, stratifying lake in northern Germany.

# Methods

## Study site

Plußsee is a small but relatively deep eutrophic kettle lake [14.3 ha surface area, max. depth = 29.2 m, Zr (relative depth: WETZEL 2001) = 6.6 %] situated in Schleswig-Holstein, Germany (54° 10′ N, 10° 23′ E). Basin morphometry, the surrounding catchment and a densely wooded shoreline combine to protect the lake from wind mixing, allowing the development of very stable stratification. The typical limnological features of Plußsee have been described in detail by KRAMBECK et al. (1994).

The Plußsee fish community is dominated by dense stocks of perch *Perca fluviatilis* and roach *Rutilus rutilus*. Commonly recorded, but in lower numbers, are ruffe *Gymnocephalus cernuus*, European eel *Anguilla anguilla*, bream *Abramis brama,* pike *Esox lucius,* carp *Cyprinus carpio* and spined loach *Cobitis taenia*. Other, less common species, that were previously described (KRAMBECK et al. 1994, ARZBACH 1997) from the lake, but have not been captured in recent surveys, include: tench *Tinca tinca*, rudd *Scardinius erythrophthalmus*, sunbleak *Leucaspius delineatus*, bleak *Alburnus alburnus* and crucian carp *Carassius carassius*.

## Sampling methods

Temperature and oxygen concentration data were collected on a weekly basis during 2005 from a fixed station over the deepest point of the lake using a WTW probe. We collected bulk zooplankton every two weeks using a 250 µm mesh net towed through the surface waters (0–2 m) following a transect between the fixed station and the shore. Surface waters were sampled as both fish and zooplankton concentrate there during the bulk of the growth period of most fishes (KRAMBECK et al. 1994, ARZBACH 1997). Mussels and other macroinvertebrates were collected by pond net or Ekman grab from around the lake littoral. Crayfish (*Orconectes limosus*) were collected from fyke nets set for fish (see below).

Fish were captured using a combination of multipanel gillnets (modified S-type, Lundgrens Fiskredskapsfabrik) and summer fyke nets (Doppelreuse Typ 3, Engel-Netze GmbH & Co. Kg). Surface set gillnets were fished in the pelagic zone of Plußsee whilst bottom-set gillnets and fyke nets were set in the littoral zone in depths of 2–8 m. Nets were deployed overnight, and fish were removed from nets and returned to the laboratory on ice. Fork length (total length for eels) (± 1 mm) and blotted mass (± 0.1 g) were recorded.

## Sample preparation

Upon return to the laboratory, the bulk zooplankton was split and one part placed into filtered water for several hours to reduce the influence of gut contents on stable isotope results (FEUCHTMAYR & GREY 2003). The remainder was separated manually into calanoids, cyclopoids, cladocerans and *Chaoborus* using carbonated water to narcotise the organisms. Each group was then placed into filtered water as above. All separate zooplankton samples were filtered onto 25 mm Whatman GF/C filter papers. Mussels

and snails were separated from shell material, the digestive gland removed, and the remaining tissues macerated; other invertebrates were maintained alive in filtered water for several hours to allow for gut evacuation, except for crayfish which were sacrificed by freezing, prior to dissection of the tail muscle. Fish muscle was excised from above the lateral line and macerated. All samples for stable isotope analysis were oven-dried at 60 ˚C for 24 h, homogenised using an agate pestle and mortar, and stored in a desiccator.

Carbon and nitrogen stable isotope ratios were determined by continuous flow isotope ratio mass spectrometry. Stable isotope ratios are given using the δ notation expressed in units per mil as follows: $\delta\ (‰) = [(R_{sample}/R_{standard})-1] \times 1000$, and $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The reference materials used were secondary standards of known relation to the international standards of Vienna Pee Dee belemnite for carbon and atmospheric $N_2$ for nitrogen. Typical precision for a single analysis was ± 0.1 ‰ for $\delta^{13}C$ and ± 0.3 ‰ for $\delta^{15}N$.

As lipids are depleted in $^{13}C$ (DeNiro & Epstein 1977), any variation in lipid concentrations between fish species could influence comparisons of $\delta^{13}C$. Mean C : N ratios (a correlate of lipid concentration) varied both between (ANOVA: $F_{5,149} = 18.73$, $P < 0.001$), and within species: e. g. eel C : N values were positively correlated with length ($r = 0.85$, $P < 0.001$). Therefore, fish $\delta^{13}C$ data were arithmetically lipid-normalised according to Kiljunen et al. (in press). Kiljunen et al developed a modification of the McConnaughey & McRoy (1979) model that allows lipid-free $\delta^{13}C$ values for fish muscle tissues to be predicted from sample C : N and $\delta^{13}C$ values. Zooplankton and macroinvertebrate $\delta^{13}C$ values were left uncorrected.

## Results

During 2005, Plußsee exhibited an extremely stable and pronounced period of thermal stratification that extended between April and November – a characteristic of this water body (Krambeck et al. 1994). Anoxic conditions were first recorded from the hypolimnon in June (Fig. 1), and extended through to late November. The oxygenated epilimnetic zone extended to a depth of ca. 6 m for much of the summer.

### Stable isotope data

The mean isotopic composition of Plußsee consumers ranged extensively (see Fig. 2 and Tables 1 and 2): $\delta^{13}C$ values ranged between –56 ‰ and –18.7 ‰ ($range_{\delta 13C} = 37.3$ ‰), and $\delta^{15}N$ values between –7.8 and 10.9 ‰ ($range_{\delta 15N} = 18.7$ ‰). These ranges are strongly influenced by the depleted values recorded from the two chironomid species (see inset in Fig. 2). When the chironomid species are discounted, the range of $\delta^{13}C$ values remains large ($range_{\delta 13C} = 12.4$ ‰), but follows a pattern typical of temperate freshwater lakes spanning from the filter-feeder *Anodonta cygnea* (–31.1 ‰) to the littoral gastropod *Theodoxus fluviatilis* (–18.7 ‰). Without the inclusion of the chironomids, the

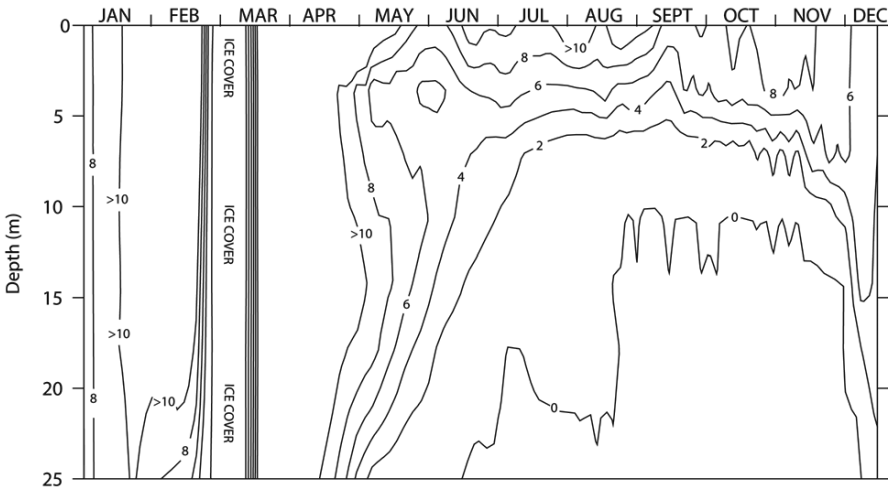


**Fig. 1.** Seasonal variation in the dissolved oxygen concentration (mg $l^{-1}$) of Plußsee during 2005. Note that for the bulk of the fish-growing period (e. g. May–October) Plußsee is stratified, with a hypoxic hypolimnon restricting potential habitat to fishes to areas ≤6 m.

**Table 1.** Mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values for various invertebrate taxa collected from Plußsee, with species code (see Fig. 2) and putative source of carbon. Note that two values are given for zooplankton: the first represents means calculated for the summer growth period of most fishes (see Fig. 3) and the second, an annual mean.

| Species (Code) | | Putative C source<br>P = Pelagic<br>B = Benthic<br>BL = Benthic-littoral | Mean $\delta^{13}C$ (±SD) | Mean $\delta^{15}N$ (±SD) | n |
|---|---|---|---|---|---|
| *Anodonta cygnea* (An) | | P | −31.1 (±1.53) | 5.5 (±0.83) | 7 |
| Calanoid zooplankton | April–August 2005 | P | −29.7 (±2.60) | 6.5 (±1.42) | 10 |
| | Jan–December 2005 | | −33.6 (±6.76) | 5.7 (±2.05) | 22 |
| *Chaoborus* (Cr) | April–August 2005 | P | −27.3 (±1.64) | 7.2 (±0.81) | 9 |
| | Jan–December 2005 | | −26.1 (±3.12) | 6.7 (±1.45) | 18 |
| Cladoceran zooplankton | April–August 2005 | P | −26.7 (±3.42) | 4.0 (±1.24) | 11 |
| | Jan–December 2005 | | −31.4 (±8.28) | 2.4 (±3.13) | 21 |
| Cyclopoid zooplankton | April–August 2005 | P | −29.0 (±3.63) | 3.6 (±1.50) | 9 |
| | Jan–December 2005 | | −32.0 (±5.55) | 6.1 (±1.53) | 19 |
| Mixed zooplankton (Zoo) | April–August 2005 | P | −29.0 (±2.45) | 6.0 (±1.11) | 30 |
| | Jan–December 2005 | | −30.9 (±6.82) | 4.8 (±2.88) | 66 |
| *Asellus aquaticus* (As) | | BL | −27.5 (±0.43) | 2.5 (±0.41) | 5 |
| *C. anthracinus* (*C. ant*) | | B | −41.8 (±2.34) | −2.8 (±1.38) | 10 |
| *C. plumosus* (*C. plu*) | | B | −56.2 (±2.25) | −7.8 (±0.60) | 10 |
| Crayfish *Orconectes limosus* (Cr) | | BL | −24.5 (±1.0) | 6.0 (±0.96) | 23 |
| Damselfly larvae (Da) | | BL | −25.8 (±1.04) | 4.8 (±0.21) | 4 |
| *Polycentropus* sp. larvae (Po) | | BL | −27.5 (±0.32) | 5.4 (±0.29) | 3 |
| *Theodoxus fluviatilis* (Th) | | BL | −18.7 | 5.1 | 1 |

**Table 2.** Mean $\delta^{13}C$ (lipid-corrected and uncorrected values shown) and $\delta^{15}N$ values for different fishes collected from Plußsee. Individuals of both bream and eel were separated into different length classes as both species showed significant correlations between fish length and $\delta^{13}C$ and $\delta^{15}N$. Dietary information taken from ARZBACH (1997). S – small, M – medium, L – large.

| Species | | Mean (±SD) lipid-corrected $\delta^{13}C$ (‰) | Mean (±SD) $\delta^{13}C$ (‰) | Mean (±SD) $\delta^{15}N$ (‰) | n | Size range (mm) | Principal diet in Plußsee (contribution by wet mass) |
|---|---|---|---|---|---|---|---|
| Bream | S | −23.2 (±0.44) | −26.0 (±0.32) | 8.4 (±0.45) | 3 | 205–250 | Chironomids, bivalves & |
| (*Abramis brama*) | M | −27.2 (±0.52) | −29.9 (±0.45) | 6.2 (±0.42) | 3 | 442–487 | gastropods |
| | L | −29.5 (±0.92) | −32.4 (±0.57) | 5.3 (±0.11) | 3 | 512–516 | |
| European eel | S | −23.7 (±0.93) | −25.1 (±1.10) | 7.5 (±0.45) | 4 | 405–464 | Fish & insect larvae |
| (*Anguilla anguilla*) | M | −23.0 (±0.50) | −24.4 (±0.72) | 8.4 (±0.53) | 8 | 479–644 | |
| | L | −22.8 (±0.20) | −27.3 (±0.53) | 10.0 (±0.36) | 4 | 716–820 | |
| Perch (*Perca fluviatilis*) | | −25.0 (±0.66) | −25.8 (±0.67) | 8.8 (±0.67) | 85 | 78–228 | <100 mm = Zooplankton<br>>100 mm = Zooplankton & fish |
| Pike (*Esox lucius*) | | −22.3 (±0.36) | −23.5 (±0.31) | 10.9 (±1.01) | 4 | 580–840 | Cyprinid fishes |
| Roach (*Rutilus rutilus*) | | −24.5 (±0.78) | −25.4 (±0.72) | 7.7 (±0.58) | 31 | 76–245 | Zooplankton & insect larvae |
| Ruffe (*Gymnocephalus cernuus*) | | −25.2 (±1.11) | −26.6 (±0.83) | 7.5 (±0.63) | 10 | 65–120 | Insect larvae |
| Spined loach (*Cobitis taenia*) | | −21.8 | −23.5 | 6.4 | 1 | 80 | Not recorded |

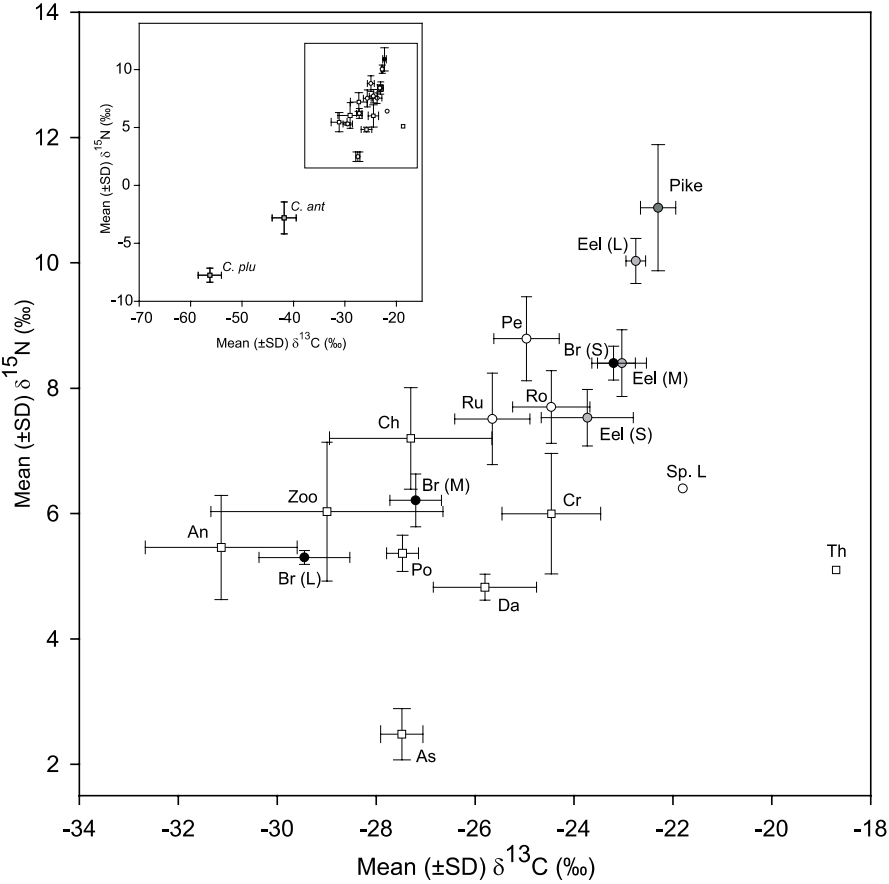


**Fig. 2.** Isotopic biplot showing mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ for different Plußsee consumers. Species codes: invertebrates (squares) – *Anodonta cygnea* (An), *Asellus aquaticus* (As), *Chaoborus* (Ch), crayfish (Cr), Damselfly larvae (Da), *Polycentropus* sp. larvae (Po), *Theodoxus fluviatilis* (Th), mixed zooplankton (Zoo); and fishes (circles) – bream (Br), eel, perch (Pe), pike, roach (Ro), ruffe (Ru) and spined loach (Sp. L). Eel and bream samples were divided into small (S), medium (M) and large (L) size categories. The inset shows the depleted isotopic signatures of larvae of two *Chironomus* spp. (*C. anthracinus* (*C. ant*) and *C. plumosus* (*C. plu*)) relative to the rest of the Plußsee food web.

range of mean $\delta^{15}N$ values falls ($range_{\delta 15N}$ = 8.4‰), from the benthic herbivore *Asellus aquaticus* (2.5‰) to pike (10.9‰).

## Invertebrates

Invertebrate consumer stable isotope values generally exhibited lighter $\delta^{13}C$ and $\delta^{15}N$ values relative to those of predatory fishes (but see values for large

bream). The mean $\delta^{13}C$ data lend some apparent support for segregation of invertebrates between pelagic and benthic-littoral energy sources: those considered to be part of the pelagic food web, e. g. *Anodonta* (mean $\delta^{13}C = -31‰$) and mixed zooplankton (−29.0‰) were $^{13}C$-depleted relative to macroinvertebrates typical of the benthic-littoral zone e. g. *Asellus* (−27.5‰), crayfish (−24.5‰), and Polycentropid (−27.5‰) and damselfly larvae (−25.8‰). Predatory taxa were $^{15}N$-enriched relative to herbivorous consumers. In benthic-littoral taxa, mean $\delta^{15}N$ in larval *Polycentropus* (5.4‰) and damselflies (4.8‰) were $^{15}N$-enriched by 2.3 – 2.9‰, and crayfish (6.0‰) by 3.5‰ compared to *Asellus* (2.5‰). *Chaoborus* (7.2‰) was $^{15}N$-enriched by only 1.2‰ relative to mixed zooplankton (6‰). All invertebrates were enriched in both $^{13}C$ and $^{15}N$ relative to the extremely depleted *Chironomus anthracinus* ($\delta^{13}C = -41.8‰$, $\delta^{15}N = -2.8‰$) and *C. plumosus* ($\delta^{13}C = -56.2‰$, $\delta^{15}N = -7.8‰$).

Summer and annual estimates of mean $\delta^{13}C$ and $\delta^{15}N$ for various zooplankton taxa included substantial variation around the mean (see standard deviations in Table 1 and Fig. 2). This variation was due to marked seasonal varia-

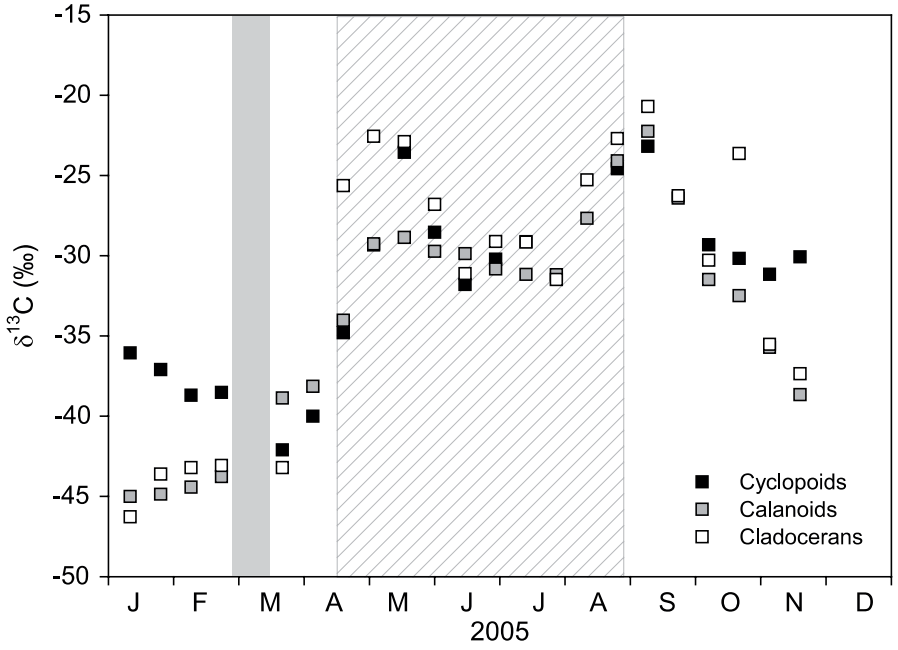


**Fig. 3.** Seasonal variation in Plußsee zooplankton $\delta^{13}C$ samples collected ca. fortnightly during 2005. The greyed bar shows the period of ice-cover, and the hatched area illustrates the period during which mean summer values were calculated for use in Fig. 2.

bility in both $\delta^{13}C$ and $\delta^{15}N$, typically showing a winter-depletion and summer-enrichment pattern (see Fig. 3 for $\delta^{13}C$ values). Within-taxa isotopic variation measured at each sampling date was low (e. g., mean SD calculated from mixed zooplankton: $\delta^{13}C = 0.68$, $\delta^{15}N = 0.44$).

Cladocerans exhibited the greatest amplitude in both $\delta^{13}C$ (25.6 ‰) and $\delta^{15}N$ (9.4 ‰), being most $^{13}C$-depleted during January but showing two peaks of $^{13}C$-enrichment in early May and early September. Calanoid copepods exhibited a similar seasonal pattern to cladocerans with a reduced amplitude ($\delta^{13}C$: 22.8 ‰, $\delta^{15}N$: 6.5 ‰) without a pronounced peak of $^{13}C$-enrichment in early May. Cyclopoid copepods were relatively $^{13}C$-enriched in January compared to other zooplankters and appeared to deviate from them again in November, but from March to October tracked the calanoids and cladocerans closely; thus, cyclopoids exhibited the least seasonal variability in isotope ratios ($\delta^{13}C$: 18.9 ‰, $\delta^{15}N$: 4.9 ‰). The most marked shifts occurred in the period immediately following ice-break, when cladoceran $\delta^{13}C$ increased by 17.6 ‰ in just four weeks (Fig. 3).

## Fishes

Mean stable isotope values differed between species (see Fig. 2 and Table 3). Lipid-normalised $\delta^{13}C$ values were enriched relative to untreated $\delta^{13}C$ values (Table 2). We used lipid-normalised $\delta^{13}C$ data for all statistical analyses due to significant variation in C : N ratios between individuals and species. Where significant correlations were shown between isotope values and size (e. g. bream and eels: Table 3), fish were classified according to size, based on percentiles of length measurements (see below).

Although comparisons were limited due to differences in sample sizes, there was clear statistical evidence of differences in mean $\delta^{13}C$ between the different fishes (ANOVA: $F_{5,149} = 25.7$, $P < 0.001$). A single spined loach was discounted from this and subsequent analyses due to lack of replication. Correlations between $\delta^{13}C$ and length were only significant for bream, which became increasingly $^{13}C$-depleted with size (Table 4: $r = -0.94$, $P < 0.001$). In the

**Table 3.** Relationships between fish size and carbon and nitrogen stable isotope values. Sample sizes are shown in Table 2.

| Species | Length v $\delta^{13}C$ | Length v $\delta^{15}N$ |
|---|---|---|
| Bream | $r = -0.94$, $P < 0.001$ | $r = -0.96$, $P < 0.001$ |
| Eel | $r = 0.45$, $P = 0.08$ | $r = 0.93$, $P < 0.001$ |
| Perch | $r = 0.09$, $P = 0.37$ | $r = 0.05$, $P = 0.68$ |
| Pike | $r = 0.88$, $P = 0.12$ | $r = 0.99$, $P = 0.005$ |
| Roach | $r = -0.33$, $P = 0.07$ | $r = 0.36$, $P = 0.05$ |
| Ruffe | $r = -0.56$, $P = 0.09$ | $r = 0.54$, $P = 0.11$ |

fish community as a whole, mean $\delta^{13}C$ values varied between −29.5‰ (large bream) and −21.8‰ (spined loach), a difference of 7.7‰. Of all the fishes, bream were most isotopically distinct, and mean $\delta^{13}C$ values recorded from both large and medium bream (−27.2‰) did not overlap with those of any other fishes. Amongst the remaining fishes, there was evidence of two separate clusters based on mean $\delta^{13}C$ values (Fig. 2 and Table 2). For instance, there was evidence of isotopic overlap between the mean $\delta^{13}C$ values of perch (−25‰), roach (−24.5‰), and ruffe (−25.2‰), which due to their lighter $\delta^{13}C$ values may imply partial foraging on pelagic food resources. The remaining fishes, eels (range of means −23.7 to −22.8‰), pike (−22.3‰), and small bream (−23.2‰) were more $^{13}C$-enriched suggesting a greater reliance on benthic-littoral food sources. On average, pike were enriched by 1.3‰ relative to other fishes, except for the medium and large bream, which we have not included in this comparison due to their large individual size effectively removing them from risk of predation by pike.

Mean $\delta^{15}N$ (Fig. 2 and Table 2) ranged between 5.3‰ (large bream) and 10.9‰ (pike), and varied significantly between species ($ANOVA_{\delta 15N}$ $F_{5,149}$ = 29.9, $P < 0.001$). There were significant correlations between $\delta^{15}N$ and length in bream ($r = -0.96$, $P < 0.001$), pike ($r = 0.99$, $P = 0.005$) and eel ($r = 0.93$, $P < 0.001$). To illustrate potential isotopic variation according to size, bream and eels were subsequently classified into small, medium and large size groups, using percentiles from length data: small ≤ 25 percentile, medium > 25 – ≤ 75 percentile and large > 75 percentile. Although a strong correlation was shown for pike, samples sizes were small and we did not classify them into size-groups.

Mean $\delta^{15}N$ values of both large and medium bream (6.2‰) were depleted relative to other fishes. Mean $\delta^{15}N$ values of roach, ruffe, and small eels were considered isotopically identical and overlapped (range = 7.5–7.7‰). Slightly enriched relative to these fishes were perch, medium eel and small bream, whose $\delta^{15}N$ values overlapped (range = 8.4–8.8‰). Large eels (10.0‰) and pike (10.9‰) were most enriched in $^{15}N$. Pike were enriched, on average by 2.9‰, relative to other fishes (again, not including large and medium bream).

## Discussion

Our stable isotope data could be loosely interpreted as providing evidence for the existence of separate pelagic and benthic-littoral food sources in the Plußsee food web, as shown in many other lakes worldwide (France 1995, Hecky & Hesslein 1995, Post 2002). However, the degree of isotopic separation between fish species, and the apparent truncation of the food web (if one excludes chironomids, see below) renders it extremely difficult to unravel

trophic linkages with any confidence from the isotope data alone. The problem stems from the fact that the zooplankton isotopic composition displayed extreme temporal variability, and at times during the summer of 2005 showed overlap with consumers typically considered part of the benthic-littoral food-web (see Table 1 and Fig. 3). Intra-annual variation in both zooplankton $\delta^{13}C$ and $\delta^{15}N$ has been shown in other lake systems, both large (YOSHIOKA et al. 1994, ZOHARY et al. 1994, GREY et al. 2001, PERGA & GERDEAUX 2005), and small (GU et al. 1999). However, the interannual isotopic variation described in these studies (median reported interannual amplitude in $\delta^{13}C = 8.8‰$) was typically far less extreme than that shown from Plußsee zooplankton (>25‰). Our data clearly demonstrate how variable zooplankton isotopic signatures can be in small deep stratifying lakes (for further discussion, see SANTER et al. 2006) and are likely to be in other highly productive stratifying lakes. Attempts to definitively assign fishes to pelagic or benthic-littoral food webs are further complicated because in small lakes like Plußsee fish are readily able to move between littoral and pelagic habitats and integrate energy from both (SCHINDLER & SCHEUERELL 2002, VANDER ZANDEN & VADEBONCOEUR 2002).

We calculated both annual and summer zooplankton mean $\delta^{13}C$ and $\delta^{15}N$ values in an attempt to qualify the pelagic baseline, and we compared these to *Anodonta*, which are recognised as long-term temporal integrators of pelagic production (CABANA & RASMUSSEN 1996). Mean annual zooplankton $\delta^{13}C$ and $\delta^{15}N$ values were actually rather consistent with *Anodonta* (Table 1) indeed indicating that assimilation had occurred throughout the year. If the mean values of *Anodonta* truly reflect the pelagic baseline, which is incorporated into fish, then it appears that very little of the Plußsee food web was reliant upon zooplankton, especially when one considers the biomass available during the summer [e. g. mean (± 95 % CI) biomass in 1981 = 5.4 (± 1.4) g $m^{-2}$ dry weight (calculated from data in KRAMBECK et al. 1994)]. Increasingly, there is the realisation that temperate fishes do not typically accumulate biomass throughout the year (CONOVER 1992, GRIFFITHS & KIRKWOOD 1995), and hence we chose to calculate a mean summer zooplankton $\delta^{13}C$ and $\delta^{15}N$ baseline more closely attuned to the period of fish growth (PERGA & GERDEAUX 2005). Even then, temporal isotopic variation was still high, and effectively, zooplankton overlapped isotopically with the majority of littoral-benthic baseline organisms at some point during the summer. Although we can be relatively confident of the existence of semi-separate littoral-benthic (e. g. *Asellus*/crayfish) and pelagic (*Daphnia/Chaoborus*) food webs, it is extremely difficult to accurately partition the relative contribution of pelagic and benthic-littoral energy sources to individual consumer taxa using mixing models (e. g. VANDER ZANDEN & VADEBONCOEUR 2002). For example, we estimated the approximate contribution of pelagic and littoral-benthic prey to the most common fish consumer (perch)

using a two-source isotope mixing model (PHILLIPS & GREGG 2001), with mean mixed zooplankton $\delta^{13}C$ as the pelagic end member, *Asellus* $\delta^{13}C$ as the littoral-benthic end member incorporating a trophic fractionation of 1‰ for each, and perch $\delta^{13}C$ as the mixture. Use of annual (−30.9‰) and summer (−29‰) mean mixed zooplankton $\delta^{13}C$ values as end-members indicated that zooplankton made no contribution to perch biomass. In order to provide an indication of the effects of interannual variation in zooplankton $\delta^{13}C$ values, the value of the zooplankton end member was adjusted to reflect mean mixed zooplankton $\delta^{13}C$ during four different time periods in 2005: January–March (mean $\delta^{13}C$ = −41.5‰), April–June (−30.3‰), July–September (−25.7‰) and October–December (−26.4‰). Results indicated that the variation in mixed zooplankton $\delta^{13}C$ was such that estimates of the contribution of pelagic prey to the assimilated diet of perch varied between 0 (January–March and April–June) and 100% (July–September and October–December).

MATTHEWS & MAZUMDER (2005) illustrate the potential difficulties of modelling fish trophic level (TL) due to intra-annual variation in zooplankton $\delta^{15}N$. Clearly, using conventional tissue samples taken from fish consumers for isotope analysis (i.e. muscle), it is extremely difficult to track the temporal variability shown by Plußsee zooplankton. A potential solution from an isotopic perspective would be to use tissues with faster turnover e.g. liver or blood (TIESZEN et al. 1983, HOBSON 1999, PERGA & GERDEAUX 2005). Although analyses of gut or stomach contents only provide a snapshot of consumer diet (GREY 2001), their use in parallel with stable isotope analyses would permit the use of a combined stable isotope/bioenergetics approach (HARVEY et al. 2002).

The Plußsee food web appears to be very short. For instance the total difference in mean $\delta^{15}N$ from the primary consumer *Asellus* to the top predator pike is 8.4‰. Using the typically quoted fractionation factor of 3.4‰ per trophic level (POST 2002), it appears that pike have a mean TL of 4.7, with only 2.7 trophic levels separating this top predator and the most $^{15}N$ depleted littoral primary consumer. If we switch to a consumer that is considered part of the pelagic, the food web appears even shorter. The mean $\delta^{15}N$ values for *Anodonta* sit only 5.4‰ below pike. Again, using a typical 3.4‰ trophic fractionation factor per trophic level, this indicates that the pelagic component of the Plußsee foodweb is extremely short – only 1.6 TL from primary consumer to top predator. To what degree the pelagic food chain is impacted by the zooplankton temporal variability, we are unable to say from our data. Note that in both of these cases, we have ignored the extremely isotopically depleted chironomids; although chironomids may be important as fish food in many lakes (e.g. LAMMENS et al. 1985, LAMMENS & HOOGENBOEZEM 1991), they occur in Plußsee in very low numbers (abundance < 50 ind $m^{-2}$, GREY, unpubl.) and appear to be restricted to a narrow band of sediment adjacent to the summer

oxycline (ca. 6 m). There was little evidence of them contributing substantially to the food web, except to the larger bream (see below).

Both putative food webs appear short, which indicate considerable omnivory by Plußsee consumers. It is difficult to conclude whether this is due to classical omnivory (i. e. consumers feed at more than one trophic level), multichain omnivory [i. e. consumers feed in both pelagic and benthic-littoral foodwebs (VADEBONCOEUR et al. 2005)], or is a consequence of isotopic variation at the base of the foodweb (Fig. 3). Omnivory is seemingly common in the food webs of small, shallow eutrophic lakes (BEAUDOIN et al. 2001, JONES & WALDRON 2003), but it is currently unclear how common it is in small, stratified lakes.

During 2005, Plußsee stratified following a pattern typical for the lake (KRAMBECK et al. 1994): initial thermal stratification appeared during April, subsequently followed by deoxygenation of the hypolimnon for much of the summer (Fig. 1), with the epilimnion extending to a depth of only 6 m. Due to intolerance of oxygen stress by most freshwater fishes (ALABASTER & LLOYD 1980), this indicates that almost 60 % of the potentially available habitat (by volume) were unavailable to the fish community (KRAMBECK et al. 1994) during the crucial summer growth period (CONOVER 1992). There are many reports in the literature of how stratification can restrict fish to epilimnetic areas, and prevent access to other potential habitats for different biological functions, e. g. foraging, predator avoidance and reproduction (COUTANT 1985, HEADRICK & CARLINE 1992, RAHEL & NUTZMAN 1994, AKU & TONN 1999, WANINK et al. 2001).

HEADRICK & CARLINE (1992) recorded pike encountering restricted foraging opportunities following lake stratification. Although typically considered a specialist predator of the macrophyte-open water interface, pike will switch habitats and forage in open water if conditions become unsuitable (JEPSEN et al. 2001). During periods of stratification, pike are often captured in pelagic areas of Plußsee, suggesting that densities of fish in the littoral may be reduced. However, the limited numbers of pike examined here were relatively enriched in $\delta^{13}C$, suggesting their diet was largely made up of fishes from a benthic-littoral source.

Perch, roach and ruffe all showed similar isotopic signatures, which could be perceived as evidence for dietary overlap (GENNER et al. 1999). However, pelagic (e. g. *Chaoborus* mean $\delta^{13}C = -27.3$ ‰) and benthic-littoral (e. g. *Asellus* mean $\delta^{13}C = -27.5$ ‰) prey often had similar isotope values, indicating that predator isotope signatures could be realised from more than one source. The level of isotopic variation in zooplankton effectively precludes attempts to definitively assign consumers to pelagic or benthic-littoral food web.

Fish populations often include groups of individuals that differ in their long-term foraging behaviour, either due to ontogenetic diet shifts or due to in-

dividual specialism (Grey 2001, Harrod et al. 2005). Typically, changes in isotopic signatures with increased individual size are often considered to provide evidence of ontogenetic dietary shifts (Grey 2001). Such patterns were not generally obvious in the Plußsee fish community (Table 3), although both eel ($\delta^{15}N$) and bream ($\delta^{13}C$ & $\delta^{15}N$) showed clear correlations between size and isotope values, but in opposite directions. Eels demonstrated a pattern of increased $\delta^{15}N$ with size, where the largest individuals had isotope signatures similar to pike, indicating increased piscivory with size. As noted above, bream demonstrated an opposite pattern to eels, and both $\delta^{13}C$ and $\delta^{15}N$ were negatively correlated with fish length. We suggest that SIA provides evidence for dietary segregation between different size classes of bream.

In situations where stratification leads to hypolimnetic deoxygenation, and subsequently reduces access to optimal habitat (referred to as habitat squeeze by Coutant 1985) some fishes may enter sub-optimal areas to forage (Malinin et al. 1992, Rahel & Nutzman 1994). Our isotope data may provide indirect evidence that some large bream are able to forage in deoxygenated areas. The most isotopically depleted component of the Plußsee food web comprised the two congeneric *Chironomus* species. This appears to be a common phenomenon in productive lakes which undergo stratification (Kelly et al. 2004, Deines & Grey 2006) and is suggested to reflect assimilation of $^{13}C$-depleted carbon associated with methanogenesis and methanotrophy (Grey et al. 2004); certainly, there is abundant methane resource produced in the sediments of Plußsee (Nüsslein & Conrad 2000). *Chironomus plumosus* was >25‰ ($\delta^{13}C$) and >13‰ ($\delta^{15}N$) depleted relative to *A. cygnea* and the remainder of the Plußsee food web (excluding its congener *C. anthracinus*). Thus, the distinct isotopic signature of these two chironomid species should allow for contributions from their biomass to be traced into the food web.

For the purposes of estimating dietary contributions of chironomids to large bream using a two-source isotope mixing model (Phillips & Gregg 2001), we assumed the end-members of the model to be mean chironomid $\delta^{13}C$ and *Asellus* $\delta^{13}C$ (incorporating a trophic fractionation of 1‰ for each), and bream $\delta^{13}C$ to represent the mixture. The model suggested that to exhibit such a $\delta^{13}C$ value, large bream would have to assimilate carbon from a diet comprising ~10% *C. plumosus* or ~21% *C. anthracinus* biomass. *Asellus* was chosen because it was the most $^{13}C$-depleted benthic-littoral invertebrate sampled and therefore the estimates for dietary contributions from chironomids derived from the model are likely to be conservative.

Bream are certainly capable of tolerating anoxic conditions for short periods, and Malinin et al. (1992) suggested that the movements into areas of low oxygen they recorded by acoustically-tagged bream were made in order to exploit chironomid larvae. Other benthivorous fishes do feed on chironomids in Plußsee (Arzbach 1997), but the isotopic evidence indicates that only large

bream are able to exploit the chironomids when they are found in sub-optimal areas at low densities. It is interesting that no eels were recorded with depleted $\delta^{13}C$ signatures. Eels are benthivorous, will compete with bream for chironomid prey (LAMMENS et al. 1985) and like bream, eels will make short foraging trips into deoxygenated waters (HARROD, unpubl.). A difference in foraging behaviours may explain why eels seemingly do not exploit chironomids from low-oxygen areas. Bream are extremely well adapted for feeding on sediment dwelling chironomids – they have specialised mouthparts that allow them to penetrate deep into sediments and to sort and retain food from sediments, and it appears they constantly sample sediments in order to locate aggregations of chironomids (LAMMENS & HOOGENBOEZEM 1991). Eels forage by olfaction (TESCH 2003), and may therefore not be able to locate sparsely distributed chironomids, that may be located deep in the sediments. The efficiency of bream foraging on buried chironomids is a function of fish size (LAMMENS & HOOGENBOEZEM 1991), and smaller bream may simply be unable to penetrate sediments to a suitable depth in order to exploit the chironomid resource. Hence, our data may provide isotopic evidence for ontogenetic niche shifts in bream.

## Conclusions

The use of stable isotope analysis to examine the food web of Plußsee, a stratified eutrophic lake demonstrated that patterns reported from studies of larger lake systems might not be representative of smaller lake systems. Isotopic variation in pelagic consumers (zooplankton) was extreme, and such that values overlapped with members of the putative benthic-littoral foodweb: during 2005, mixed zooplankton $\delta^{13}C$ values ranged between $-46.3$ and $-20.7$ ‰, precluding attempts to definitively assign consumers to pelagic or benthic-littoral food webs (cf. VANDER ZANDEN & VADEBONCOEUR 2002). We provide further evidence that food webs in small, productive lakes may be short (POST et al. 2000, BEAUDOIN et al. 2001, JONES & WALDRON 2003): this may be due to omnivory (VADEBONCOEUR et al. 2005) or to the influence of isotopic variation at the base of the foodweb.

Our data provide incidental evidence for population-level variation in the foraging strategies of eels (increased piscivory with size) and bream (use of deoxygenated habitats). The $^{13}C$-depleted signatures of large bream provide evidence that some methanogenic carbon is ultimately assimilated into the upper trophic levels of the Plußsee food web.

## Acknowledgements

The Max Planck Society provided funding. We would like to thank H. Deiwick, H. Paul-Wardenga, S. Dembeck and D. Albrecht for routine data collection, H. Buhtz, A. Möller and I. Dankert for sample preparation and stable isotope analyses. We would also like two anonymous reviewers for comments that strengthened the manuscript. Finally, Winfried – So long, and thanks for all the fish….

## References

Aku, P. M. K. & Tonn, W. M. (1999): Effects of hypolimnetic oxygenation on the food resources and feeding ecology of cisco in Amisk Lake, Alberta. – Trans. Amer. Fish. Soc. **128:** 17–30.

Alabaster, J. S. & Lloyd, R. (1980): Water Quality Criteria for Freshwater Fishes. – Butterworth Scientific, London and others.

Arzbach, H.-H. (1997): Untersuchungen zur allgemeinen Ökologie, Radioökologie, und Trophodynamik am Fischbestand des Plußsees in Schleswig-Holstein, Norddeutschland. – Ph. D. Thesis, University of Hamburg.

Beaudoin, C. P., Prepas, E. E., Tonn, W. M., Wassenaar, L. I. & Kotak, B. G. (2001): A stable carbon and nitrogen isotope study of lake food webs in Canada's Boreal Plain. – Freshwat. Biol. **46:** 465–477.

Cabana, G. & Rasmussen, J. B. (1996): Comparison of aquatic food chains using nitrogen isotopes. – Proc. Natn. Acad. Sci. U.S.A. **93:** 10844–10847.

Conover, D. O. (1992): Seasonality and the scheduling of life history at different latitudes. – J. Fish Biol. **41:** 161–178.

Coutant, C. C. (1985): Striped bass, temperature and dissolved oxygen: a speculative hypothesis for environmental risk. – Trans. Amer. Fish. Soc. **114:** 31–61.

Deines, P. & Grey, J. (2006): Site-specific methane production and subsequent midge mediation within Esthwaite water, UK. – Arch. Hydrobiol. **167:** 317–334, this issue.

DeNiro, M. & Epstein, S. (1977): Mechanism of carbon isotope fractionation associated with lipid synthesis. – Science **197:** 261–263.

Eggers, T. & Jones, T. H. (2000): You are what you eat... or are you? – T. R. E. E. **15:** 265–266.

Estep, M. L. F. & Vigg, S. (1985): Stable carbon and nitrogen isotope tracers of trophic dynamics in natural populations and fisheries of the Lahontan Lake system, Nevada. – Can. J. Fish. Aquat. Sci. **42:** 1712–1719.

Feuchtmayr, H. & Grey, J. (2003): Effect of preparation and preservation procedures on carbon and nitrogen stable isotope determinations from zooplankton. – Rapid Commun. Mass Spectrom. **17:** 2605–2610.

France, R. L. (1995): Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. – Limnol. Oceanogr. **40:** 1310–1313.

Fry, B., Mumford, P. L., Tam, F., Fox, D. D., Warren, G. L., Havens, K. E. & Steinman, A. D. (1999): Trophic position and individual feeding histories of fish from Lake Okeechobee, Florida. – Can. J. Fish. Aquat. Sci. **56:** 590–600.

Genner, M. J., Turner, G. F. & Hawkins, S. J. (1999): Niche separation among Lake Malawi cichlid fishes? Evidence from stable isotope signatures. – Ecology Letters **2:** 185–190.

Grey, J. (2001): Ontogeny and dietary specialization in brown trout (*Salmo trutta* L.) from Loch Ness, Scotland, examined using stable isotopes of carbon and nitrogen. – Ecol. Freshwat. Fish **10:** 168–176.

Grey, J., Jones, R. I. & Sleep, D. (2001): Seasonal changes in the importance of allochthonous organic matter to the diet of zooplankton in Loch Ness indicated by stable isotope analysis. – Limnol. Oceanogr. **46:** 505–513.

Grey, J., Kelly, A. & Jones, R. I. (2004): High intraspecific variability in carbon and nitrogen stable isotope ratios of lake chironomid larvae. – Limnol. Oceanogr. **49:** 239–244.

Griffiths, D. & Kirkwood, R. C. (1995): Seasonal variation in growth, mortality and fat stores of roach and perch in Lough Neagh, Northern Ireland. – J. Fish Biol. **47:** 537–554.

Gu, B., Alexander, V. & Schell, D. M. (1999): Seasonal and interannual variability of plankton carbon isotope ratios in a subarctic lake. – Freshwat. Biol. **42:** 417–426.

Gu, B., Schelske, C. L. & Hoyer, M. V. (1996): Stable isotopes of carbon and nitrogen as indicators of diet and trophic structure of the fish community in a shallow hypereutrophic lake. – J. Fish Biol. **49:** 1233–1243.

Harrod, C., Grey, J., McCarthy, T. K. & Morrissey, M. (2005): Stable isotope analyses provide new insights into ecological plasticity in a mixohaline population of European eel. – Oecologia **144:** 673–683.

Harvey, C. J., Hanson, P. C., Essington, T. E., Brown, P. B. & Kitchell, J. F. (2002): Using bioenergetics models to predict stable isotope ratios in fish. – Can. J. Fish. Aquat. Sci. **59:** 115–124.

Headrick, M. R. & Carline, R. F. (1992): Restricted summer habitat and growth of northern pike in two southern Ohio impoundments. – Trans. Amer. Fish. Soc. **122:** 228–236.

Hecky, R. E. & Hesslein, R. H. (1995): Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. – J. N. Amer. Benthol. Soc. **14:** 631–653.

Hobson, K. A. (1999): Tracing origins and migration of wildlife using stable isotopes: a review. – Oecologia **120:** 314–326.

Hughes, M., Hornby, D. D., Bennion, H., Kernan, M., Hilton, J., Phillips, G. L. & Thomas, T. (2004): The development of a GIS-based inventory of standing waters in Great Britain together with a risk-based prioritisation protocol. – Water Air Soil Pollut.: Focus **4:** 73–84.

Hutchinson, G. E. & Löffler, H. (1956): The thermal classification of lakes. – Proc. Natn. Acad. Sci. U.S.A. **42:** 84–86.

Jepsen, N., Beck, S., Skov, C. & Koed, A. (2001): Behavior of pike (*Esox lucius* L.) > 50 cm in a turbid reservoir and in a clearwater lake. – Ecol. Freshwat. Fish **10:** 26–34.

Jones, I. J. & Waldron, S. (2003): Combined stable isotope and gut contents analysis of food webs in plant-dominated, shallow lakes. – Freshwat. Biol. **48:** 1396–1407.

Kelly, A., Jones, R. I. & Grey, J. (2004): Stable isotope analysis provides fresh insights into dietary niche separation between larvae of *Chironomus anthracinus* and *C. plumosus*. – J. N. Amer. Benthol. Soc. **23:** 287–296.

Keough, J. R., Sierszen, M. E. & Hagley, C. A. (1996): Analysis of a Lake Superior coastal food web with stable isotope techniques. – Limnol. Oceanogr. **41:** 136–146.

Kiljunen, M., Grey, J., Sinisalo, T., Harrod, C., Immonen, H. & Jones, R. I. (in press): A revised model for lipid normalising $\delta^{13}C$ values from aquatic organisms, with implications for mixing models. – J. Appl. Ecol.

Krambeck, H.-J., Albrecht, D., Hickel, B., Hofmann, W. & Arzbach, H.-H. (1994): Limnology of the Plußsee. – In: Overbeck, J. & Chróst, R. (eds): Microbial Ecology of Lake Plußsee. – Springer-Verlag, New York, pp. 1–23.

Lammens, E. H. R. R., de Nie, H. W., Vijverberg, J. & van Densen, W. L. T. (1985): Resource partitioning and niche shifts of bream (*Abramis brama*) and eel (*Anguilla anguilla*) mediated by predation of smelt (*Osmerus eperlanus*) on *Daphnia hyalina*. – Can. J. Fish. Aquat. Sci. **42:** 1342–1351.

Lammens, E. H. R. R. & Hoogenboezem, W. (1991): Diet and feeding behaviour. – In: Winfield, I. J. & Nelson, J. S. (eds): Cyprinid Fishes: Systematics, biology and exploitation. – Chapman & Hall, London, pp. 353–376.

Lewis, W. M. (1983): A revised classification of lakes based on mixing. – Can. J. Fish. Aquat. Sci. **40:** 1779–1787.

– (2000): Basis for the protection and management of tropical lakes. – Lakes and Reservoirs: Res. Manage. **5:** 35–48.

Malinin, L. K., Kijaško, V. I. & Vääränen, P. L. (1992): Behaviour and distribution of bream (*Abramis brama*) in oxygen deficit regions. – In: Priede, I. G. & Swift, S. M. (eds): Wildlife Telemetry: remote monitoring and tracking of animals. – Ellis Horwood Ltd, Chichester, pp. 297–306.

Matthews, B. & Mazumder, A. (2005): Consequences of large temporal variability of zooplankton $\delta^{15}N$ for modelling fish trophic position and variation. – Limnol. Oceanogr. **50:** 1404–1414.

McConnaughey, T. & McRoy, C. P. (1979): Food-web structure and the fractionation of carbon isotopes in the Bering Sea. – Mar. Biol. **53:** 257–262.

Nüsslein, B. & Conrad, R. (2000): Methane production in eutrophic Lake Plußsee: seasonal change, temperature effect and metabolic processes in the profundal sediment. – Arch. Hydrobiol. **149:** 597–623.

Perga, M. E. & Gerdeaux, D. (2005): 'Are fish what they eat' all year round? – Oecologia **14:** 598–606.

Phillips, D. L. & Gregg, J. W. (2001): Uncertainty in source partitioning using stable isotopes. – Oecologia **127:** 171.

Post, D. M. (2002): Using stable isotopes to estimate trophic position: models, methods, and assumptions. – Ecology **83:** 703–718.

Post, D. M., Pace, M. L. & Hairston, N. G. (2000): Ecosystem size determines food-chain length in lakes. – Nature **405:** 1047–1049.

Rahel, F. J. & Nutzman, J. W. (1994): Foraging in a lethal environment: Fish predation in hypoxic waters of a stratified lake. – Ecology **75:** 1426–1253.

Rau, G. H., Mearns, A. J., Young, D. R., Olson, R. J., Schafer, H. A. & Kaplan, I. R. (1983): Animal $^{13}C/^{12}C$ correlates with trophic levels in pelagic food webs. – Ecology **64:** 1314–1318.

Santer, B., Sommerwerk, N. & Grey, J. (2006): Food niches of cyclopoid copepods in eutrophic Plußsee determined by stable isotope analysis. – Arch. Hydrobiol., (in press).

Schindler, D. E. & Scheuerell, M. D. (2002): Habitat coupling in lake ecosystems. – Oikos **98:** 177–189.

Tesch, F.-W. (2003): The Eel (Fifth Edition). – Blackwell Publishing, Oxford.

Tieszen, L. L. & Boutton, T. W. (1988): Stable Carbon Isotopes in Terrestrial Ecosystem Research. – In: Rundel, P. W., Ehleringer, J. R. & Nagy, K. A. (eds): Stable Isotopes in Ecological Research. – Springer-Verlag, New York, pp. 167–195.

Tieszen, L. L., Boutton, T. W., Tesdahl, K. G. & Slade, N. A. (1983): Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. – Oecologia **57:** 32–37.

Vadeboncoeur, Y., McCann, K., Zanden, M. & Rasmussen, J. (2005): Effects of multi-chain omnivory on the strength of trophic control in lakes. – Ecosystems **8:** 682–693.

Vadeboncoeur, Y., Vander Zanden, M. J. & Lodge, D. M. (2002): Putting the lake back together: reintegrating benthic pathways into lake food webs. – BioScience **52:** 44–54.

Vander Zanden, M. J. & Rasmussen, J. B. (1999): Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. – Ecology **80:** 1395–1404.

Vander Zanden, M. J. & Vadeboncoeur, Y. (2002): Fishes as integrators of benthic and pelagic food webs in lakes. – Ecology **83:** 2152–2161.

van Dover, C. L. & Fry, B. (1989): Stable isotopic compositions of hydrothermal vent organisms. – Mar. Biol. **102:** 257–263.

Wanink, J. H., Kashindye, J. J., Goudswaard, P. C. & Witte, F. (2001): Dwelling at the oxycline: does increased stratification provide a predation refugium for the Lake Victoria sardine *Rastrineobola argentea*? – Freshwat. Biol. **46:** 75–85.

Wetzel, R. G. (1990): Land-water interfaces: Metabolic and limnological regulators. – Verh. Internat. Verein. Limnol. **24:** 6–24.

– (2001): Limnology: Lake and River Ecosystems, 3rd Edition. – Academic Press, London.

Yoshii, K., Melnik, N. G., Timoshkin, O. A., Bondarenko, N. A., Anoshko, P. N., Yoshioka, T. & Wada, E. (1999): Stable isotope analyses of the pelagic food web in Lake Baikal. – Limnol. Oceanogr. **44:** 502–511.

Yoshioka, T., Wada, E. & Hayashi, H. (1994): A stable isotope study on seasonal food web dynamics in a eutrophic lake. – Ecology **75:** 835–846.

Zohary, T., Erez, J., Gophen, M., Berman-Frank, I. & Stiller, M. (1994): Seasonality of stable carbon isotopes within the pelagic food web of Lake Kinneret. – Limnol. Oceanogr. **39:** 1030–1043.

Submitted: 16 January 2006; accepted: 14 April 2006.