

Stable isotope analyses of the pelagic food web in Lake Baikal

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Abstract

Stable isotope ratios of various organisms were analyzed to elucidate food web structure in the pelagic zone of Lake Baikal. The pelagic food web of Lake Baikal is simple and consists of five major ecological groups: phytoplankton (*Aulacoseira baicalensis*), mesozooplankton (*Epischura baicalensis*), macrozooplankton amphipod (*Macrohectopus branickii*), fish (*Coregonus autumnalis migratorius* and four species of cottoid fishes), and seal (*Phoca sibirica*). Because of the low diversity and consequently small number of possible diets for each species, we were able to quantitatively estimate the diet composition of each animal with stable isotopes. Our carbon isotope data indicated that pelagic phytoplankton are the primary carbon source of the pelagic food web because $\delta^{13}\text{C}$ levels of animals were close to those of pelagic phytoplankton. The $\delta^{15}\text{N}$ levels of animals showed a clear trend of stepwise enrichment with trophic level according to the following equation: $\delta^{15}\text{N} (\text{‰}) = 3.3 (\text{Trophic Level} - 1) - 3.8$. In addition to interspecific food web analysis, important pelagic animals, such as *M. branickii*, two species of pelagic sculpin, *C. autumnalis migratorius*, and *P. sibirica*, were also examined, with emphasis on ontogenic diet changes. $\delta^{15}\text{N}$ levels of *M. branickii* and sculpins increased with body length, suggesting a change in feeding habits during growth. We demonstrate that carbon and nitrogen stable isotopes can be successfully applied to elucidate trophic relationships and conclude that the pelagic food web of Lake Baikal has an ideal, isotopically ordered structure.

Lake Baikal is located in the central part of southern Siberia (52–56°N, 104–110°E) at an altitude of 455.6 m above sea level. The lake is 635 km long and 80 km across at its widest point, covering an area of 31,500 km². Lake Baikal is endowed with many unique characteristics. First, the lake is the oldest in the world (20–25 million yr). Second, it is the deepest lake in the world, with a maximum depth of 1,637 m (Stewart 1990) and more than 80% of its area exceeding 250 m (Kozhov 1963). Lake Baikal contains as much as 20% of the world's freshwater (23,000 km³). As a result, Afanasyev (1960) reported that the residence time of water and major ions in the lake is about 330 yr. Lake Baikal is dimictic, with the surface water column turning over twice a year (Votintsev 1985). The surface layer, at least above 400 m, is known to be well mixed in May and October. Based on the vertical distribution of chlorofluorocarbons,

Weiss et al. (1991) estimated that the renewal time of the bottom water was ~8 yr. The third unique feature of Lake Baikal is that it has high dissolved oxygen concentrations in the bottom waters (Maddox 1989; Weiss et al. 1991). In contrast, large, ancient Lake Tanganyika is anoxic below 200 m. The high dissolved oxygen content of the bottom waters of Lake Baikal may have contributed to the evolution of a diverse biota; there are >2,000 species of animals in Lake Baikal, and two-thirds of them are endemic (Kozhov 1963).

The pelagic zone of Lake Baikal has several features that facilitate study of material transport and food web analysis by stable isotope composition: (1) transport of organic matter from the sediments is negligible because of extreme water depth, (2) transport of organic matter from coastal areas is minimal because of a thermal-bar system (Shimaraev et al. 1993), (3) horizontal material transport is limited compared to marine systems, (4) human impact is minimal, (5) few species inhabit the open water and thus the food web structure is relatively simple, and (6) seasonal $\delta^{13}\text{C}$ variation of the food base (phytoplankton) may be small because of the large amount of HCO_3^- in the system (66.5 mg/liter; Takamatsu et al. 1992). Therefore, the open water of Lake Baikal may be an optimal model ecosystem for stable isotope analyses.

Stable isotope analysis (SIA) can be used for both biological and nonbiological samples. Therefore, it can be a

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powerful tool to investigate energy flow through an ecosystem. SIA is also useful in analyzing food web structure, performing better than other approaches, such as gut content analysis. Although the feeding habits of aquatic organisms have frequently been assessed with gut content analysis and through feeding experiments, results from these approaches can be misleading if the gut contents are not completely assimilated (Kling et al. 1992). Furthermore, conventional stomach content analyses provide only instantaneous information on feeding habits at the time the organism was captured. In contrast, the isotopic signature of an organism provides integrated information about its feeding habits over significant time periods corresponding to taxon-specific organic carbon turnover times (Fry and Arnold 1982).

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of animals reflect their diets. Enrichment of $\delta^{15}\text{N}$ along the trophic network is widely recognized among most animals, including vertebrate and invertebrate taxa (DeNiro and Epstein 1981; Minagawa and Wada 1984). In contrast, the $\delta^{13}\text{C}$ of animals directly reflects their diet, with only slight enrichment ($<1\text{‰}$) during the feeding process (Rau et al. 1983; Fry et al. 1984). The isotopic composition of aquatic organisms can therefore provide useful information about food sources and trophic level. SIA has recently been used to examine energy flow through a variety of aquatic ecosystems, including lakes, estuaries, lagoons, and oceanic regions. However, only preliminary studies have been performed in Lake Baikal (Kiyashko et al. 1991; Kucklick et al. 1996). Data from these studies suggested that SIA would be useful for food web studies in this important lake. In this study, carbon and nitrogen isotope ratios of various pelagic organisms were measured to elucidate the structure of the pelagic food web. Our objective is to track the flow of energy through the pelagic ecosystem of Lake Baikal by establishing trophic relationships.

Materials and methods

Various kinds of pelagic organisms were collected at several sites in Lake Baikal during research expeditions performed on RV *Obruchev* (80 tonnes) from June to August 1992, 1993, and 1994 (Fig. 1, Table 1). We defined pelagic animals as those utilizing organic matter of pelagic origin as their dominant food sources and those mainly inhabiting the pelagic zone. Most of the fish samples were collected during the expeditions; however, some were obtained from fishermen in 1993. Seal samples were supplied by N. Miyazaki (University of Tokyo), who collected them on an expedition into the central and southern basins in May 1992. Their body length, weight, sex, and age were recorded by his group. Age was estimated from their teeth following the methodology of Kasuya (1976).

The lipid fraction of powdered biological samples (whole organisms in the case of planktonic samples and individual muscle tissue for fish and seals) was extracted and removed by filtration after leaving ($\sim 30\text{-mg}$) samples in 10 ml of chloroform:methanol (2:1) solution for about 24 h. These samples (2–8 mg) were then transformed into CO_2 and N_2 gases with the sealed-tube combustion method (Minagawa et al. 1984). The gases produced were separated and purified

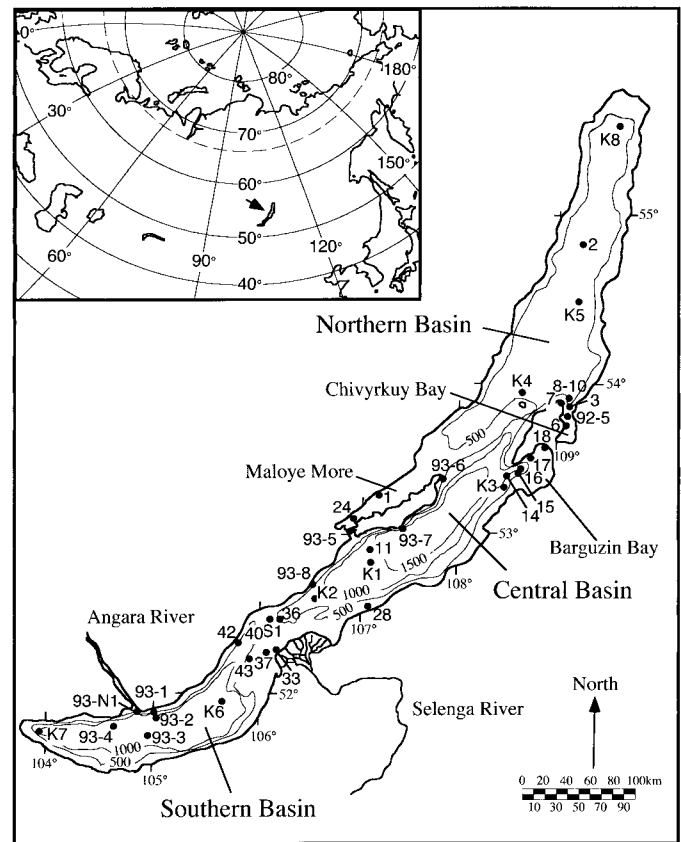


Fig. 1. Location of Lake Baikal and sampling stations.

cryogenically using a dry ice–ethanol trap and liquid nitrogen traps. The resulting N_2 and CO_2 gases were then collected in a glass tube for isotope analysis.

Nitrate in the water sample collected from the pelagic zone of Lake Baikal was reduced to ammonia by modified Kjeldahl distillation (Bremner and Edwards 1965). The ammonia was collected by steam distillation and oxidized to N_2 gas with hypobromite (Rittenberg 1946). The N_2 gas samples were further purified by passing them through two furnaces filled with copper (400°C) and cupric oxide (700°C) for 10 min.

Mass spectrometers (Delta-S and Delta-V, Finnigan-MAT) were used to analyze carbon and nitrogen stable isotope ratios. Isotope ratios are expressed as the deviation (‰) from a standard Pee Dee belemnite for carbon and atmospheric nitrogen gas for nitrogen:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N}(\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$$

where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$. Analytical precision was better than $\pm 0.2\text{‰}$ for nitrogen and $\pm 0.1\text{‰}$ for carbon. A laboratory standard of DL-alanine ($\delta^{13}\text{C} = -23.5\text{‰}$, $\delta^{15}\text{N} = -1.6\text{‰}$) was used as a running standard for isotopic measurements.

Results

$\delta^{13}\text{C}$ values of pelagic organisms exhibited a small range (-30 to -24‰), whereas $\delta^{15}\text{N}$ values were more variable

Table 1. Stable isotope ratios of planktonic samples.

Sta.	Date	Location	Water depth (m)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Remarks (sample no.)
Phytoplankton (composite sample)						
93-7	10 Aug 93	Central basin	1,000	-27.0		71
93-1	11 Aug 93	Southern basin	900	-28.8		80
93-2	22 Jul 93	Southern basin	55		4.2	8
93-5	2-4 Aug 93	Maloye More	11	-23.7		39
93-6	9 Aug 93	Central basin	3	-27.4		55
93-1	1 Apr 94	Southern basin		-29.5		B7p
Phytoplankton (Cyanophyta) <i>Gloetrichia echinulata</i>						
92-5	Jun 92	Chivirkuy Bay		-22.7±0.4 (2)	2.7±0.4 (2)	
Phytoplankton (Bacillariophyta) <i>Aulacoseira baicalensis</i>						
14	11 Jun 94	Central basin	1,286	-28.6		39p1
15	12 Jun 94	Central basin	620	-29.6	3.5	54p
16	12 Jun 94	Barguzin Bay	376	-28.6		70p
17	12 Jun 94	Barguzin Bay	110	-28.6		87p
18	12 Jun 94	Barguzin Bay	24	-28.8		99p
24	14 Jun 94	Maloye More	13	-17.7	5.0	100p
28	15 Jun 94	Central basin	57	-27.7		101p1
36	16 Jun 94	Central basin	300	-27.6	4.1	103p
37	16 Jun 94	Southern basin	100	-25.3		106p
40	16 Jun 94	Southern basin	500	-27.1		107p
33	16 Jun 94	Southern basin	25	-28.6		102p
43	17-18 Jun 94	Southern basin	1,137	-28.3	4.4	108p
Mesozooplankton (Calanoida) <i>Epischura baicalensis</i>						
93-7	10 Aug 93	Central basin	1,000	-26.6	7.1	73
93-1	11 Aug 93	Southern basin	900	-27.1	6.5	81
93-9	11 Aug 93	Southern basin	700	-26.8	6.6	79
93-8	11 Aug 93	Central basin	1,000	-26.6		76
93-2	22 Jul 93	Southern basin	55	-27.8	5.9	10
93-4	2-4 Aug 93	Southern basin	1,350	-26.9	6.5	21
93-5	8 Aug 93	Maloye More	11	-22.8	6.5	41
93-6	9 Aug 93	Central basin	3	-25.3	7.5	57
8	9 Jun 94	Chivirkuy Bay	210-260	-27.7	6.0	11p
94-11	10-11 Jun 94	Central basin	1,000	-26.6	7.2	35p
14	11 Jun 94	Central basin	1,286	-26.4	6.5	40p1
15	12 Jun 94	Barguzin Bay	620	-26.2	5.7	55p
16	12 Jun 94	Barguzin Bay	376	-25.4	6.5	71p
17	12 Jun 94	Barguzin Bay	110	-26.7	5.7	88p
36	16 Jun 94	Central basin	300	-25.8	7.5	104p
43	17-18 Jun 94	Southern basin	1,137	-27.2	7.0	109p
2	7 Jun 94	Northern basin	940	-29.9	6.6	4p
3	8 Jun 94	Chivirkuy Bay	225	-28.0	6.4	8p
10	9 Jun 94	Chivirkuy Bay	510	-26.0	5.6	23p
Mesozooplankton (Cyclopoida) <i>Cyclops kolensis</i>						
6	9 Jun 94	Chivirkuy Bay	6	-26.4	8.4	10p
28	15 Jun 94	Central basin	57	-26.5	7.2	101p2
43	17-18 Jun 94	Southern basin	1,137	-25.9	7.4	109p1

(4–16‰; Table 1, Figs. 2, 3). $\delta^{15}\text{N}$ values of the pelagic samples showed general trends of enrichment with trophic level from phytoplankton to seals. $\delta^{15}\text{N}$ of nitrate in water samples collected at a depth of 1,000 m in central Baikal was 3.0‰. The pelagic phytoplankton of Lake Baikal are generally dominated by the endemic diatom species *Cyclotella baicalensis*, *Cyclotella minuta*, and *Aulacoseira baicalensis* (Kozhov 1963). However, in 1994, *A. baicalensis* alone dominated, whereas in 1993, the phytoplankton con-

tained many European–Siberian species, including *Gloetrichia* sp. (Table 1). $\delta^{15}\text{N}$ of the cyanophyte *Gloetrichia* sp. collected in shallow water was less enriched than samples collected from deeper sites. $\delta^{13}\text{C}$ of *A. baicalensis* collected in a shallow bay (-17.7‰) was also more enriched than that of phytoplankton collected in the open water (-28.0 ± 1.1‰, $N = 11$), whereas the cyanophyte *Gloetrichia* sp. (collected in Chivirkuy Bay) had high $\delta^{13}\text{C}$ values of -22.7 ± 0.4‰. No clear difference was observed between the $\delta^{13}\text{C}$

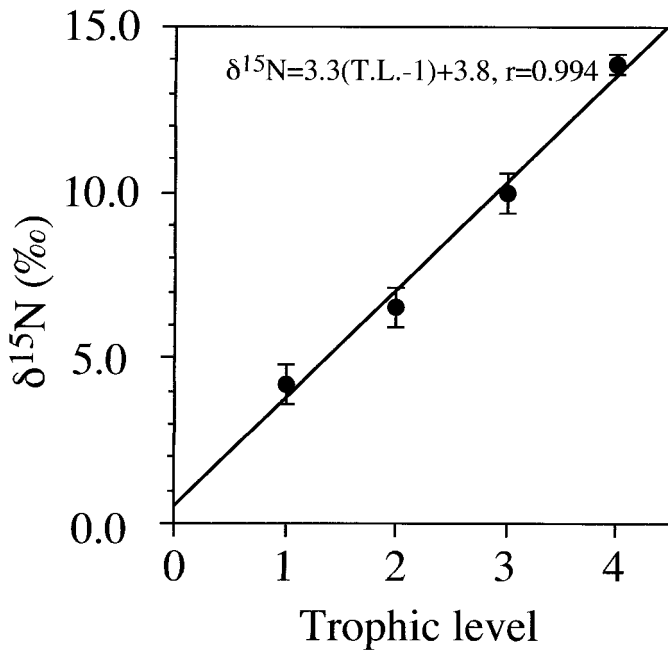


Fig. 2. Relationship between $\delta^{15}\text{N}$ and trophic level (T.L.) for the pelagic food web. Trophic level was estimated from our previous knowledge of each animal's feeding habits: phytoplankton, T.L. = 1; zooplankton (*E. baicalensis*), T.L. = 2; fish (*C. autumnalis migratorius*), T.L. = 3; seal (*P. sibirica*), T.L. = 4. Solid lines are derived from linear regression of the mean isotope ratio and trophic level.

of *A. baicalensis* in the open water of the southern and central basins. Similarly, no significant change in phytoplankton $\delta^{15}\text{N}$ was observed from April to August ($4.2 \pm 0.6\text{‰}$, $N = 4$; Table 1). Thus, the $\delta^{13}\text{C}$ signature of phytoplankton was relatively constant both spatially and temporally throughout the sampling period, except in the shallow water of the inner bays.

Epischura baicalensis was the dominant zooplankton species at most open-water sites. Although an enriched $\delta^{13}\text{C}$ value was observed in the shallow water of the inner bay (-22.8‰), the $\delta^{13}\text{C}$ values of pelagic *E. baicalensis* were constant ($-26.5 \pm 0.8\text{‰}$, $N = 18$). $\delta^{15}\text{N}$ of *Cyclops* sp. ($7.6 \pm 0.6\text{‰}$, $N = 3$) was enriched relative to pelagic *E. baicalensis* ($6.5 \pm 0.6\text{‰}$, $N = 17$). Finally, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the pelagic amphipod *Macrohectopus branickii* ($\delta^{13}\text{C} = -25.8 \pm 0.8\text{‰}$, $N = 91$; $\delta^{15}\text{N} = 7.8 \pm 1.0\text{‰}$, $N = 86$) generally increased with increasing body length (Fig. 4).

Four endemic sculpins (Comephoridae: *Comephorus baicalensis*, *Comephorus dybowskii*; Cottocomephorinae: *Cottocomephorus inermis*, *Cottocomephorus grewingki*) and one Coregonidae (*Coregonus autumnalis migratorius* [Omul]) inhabit the pelagic area of Lake Baikal. Variation in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *C. autumnalis migratorius* was small ($\delta^{13}\text{C} = -25.5 \pm 0.8\text{‰}$, $N = 21$; $\delta^{15}\text{N} = 10.0 \pm 0.6\text{‰}$, $N = 20$). $\delta^{15}\text{N}$ of this species was constant at $\sim 10.0\text{‰}$, changing little with body length (115–331 mm). Variation in $\delta^{15}\text{N}$ with size was also analyzed for two sculpin species (*C. baicalensis*, *C. dybowskii*). For both of these taxa, $\delta^{15}\text{N}$ in-

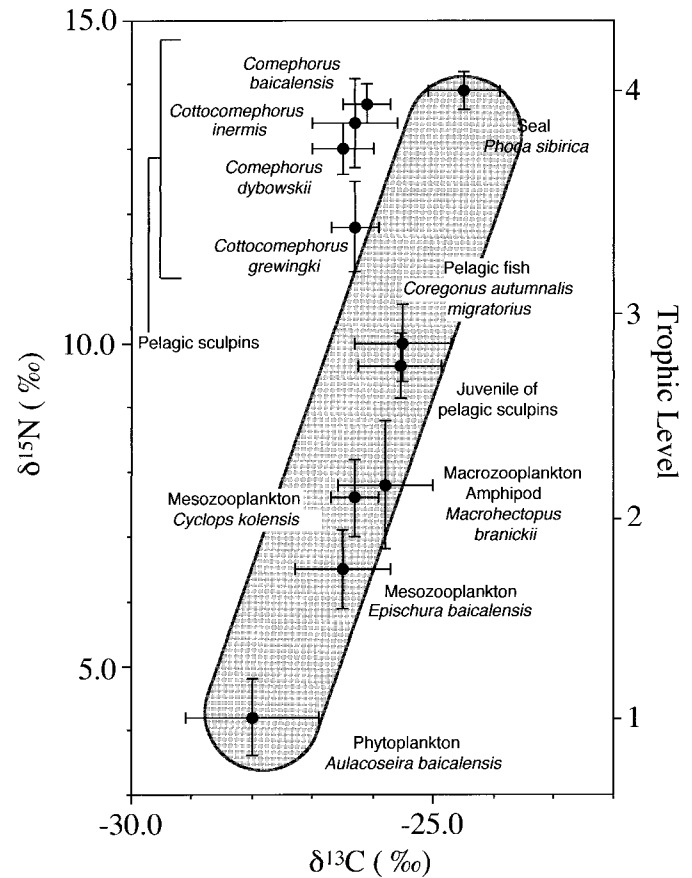


Fig. 3. $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ plot of pelagic organisms. ●, mean \pm SD.

creased with body length (Fig. 5). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of adult *C. inermis* ($\delta^{13}\text{C} = -26.1 \pm 0.4\text{‰}$, $N = 3$; $\delta^{15}\text{N} = 13.7 \pm 0.3\text{‰}$, $N = 3$) were more enriched than values of any other adult pelagic sculpin species (*C. baicalensis*: $\delta^{13}\text{C} = -26.3 \pm 0.7\text{‰}$, $N = 34$; $\delta^{15}\text{N} = 13.4 \pm 0.7\text{‰}$, $N = 33$; *C. dybowskii*: $\delta^{13}\text{C} = -26.5 \pm 0.5\text{‰}$, $N = 62$; $\delta^{15}\text{N} = 13.0$

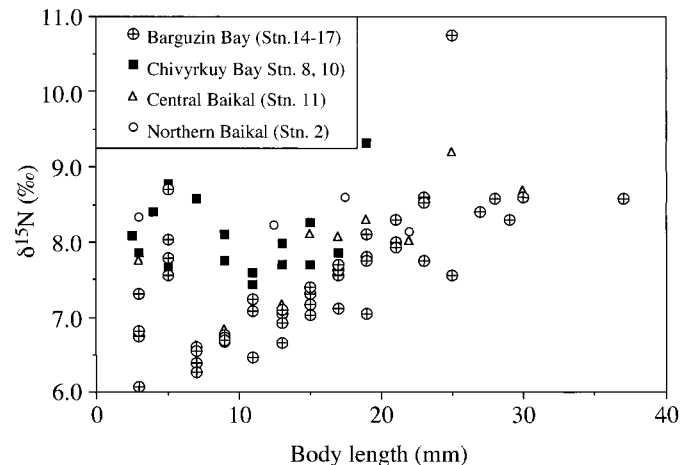


Fig. 4. Relationship between $\delta^{15}\text{N}$ and body length of *M. branickii*. Each point is a mean of several individuals.

$\pm 0.4\text{‰}$, $N = 59$; *C. grewingki*: $\delta^{13}\text{C} = -26.3 \pm 0.4\text{‰}$, $N = 6$; $\delta^{15}\text{N} = 11.8 \pm 0.7\text{‰}$, $N = 5$).

Forty-four individuals of the endemic seal *Phoca sibirica* collected from various regions of the lake were also analyzed for stable isotopes. The $\delta^{15}\text{N}$ value of seals depended on their age (Fig. 6). Seals older than 1 yr had a constant $\delta^{15}\text{N}$ value, but the $\delta^{15}\text{N}$ value of those <1 yr old was 1–2‰ higher than that of older animals and thus is one of the highest $\delta^{15}\text{N}$ values among the organisms we assessed. For older seals, no significant differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were observed among individuals, between sexes, or among locations ($\delta^{13}\text{C} = -24.5 \pm 0.6\text{‰}$, $N = 39$; $\delta^{15}\text{N} = -13.9 \pm 0.3\text{‰}$, $N = 39$).

Discussion

Stable isotope ratios of nitrate and primary producers—Carbon and nitrogen isotope ratios of phytoplankton vary spatially and temporarily according to environmental conditions (Wada 1980). The $\delta^{13}\text{C}$ value of aquatic plants, including microalgae, is determined largely by the plant's CO_2 assimilation systems (i.e., C3 vs C4 metabolism and growth rate). The $\delta^{13}\text{C}$ value of phytoplankton becomes enriched in temperate and tropical environments when the growth rate of phytoplankton is high (Sweeney et al. 1978; Wada et al. 1987). On the other hand, the $\delta^{15}\text{N}$ of phytoplankton is closely correlated with the form of nitrogen used for growth as well as with phytoplankton growth rate (Wada 1980).

Seasonal variability in $\delta^{13}\text{C}$ of plankton and particulate organic matter has been well studied in both freshwater (Yoshioka et al. 1994; Zohary et al. 1994; Hecky and Hesselein 1995; Bootsma et al. 1996) and marine systems (Rau et al. 1992). In general, the seasonal amplitude of phytoplankton $\delta^{13}\text{C}$ is large in freshwater ecosystems. For example, Zohary et al. (1994) reported seasonal $\delta^{13}\text{C}$ variations in planktonic organic matter ranging from -5.3 to -20.0‰ in various freshwater ecosystems. In contrast, the seasonal change of phytoplankton $\delta^{13}\text{C}$ in open waters of Lake Baikal from April to June was negligible, with $\delta^{13}\text{C}$ almost constant at around -28‰ (Table 1). Nakatsuka et al. (1992) reported dynamic changes in $\delta^{13}\text{C}$ ratios of suspended and sedimented particulate organic matter in a controlled ecosystem enclosure. They suggested that the main factor controlling variation in the $\delta^{13}\text{C}$ level of particulate organic matter during phytoplankton blooms was not a change in the CO_2 system or phytoplankton community composition but a change in phytoplankton growth rates. According to Takamatsu et al. (1992), the main ionic components in Lake Baikal waters are Ca^{2+} (15.7 mg/liter) and HCO_3^- (66.5 mg/liter) with a large quantity of carbonate was present in the water. Thus, the growth rates of phytoplankton may not be restricted by a shortage of inorganic carbon in the open water, and constant isotope discrimination ratios may contribute to the relatively constant $\delta^{13}\text{C}$ value of phytoplankton from April to June. Small geographical variation may also have contributed to the uniformity of $\delta^{13}\text{C}$ ratios. Except for stations located very close to the lake shore in littoral bays (Sta. 24 in Fig. 1), $\delta^{13}\text{C}$ is almost constant (Table 1). According to Descolas-Gros and Fontugne (1990), a high $\delta^{13}\text{C}$ value of

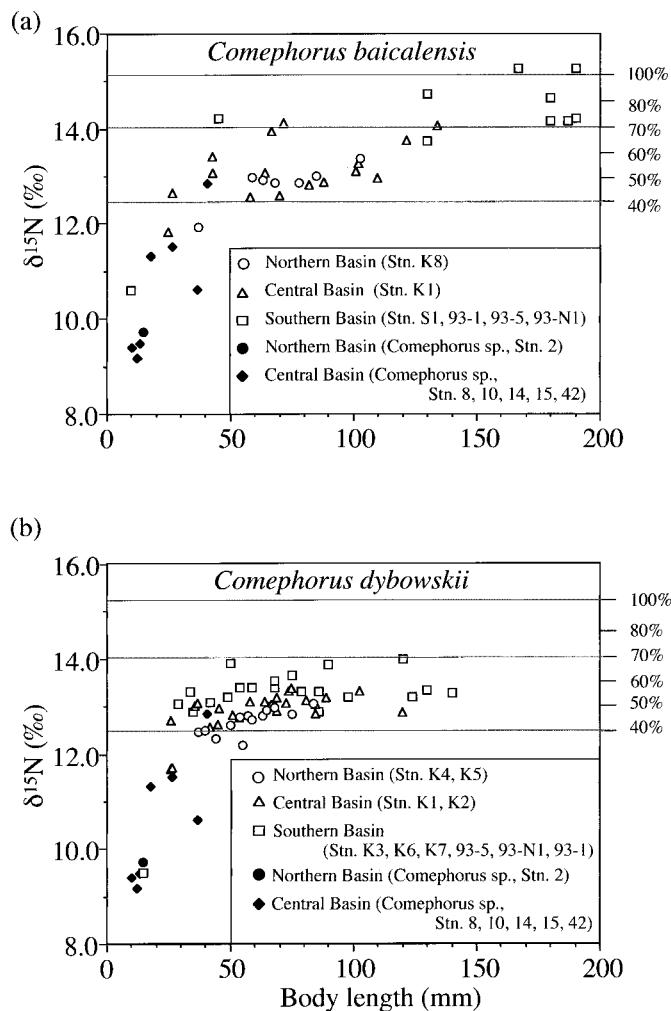


Fig. 5. Relationships between $\delta^{15}\text{N}$ and body length of pelagic sculpins *C. baicalensis* (a) and *C. dybowskii* (b) collected at various locations. Solid lines denote the percentage of pelagic sculpin larvae (body length, <30 mm) contributing to their diets. Data were calculated assuming that the diet of each fish is composed of *M. brankii* and pelagic sculpin larvae having average $\delta^{15}\text{N}$ values. Each symbol corresponds to an individual except for those whose body length is <20 mm.

phytoplankton near the lake shore of littoral bays may be associated with low CO_2 diffusion rates relative to photosynthetic CO_2 fixation in aquatic environments, which suppress the occurrence of carbon isotopic discrimination. In addition to the small geographical variation, we observed little seasonal (from April to June) variation in phytoplankton $\delta^{13}\text{C}$. This is an exceptional feature among freshwater ecosystems, and thus Lake Baikal's pelagic ecosystem is clearly advantageous for steady-state food web analysis using stable isotopes.

On the other hand, $\delta^{15}\text{N}$ of nitrate collected at a depth of 1,000 m in the central basin of Lake Baikal was 3.0‰, whereas that of postbloom phytoplankton was 4.0‰ on average. A fractionation factor of 1.005 has been reported for nitrate uptake processes by phytoplankton under high nitrate concentrations (>10 $\mu\text{g N/liter}$) in the boreal marine system

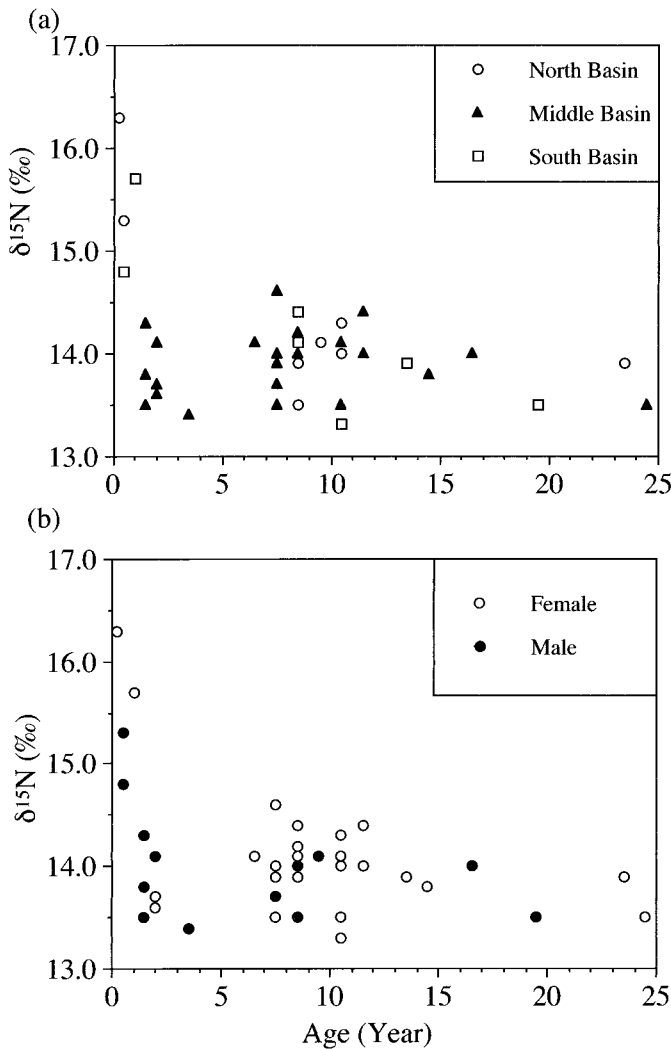


Fig. 6. Relationship between the $\delta^{15}\text{N}$ value of seals (*P. sibirica*) and age (a) and sex (b). Each symbol denotes an individual.

(Wada and Hattori 1991). Lake Baikal is dimictic, and vertical mixing down to 300 m in the spring and autumn supplies nutrients to the upper layers (NO_3^- , 0.33 mg/liter; PO_4^{3-} , 0.033 mg/liter; SiO_2 , 1.8 mg/liter at 300 m depth; Wada et al. 1995). After the vertical mixing of lake water in May, the $\delta^{15}\text{N}$ level of nitrate is uniform throughout the water column. From June to August, almost all nitrate in the euphotic zone is consumed by phytoplankton. Surface nitrate and phosphate concentrations were 0.05 and 0.001 mg/liter, respectively, at the beginning of July 1992 yet were below detection limits by the end of the month (Wada et al. 1995). Watanabe (1994) reported that enrichment of NO_3^- and PO_4^{3-} into the surface water of Lake Baikal enhanced the chlorophyll concentrations significantly. Although no precise examination has been made to determine whether primary production is limited by light, inorganic nitrogen, or phosphorus, clearly we would not expect the occurrence of nitrogen isotope fractionation during the uptake of nitrate, because almost all nitrate was used for primary production. Therefore, phytoplankton $\delta^{15}\text{N}$ values in Lake Baikal just

after the vertical mixing of water (June) might reflect the $\delta^{15}\text{N}$ signature of deep-water nitrate. Because our sampling of *A. baicalensis* was performed just after its blooming stage, when almost all inorganic nitrogen was consumed, it could be assumed that the average $\delta^{15}\text{N}$ value of *A. baicalensis* of 4.2‰ is within the expected range.

Food web analysis with stable isotopes— $\delta^{13}\text{C}$ data have been used to trace carbon flow along food chains from primary producers (food base) to higher trophic levels (Rau 1980, 1981). A $\delta^{13}\text{C}$ enrichment of $<1\%$ is generally the case for animals (del Giorgio and France 1996). The $\delta^{15}\text{N}$ of animals also reflects their diets. Minagawa and Wada (1984) reported that $\delta^{15}\text{N}$ enrichment during a single feeding process was $3.4 \pm 1.1\%$. Similarly, Wada et al. (1987) observed a constant $\delta^{15}\text{N}$ trophic effect of 3.3‰ in an Antarctic marine ecosystem.

To confirm the suitability of using a conventional stable isotope fractionation factor in this study, we compared $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of pelagic Omul with its prey estimated by gut content analysis. Omul is composed of three ecological-morphological groups: pelagic Omul, coastal-pelagic Omul, and benthic-deep-water Omul (Smirnov 1992). Smirnov found that the diet of pelagic Omul, the largest of the three groups, is composed of mesozooplankton (41%), *M. braniczkii* (23%), larva of pelagic sculpins (27%), and other organisms (9%). We calculated the average $\delta^{13}\text{C}$ of the diet of pelagic Omul to be -26.3% based on the assumptions that their diet was composed only of the former three food categories and that each category had the average $\delta^{13}\text{C}$ value we measured. Because pelagic Omul had a $\delta^{13}\text{C}$ of -25.5% , the estimated enrichment $\delta^{13}\text{C}$ value is 0.8‰. This value is within the range ($<1\%$) of previous reports for trophic ^{13}C enrichment. The $\delta^{15}\text{N}$ of pelagic Omul was estimated in the same way from reported gut compositions, $\delta^{15}\text{N}$ data of prey species, and an enrichment value of 3.3‰. The estimated value (10.6‰) of Omul was close to our actual $\delta^{15}\text{N}$ data for Omul ($10.0 \pm 0.6\%$).

Furthermore, we estimated the relationships between the trophic level of major species and their $\delta^{15}\text{N}$ ratio (Fig. 2). A clear relationship was observed between $\delta^{15}\text{N}$ and trophic level, with an enrichment factor of 3.3‰. These data indicated that standard SIA is readily applicable to Lake Baikal. Consequently, a ^{15}N enrichment value of 3.3‰ was applied to subsequent quantitative analyses.

Figure 3 illustrates stepwise enrichment of $\delta^{15}\text{N}$ with trophic level. The clear enrichment of $\delta^{15}\text{N}$ with trophic level in Lake Baikal's pelagic food web agrees well with many other isotope-based views of lake and marine trophic structures. Clear stepwise enrichment of $\delta^{15}\text{N}$ has also been demonstrated in the Antarctic marine ecosystem (Wada et al. 1987) and in an Arctic marine food web (Hobson and Welch 1992). Several factors might contribute to the simple and clear enrichment of $\delta^{15}\text{N}$ throughout the pelagic food web of Lake Baikal: (1) pelagic phytoplankton are the primary food base with little contribution from other primary producers, such as benthic plants, which usually have lower $\delta^{15}\text{N}$ values than phytoplankton; (2) there was little seasonal variation in $\delta^{15}\text{N}$ of phytoplankton during our sampling periods; (3) spe-

cies composition is simple; and (4) there is little geographical variation in phytoplankton $\delta^{15}\text{N}$.

On the other hand, ^{13}C enrichment was not as clear as indicated in Fig. 3. Lipid fractions of organisms generally have lower $\delta^{13}\text{C}$ values relative to whole organisms and other protein-rich fractions. The absence of stepwise enrichment of $\delta^{13}\text{C}$ throughout a food web has frequently been reported and is thought to be due to differential lipid content in organisms (Wada et al. 1987; Fry 1988). Thus, lipid fractions were removed from animal materials in this study so that we could exclude the effect of lipids. Nevertheless, consistent ^{13}C enrichment was not observed for the four pelagic sculpin species. These fish contain very high levels of lipids that are low in $\delta^{13}\text{C}$ as compared with other components like protein. A difference in the dynamics of the metabolic pathway is one possible factor. Further examination at the molecular level will be required at this point. However, because $\delta^{15}\text{N}$ is closely related to trophic level (Fig. 2), we obtain the following relationship between $\delta^{13}\text{C}$ and trophic level from Fig. 3:

$$\delta^{13}\text{C} (\text{‰}) = 1.2 (\text{Trophic Level} - 1) - 27.8$$

Therefore, because the pelagic ecosystem of Lake Baikal is endowed with many advantageous factors that facilitate detailed examination of food web structure, it is an ideal aquatic ecosystem for studying food webs using stable isotopes.

In this study, we analyzed the diet composition of each animal sampled. We also analyzed the size distribution of the amphipod *M. branickii*, two pelagic sculpins, and seals because there are indications that dietary changes may alter animal $\delta^{15}\text{N}$ values during development. For example, Rau et al. (1981) found a positive correlation between $\delta^{15}\text{N}$ of sole and individual body weight. In contrast, a constant $\delta^{15}\text{N}$ value was observed for two marine mussel species irrespective of age (Minagawa and Wada 1984). We also examined potential differences in $\delta^{15}\text{N}$ among three basins for *M. branickii* and two pelagic sculpins and between sexes of seals.

The $\delta^{15}\text{N}$ signatures of mesozooplankton *E. baicalensis* and *Cyclops kolensis* and macrozooplankton *M. branickii* suggest a trophic level of about 2 (Fig. 3). $\delta^{15}\text{N}$ of *C. kolensis* and *M. branickii* was higher than that of *E. baicalensis*, suggesting that they are feeding on both phytoplankton and *E. baicalensis*. *M. branickii* and *E. baicalensis* are the dominant zooplankton species, and they can be important prey items for animals at higher trophic levels.

As for *M. branickii*, possible food sources include phytoplankton and the mesozooplankton *E. baicalensis* (Kozhov 1963). Our data show that the $\delta^{15}\text{N}$ value of *M. branickii* increased with increasing body size (Fig. 4), suggesting that larger *M. branickii* have a higher proportion of zooplankton in their diet. However, *M. branickii* ranging in size (body length) from 4 to 6 mm also had relatively high $\delta^{15}\text{N}$ values. Different vertical migration patterns among organisms of different body sizes may influence $\delta^{15}\text{N}$. For example, the feeding habits of the pelagic amphipod *Themisto japonica* collected from the Sea of Japan were reported by Sugisaki et al. (1991) using the $\delta^{15}\text{N}$ natural abundance method. They found that juveniles inhabited the shallow layer with abundant phytoplankton, whereas adults were distributed in deeper layers where they could utilize zooplankton as their major

Table 2. Relative proportion of zooplankton (f) and mean of $\delta^{15}\text{N}$ of *M. branickii* collected in Barguzin Bay.

Body length (mm)	$\delta^{15}\text{N}$	f
12–14	6.9	–0.25
14–16	7.2	–0.02
16–18	7.5	0.10
18–20	7.7	0.16
20–22	8.1	0.34
22–24	8.3	0.42
24–26	9.2	0.81
26–28	8.5	0.49
28–30	8.4	0.45
37	8.6	0.49

food source. $\delta^{15}\text{N}$ values of adults were higher than those of juveniles. Sugisaki et al. (1991) concluded that the feeding behavior of *T. japonica* was closely associated with their vertical migration and changed from herbivorous to carnivorous during their growth. *M. branickii* in Lake Baikal also exhibit vertical migration (Melnik et al. 1993). Mature females (>15 mm in length) migrated extensively, whereas juveniles (1–2 mm), males (3–4 mm), and immature females (<15 mm) exhibited rather limited migration in comparison with the mature females. Immature females and mature males are dominant in the 4–6-mm body length class; thus, different migration patterns may be responsible for the distinct isotopic position of animals in this size class. The relatively high $\delta^{15}\text{N}$ of *M. branickii* in the 4–6-mm size class may also be explained by other food sources, such as zooplankton fecal pellets, which are estimated to be high in $\delta^{15}\text{N}$. The high $\delta^{15}\text{N}$ value of large (>11 mm long) *M. branickii* may reflect their migration to deep layers, where zooplankton are abundant.

We also tried to quantitatively estimate the relative contribution of phytoplankton and zooplankton to the diet of *M. branickii*. In this estimate, we assumed two food sources, phytoplankton and zooplankton. For example, the $\delta^{15}\text{N}$ value of an individual *M. branickii* with an initial $\delta^{15}\text{N}$ value of 6.9‰ can be expressed as follows:

$$\delta^{15}\text{N} = [6.9M_{t1} + (\delta^{15}\text{N}_{\text{diet}} + 3.3)(M_{t2} - M_{t1})]/M_{t2}, \quad (1)$$

where M_t denotes the dry mass at time t . $\delta^{15}\text{N}_{\text{diet}}$ was calculated with the following equation:

$$\delta^{15}\text{N}_{\text{diet}} = \delta^{15}\text{N}_{\text{z.p.}} \times f + \delta^{15}\text{N}_{\text{p.p.}} \times (1 - f), \quad (2)$$

where $\delta^{15}\text{N}_{\text{z.p.}}$ and $\delta^{15}\text{N}_{\text{p.p.}}$ are the mean $\delta^{15}\text{N}$ values of zooplankton *E. baicalensis* (6.5‰) and phytoplankton (4.2‰), respectively. f denotes the proportion of zooplankton in their diet. M_t can be estimated using body length because of the good correlation between dry weight and the third power of body length:

$$M_t = 0.002L_t^3 + 0.245, \quad r^2 = 0.92, \quad P = 0.00, \quad (3)$$

where L_t denotes body length (mm) at time t . By applying this relationship to Eq. 1, f was calculated by the following equation:

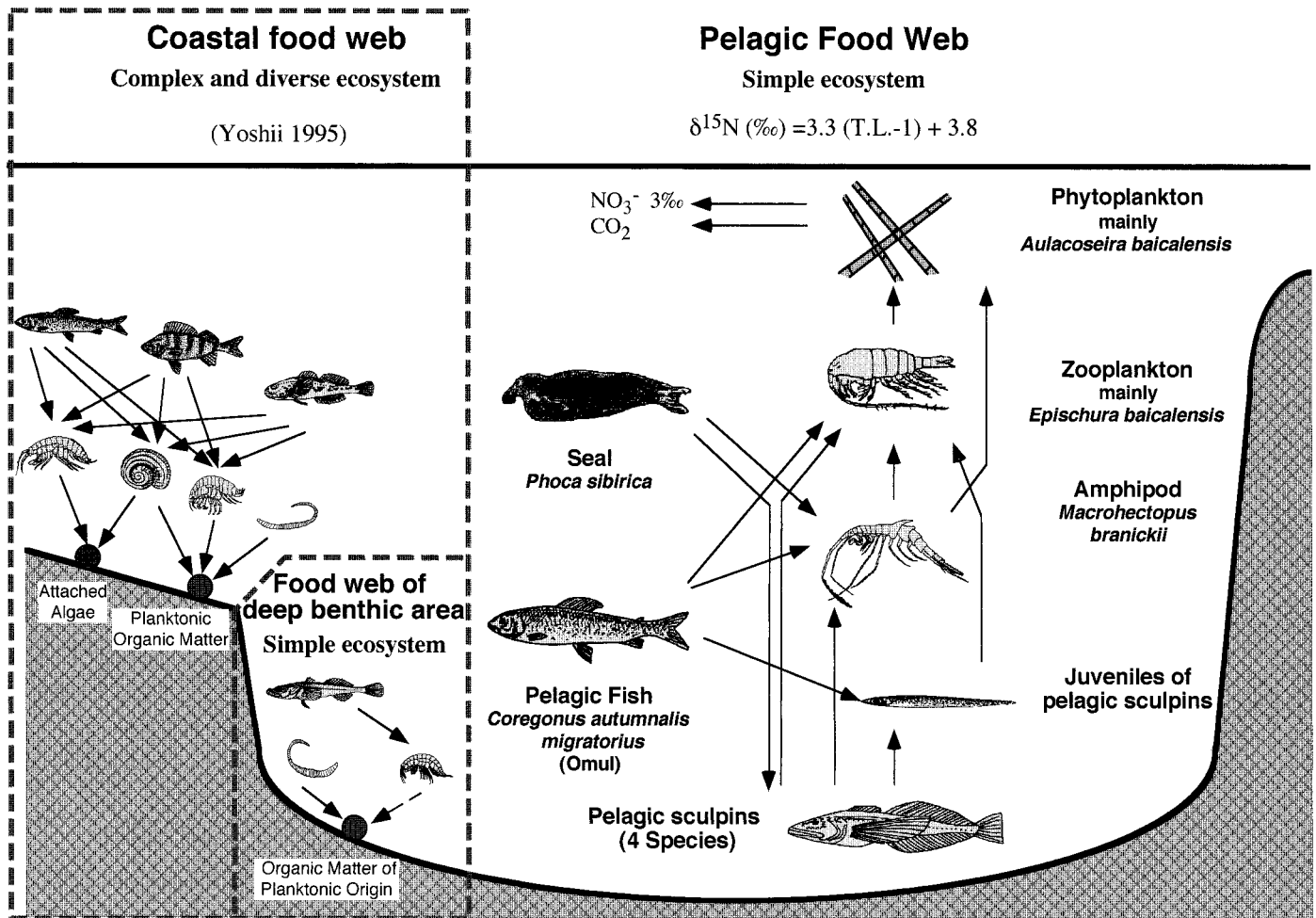


Fig. 7. Schematic illustration of Lake Baikal food webs.

$$f = \frac{[\delta^{15}\text{N}(2L_{i2}^3 + 245) - 6.9(2L_{i1}^3 + 245) - 15(L_{i2}^3 - L_{i1}^3)]}{4.6(L_{i2}^3 - L_{i1}^3)} \quad (4)$$

To obtain f , we assumed L_{i1} to be 11 mm and used samples collected in Barguzin Bay, where there is a large population of *M. branickii*. f values are summarized in Table 2. These calculations suggest that the proportion of zooplankton in the diets of large (>11 mm in body length) *M. branickii* increased as they grew but was highly variable among individuals. Furthermore, the proportion of zooplankton and phytoplankton consumed changed between sampling locations, with samples collected in Barguzin Bay having lower $\delta^{15}\text{N}$ values than samples from other sites. If *M. branickii* feed indiscriminately, differences in diet composition may reflect the distribution of phytoplankton and zooplankton in their environment.

The diet of pelagic sculpins also appears to change throughout their lifespan (Fig. 5). $\delta^{15}\text{N}$ increased sharply with body length from 0 to 50 mm for both species, suggesting ontogenetic diet shifts. In contrast, the $\delta^{15}\text{N}$ observed for the large size classes indicated rather constant diet composition. According to our isotopic data, juvenile *Comephorus* sp. (body length, <15 mm) appear to be feeding on

zooplankton. These data are consistent with the findings of Kozhov (1963), who found that the two main food sources of adult *Comephorus* were *M. branickii* and pelagic sculpin larvae. Because these two sources had distinct $\delta^{15}\text{N}$ values, we were able to evaluate the relative contribution of these animals to the diet of adult *Comephorus*. The contribution of pelagic sculpin larvae to the diet of adult *Comephorus* (body length, >40 mm) was estimated to be within the range of 40–100% for *C. baicalensis* and 40–70% for *C. dybowskii* (Fig. 5). We also investigated geographical differences in the $\delta^{15}\text{N}$ value of sculpins. Although differences in $\delta^{15}\text{N}$ between individuals were small for both species of sculpin, $\delta^{15}\text{N}$ values varied slightly at different collection sites. For both species, $\delta^{15}\text{N}$ was enriched in individuals collected in the southern basin relative to the central and northern basins. These differences might reflect variation in $\delta^{15}\text{N}$ of the food base among these basins or differences in the diet composition of sculpins.

In contrast to *C. baicalensis* and *C. dybowskii*, *C. grewingki* has been shown by conventional gut content analyses to consume mainly zooplankton, *M. branickii*, and pelagic sculpin larvae, whereas *C. inermis* were found to consume *M. branickii* and pelagic sculpin larvae (Zubin 1992). We

also estimated the possible diet composition of these species using our isotope data ($13.7 \pm 0.3\text{‰}$ for *C. inermis* and $11.8 \pm 0.7\text{‰}$ for *C. grewingki*) combined with information from the gut content analyses performed by Zubin (1992). Our analysis suggested that the diet of *C. grewingki* consists of no more than 20% pelagic sculpin larvae and at least 80% *M. branickii* and mesozooplankton, whereas the diet of *C. inermis* is 65 ± 7 to $74 \pm 7\%$ pelagic sculpin larvae and 26 ± 7 to $35 \pm 7\%$ *M. branickii* and mesozooplankton.

In the case of seals, differences in $\delta^{15}\text{N}$ between the sexes were examined together with age and geographical distribution. $\delta^{15}\text{N}$ of individuals older than 1 yr was about 14‰ and almost constant with age, whereas individuals <1 yr old had 1–2‰ higher $\delta^{15}\text{N}$ values (Fig. 6). Juvenile seals feed on milk during the first 3 months of life (Kozhov 1963). Therefore, the high $\delta^{15}\text{N}$ values of seals <1 yr old was possibly the result of feeding on milk with high $\delta^{15}\text{N}$. On the other hand, no significant difference in $\delta^{15}\text{N}$ was observed between male and female seals and among the three basins, suggesting that food sources were nearly identical irrespective of sex and sampling location. Gut content analyses suggested that the main diet of *P. sibirica* is fish, especially pelagic sculpins (Pastukhov 1966, 1977; Ivanov 1936). From an isotopic viewpoint, $\delta^{13}\text{C}$ of seals showed the typical value of pelagic animals; thus, it seems unlikely that the seals feed on benthic fish in the coastal zone that have enriched $\delta^{13}\text{C}$ or deep-dwelling fish that have high $\delta^{15}\text{N}$ (Yoshii 1995). Although our isotope data indicate that the seals may be eating Omul, gut content analyses do not strongly support this notion. Pastukhov (1993) analyzed the gut contents of seals from Lake Baikal and determined that *M. branickii* was a food source. Our $\delta^{15}\text{N}$ data suggest that the diet composition of seals could be as much as $46 \pm 6\%$ *M. branickii* and $54 \pm 6\%$ of pelagic sculpins, assuming that *M. branickii* and pelagic sculpins were their only food sources and that the $\delta^{15}\text{N}$ of the pelagic sculpins they consume have an average value of the four adult pelagic sculpin species present in Lake Baikal. The estimated diet composition of seals does, however, change depending on their relative consumption of the four pelagic sculpins and the size of *M. branickii* consumed. In any case, our $\delta^{15}\text{N}$ data suggested that *M. branickii* contribute significantly to the diet of the seals we sampled.

In conclusion, a $\delta^{15}\text{N}$ enrichment of 3.3‰ during trophic transfer was observed for Lake Baikal. This value is consistent with that observed in an Antarctic ecosystem (3.3‰; Wada et al. 1987). The food webs of polar ecosystems are generally simpler than those of tropical ecosystems; therefore, polar pelagic ecosystems are particularly well suited to food web analyses using stable isotopes techniques. Because the number of species in the pelagic food web of Lake Baikal is relatively small, and because predator–prey relationships are simple, quantitative analyses of diet composition were possible. The food sources of each animal are summarized in Fig. 7. In contrast to the $\delta^{13}\text{C}$ values of benthic animals, which varied strongly among species and individuals (Yoshii 1995), the pelagic food web is less complex than the coastal part of the benthic food web in Lake Baikal, and the two food webs are isotopically distinct.

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