

Feeding ecology of two planktonic sculpins, *Comephorus baicalensis* and *Comephorus dybowskii* (Comephoridae), in Lake Baikal

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Abstract Planktonic sculpins (*Comephorus baicalensis* and *Comephorus dybowskii*) are endemic to Lake Baikal, and their migration behavior is characterized by their strange movements, which occur only vertically. We investigated their detailed food sources at each growth stage by stable isotope analyses in combination with stomach content analysis. At all growth stages, both fishes and amphipods were the main diet for *C. baicalensis*, whereas amphipods alone were the main diet for *C. dybowskii*. Our results indicate that the relationship between the two species shifts from a competitive interaction to a predator–prey interaction with the growth stages of *C. baicalensis*.

Key words Lake Baikal · Planktonic sculpin · Stable isotope · *Comephorus* · Diet

Fishes have the potential to influence material cycles through food webs in aquatic ecosystems (see Carpenter and Kitchell, 1993) and are often categorized into two forms, i.e., swimming foragers and benthic foragers (Miyasaka et al., 2005). Interestingly, the unique planktonic foragers, another foraging form, inhabit Lake Baikal (Kozhov, 1963). Planktonic forager fishes migrate vertically, but they rarely move horizontally as do swimming foragers. They feed primarily upon planktonic invertebrates with diel vertical migration in a wide range of the pelagic water column (Kozhov, 1963). In the endemic planktonic comephorid fishes *Comephorus baicalensis* and *Comephorus dybowskii*, little is known about their feeding ecology based on quantitative analysis except the report by Sideleva (2003). In recent years, a stable isotope analysis was conducted to study the whole food-web structure including these unique planktonic fishes in the pelagic region of Lake Baikal (Yoshii et al., 1999).

The stable isotope method is a powerful tool for the study of food selection of animals, ontogenetic niche shift, food-web structure, and so on (Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 2001). The nitrogen signatures (often described as $\delta^{15}\text{N}$ values) of animals reflect their diets. Enrichment of $\delta^{15}\text{N}$ along a trophic network is widely recognized among many animals (e.g., Minagawa and Wada, 1984). However, stable isotope analysis sometimes provides

different results when the species utilizes more than two food resources (Phillips and Gregg, 2003). In contrast, stomach content analysis is able to provide information on multiple food resources, although the information is instantaneous, i.e., at the time the organism is captured. The planktonic *C. baicalensis* and *C. dybowskii* are known to consume mainly a zooplankton (*Epishura baicalensis*), an amphipod (*Macrohectopus branickii*), and pelagic sculpin larvae (see Sideleva, 2003). We report the detailed feeding ecology of these two species, combining stable isotope and stomach content analyses throughout almost the entire region of Lake Baikal.

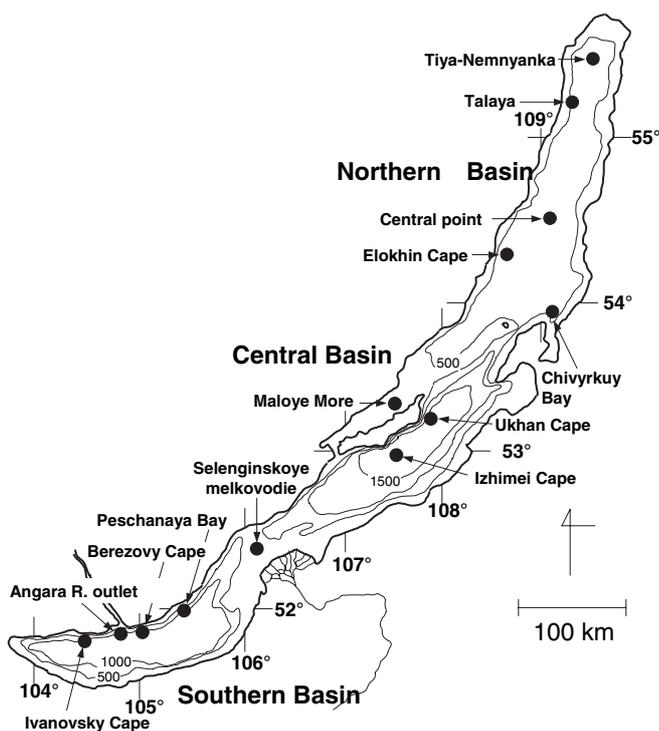
Materials and Methods

Surveys were conducted from 16 March through 6 November 1999 at 13 sampling sites in the pelagic region of all basins aboard R/V *Vereshchagin* (Table 1, Fig. 1). *Comephorus baicalensis* and *C. dybowskii* were collected from the water column (0–750 m) using a large plankton net (DOJN; 2 m diameter, 1-mm mesh) or a trawl (Isaack–Kidd midwater trawl; 2 × 5 m mouth opening). We measured the standard body length of fish samples to the nearest 1 mm and their body wet mass to the nearest 0.1 g. Then we removed their stomach and part of the muscle tissue,

Table 1. Depth, sampling layer, date, and specimen number for diet and stable isotope analyses (SI) at each sampling site in Lake Baikal

Sampling site	Depth (m)	Maximum sampling layer (m)	Date	<i>C. baicalensis</i>		<i>C. dybowskii</i>	
				Diet	SI	Diet	SI
Northern Basin (total numbers)				(29)	(35)	(73)	(60)
Tiya-Nemnyanka	620	600	22 Sept.	2	2	17	4
Talaya	635	400	1 Nov.	0	5	0	5
Central point	500	400	6 July, 1 Nov.	14	9	24	14
Elokhin Cape	600	520	5 July, 16 Aug.	6	7	8	11
Chivyrkuy Bay	800	750	8 July, 17 Aug.	7	12	24	26
Middle Basin (total numbers)				(13)	(9)	(49)	(29)
Maloye More	350	300	4 July	0	0	9	9
Ukhan Cape	1500	400	9 July, 30 Oct.	13	9	40	17
Izhimei Cape	1020	250	18 Aug.	0	0	0	3
Southern Basin (total numbers)				(29)	(24)	(115)	(47)
Selenginskoye Melkovodie	400	250	11 July	0	6	0	3
Peschanaya Bay	1400	400	12 July, 6 Nov.	6	5	25	10
Berezovy Cape	1465	500	28 May–30 Oct.	23	11	90	25
Angara River outlet	40	40	11 Apr.	0	2	0	7
Ivanovsky Cape	1400	500	16 Mar.	0	0	0	2
All Lake Baikal (total numbers)				(71)	(67)	(237)	(136)

SI, stable isotope analysis

**Fig. 1.** Thirteen sampling sites (●) in Lake Baikal

excluding skin (approximately 1 g wet mass), and identified sex. Fish individuals that were too small to identify to sex were categorized as juveniles (approximately <60 mm). Muscle samples were frozen at -5°C for stable isotope analyses. Stomach samples were preserved in 10% buffered formalin solution for diet analysis.

Prey organisms in fish stomachs were identified at the species level using a binocular microscope. The biomass

of four prey categories, one zooplankton (*Epischura baicalensis*), one amphipod (*Macrohectopus branickii*), and two fishes (*C. baicalensis* and *C. dybowskii*), were measured as wet mass (nearest 0.01 g). The percentage of wet mass contributed by each prey category was determined for each individual fish and averaged over each growth stage for each sculpin species in each basin. Collected muscle tissues were dried at 60°C for 24 h and then ground to fine powder. We did not conduct lipid extraction from muscle tissues for stable isotope analyses. Stable isotope ratios of nitrogen and carbon were measured using a CHN analyzer combined with a Finnigan MAT Delta-S (Thermo Electron, Waltham, MA, USA) mass spectrometer through a ConFlo-II interface. Isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) were expressed as permil deviations from the standard as defined by the following equation:

$$\delta^{15}\text{N} \text{ (or } \delta^{13}\text{C}) = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000 \text{ (‰)}$$

where $R = {}^{15}\text{N}/{}^{14}\text{N}$ (or ${}^{13}\text{C}/{}^{12}\text{C}$). Atmospheric nitrogen and belemnite (PDB) were used as the isotope standards for nitrogen and carbon, respectively. Analytical precision was greater than $\pm 0.2\text{‰}$ and $\pm 0.1\text{‰}$ for nitrogen and carbon, respectively. Data were log-transformed for exact value, and arcsine square-root transformation was applied for percentage to standardize variances and improve normality if necessary. For any ANOVA model, multiple comparison using the Scheffe test was conducted after one-way ANOVA when necessary. The α level was set at 0.05.

Results

Size distribution and diet variation. The frequency distribution of body length differed between the two sculpin species (Fig. 2). Adults of *C. baicalensis* were mechanically

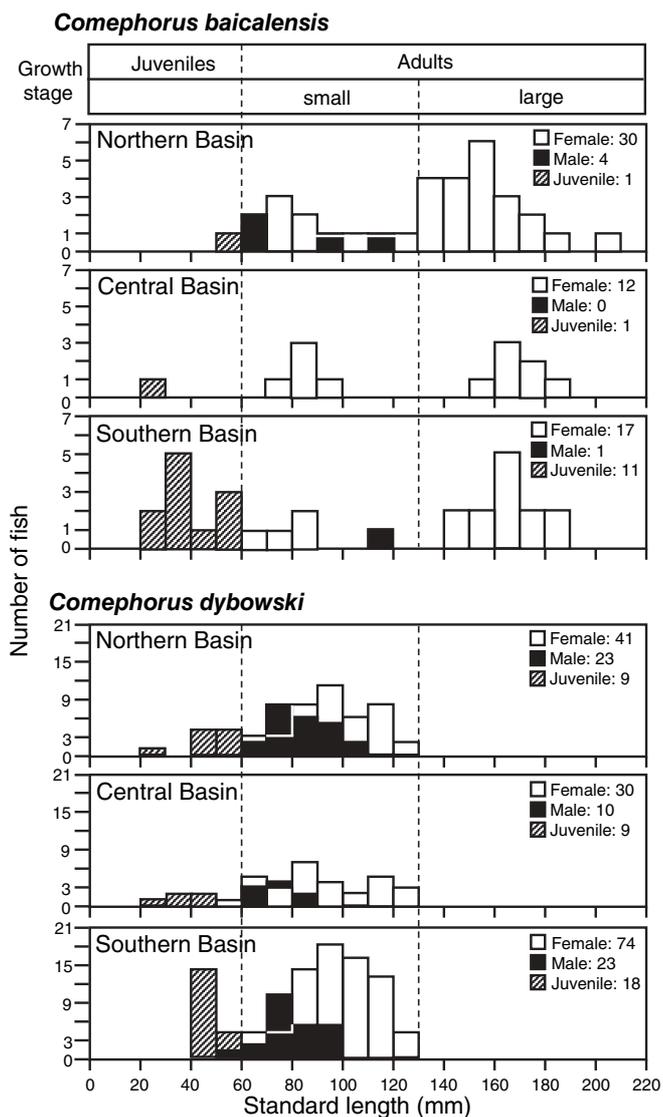


Fig. 2. Standard body length distribution of two pelagic sculpin, *Comephorus baicalensis* and *Comephorus dybowskii*, in three basins

divided into two size groups: individuals >130mm in standard length (SL) (hereafter we refer to this group as large adults) and <130mm (small adults). All adults of *C. dybowskii* were smaller than 130mm SL. No remarkable difference in distribution was found between the basins in either species.

One-way MANOVA revealed that there was no significant difference between basins in diet composition at any growth stage of *C. baicalensis* or *C. dybowskii* ($P > 0.056$ for all stages) (Fig. 3).

Diet composition differed considerably between *C. baicalensis* and *C. dybowskii* in all basins (Fig. 3). At all growth stages, fishes (two *Comephorus* species, 18–80%) and an amphipod (*Macrohectopus branickii*, 36–86%) were the main diet for *C. baicalensis*, whereas amphipods were the main diet (25–87%) for *C. dybowskii*. One-way MANOVA revealed that overall diet composition of adults differed significantly between sculpin species on three test-

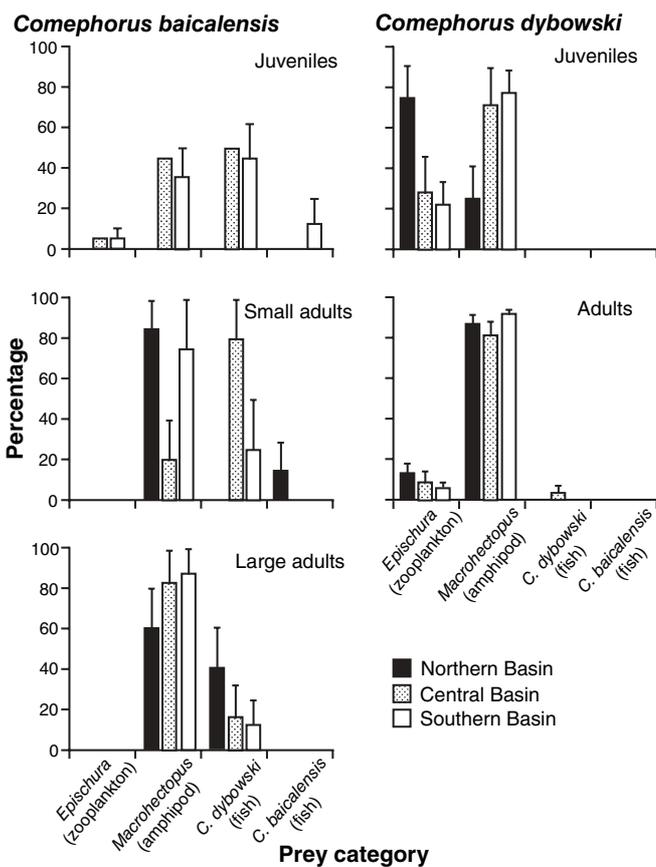


Fig. 3. Differences in diet composition by percentage of wet mass (mean \pm 1 SE) among growth stages in *Comephorus baicalensis* and *Comephorus dybowskii* in three basins

able prey categories [*Epischura*, *Macrohectopus*, and fishes; Hotelling–Lawley (H-L) trace = 0.332, $F_{3,176} = 19.48$, $P < 0.001$]. The percentage of fishes in the *C. baicalensis* diet was significantly higher than that in the *C. dybowskii* diet ($F_{1,178} = 4.31$, $P < 0.001$). In contrast, the percentage of amphipods in the *C. baicalensis* diet was significantly lower than that in the *C. dybowskii* diet ($F_{1,178} = 8.19$, $P = 0.005$).

In the *C. baicalensis* diet, one-way MANOVA revealed that overall diet differed significantly between juveniles and large adults (H-L trace = 0.782, $F_{1,25} = 6.52$, $P = 0.002$) (Fig. 3). Consumption of amphipods by large adults was significantly greater than that by juveniles ($F_{1,27} = 6.86$, $P = 0.014$). Consumption of fishes did not differ significantly between growth stages ($P > 0.058$ for all combinations). In the *C. dybowskii* diet, one-way MANOVA revealed that overall diet differed significantly between juveniles and adults (H-L trace = 0.145, $F_{2,168} = 12.17$, $P < 0.001$). The adult consumption of zooplankton (= *Epischura*) was significantly less than that of juveniles ($F_{1,169} = 23.63$, $P < 0.001$). In contrast, consumption of amphipods by adults was significantly greater than that by juveniles ($F_{1,169} = 17.77$, $P < 0.001$).

Stable isotope ratios. The $\delta^{13}\text{C}$ value of *C. baicalensis* declined significantly with standard length, whereas no significant regression line between standard length and $\delta^{13}\text{C}$ value was obtained for *C. dybowskii* (Fig. 4). The $\delta^{13}\text{C}$ value

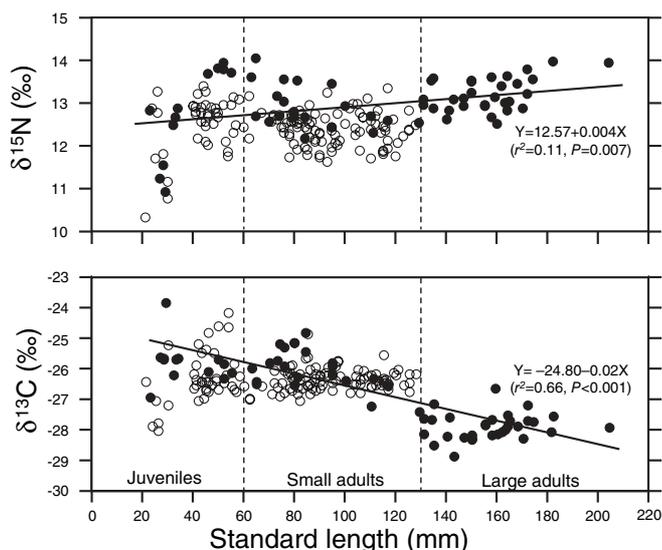


Fig. 4. The $\delta^{15}\text{N}$ (top) and the $\delta^{13}\text{C}$ (bottom) values of *Comephorus baicalensis* (●) and *Comephorus dybowskii* (○) in all basins. Regression lines for *C. baicalensis* were fitted by simple linear regression

at the large adult stage of *C. baicalensis* was significantly lower than at other stages ($P < 0.001$ for all combinations); there was no significant difference between juveniles and small adults ($P = 0.659$). There were no significant differences in $\delta^{13}\text{C}$ at each growth stage between the basins in either species ($P > 0.095$ for all combinations).

The $\delta^{15}\text{N}$ value of *C. dybowskii* adults was significantly smaller than those of *C. baicalensis* large adults ($F_{1,124} = 103.22$, $P < 0.001$) and small adults ($F_{1,115} = 25.00$, $P < 0.001$) (see Fig. 4). There was no significant difference in the $\delta^{15}\text{N}$ value between species at the juvenile stage ($P = 0.258$).

The $\delta^{15}\text{N}$ value of *C. baicalensis* increased significantly with standard length, although we were unable to obtain any significant regression line between standard length and $\delta^{15}\text{N}$ value for *C. dybowskii* ($F_{3,133} = 7.10$, $P < 0.001$) (see Fig. 4). There were no significant differences in $\delta^{15}\text{N}$ at each growth stage between the basins in either species ($P > 0.997$ for all combinations).

Discussion

The decline in the $\delta^{13}\text{C}$ value of *C. baicalensis* with body size (-25‰ to -29‰) could be attributed to lipid content in their tissues because we did not conduct lipid extraction in the present study. The $\delta^{13}\text{C}$ values often decline with the volume of lipid in tissue (DeNiro and Epstein, 1977). For *C. baicalensis*, Kucklick et al. (1996) reported that the percentage of lipid increased from 3% to 43% with age.

The planktonic populations of *C. baicalensis* were composed of three distinct size groups: juveniles, small adults, and large adults. The life span of *C. baicalensis* was longer (8–10 years) than that of *C. dybowskii* (6–8 years), and the large adults of *C. baicalensis* belonged to the oldest genera-

tion (8 to 10 years old) (Kucklick et al., 1996; Sideleva, 2003). *C. baicalensis* at all growth stages were typical piscivores. Our diet analysis and $\delta^{15}\text{N}$ values suggested an ontogenetic diet shift from low trophic food categories (zooplankton and amphipods) to high trophic food categories (amphipods and fish). $\delta^{15}\text{N}$ values of zooplankton were considerably low (5.6–7.5‰; Yoshii et al., 1999), and zooplankton were consumed only by juveniles of *C. baicalensis* (see Fig. 3). In the pelagic food web of Lake Baikal, two *Comephorus* species have been categorized as secondary consumers (Afanasyeva, 1977; Volrman and Kontorin, 1983; Sideleva, 2003). The previous study regarding isotope ratios suggested that the relationship between two species was a competitive interaction for shared food resources (Yoshii et al., 1999). However, our analysis incorporating diet analysis with stable isotope analysis indicated that the relationship shifted rather from a competitive interaction to a predator-prey interaction with growth stage.

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