

Compositional and interlake variability of zooplankton affect baseline stable isotope signatures

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Abstract

Zooplankton are commonly used to establish a baseline isotopic signature for pelagic production in lakes. Our objective was to evaluate this approach by quantifying among-lake and within-lake variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for different taxa of pelagic zooplankton. We measured the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *Daphnia*, *Holopedium*, and calanoid copepods from four lakes sampled from June to November 2001 and from eight additional lakes sampled once in midsummer. In the four lakes with temporal sampling, within-lake differences due to taxonomic grouping accounted for 36.7% of the variance in $\delta^{15}\text{N}$ and 41.7% of the variance in $\delta^{13}\text{C}$. Among all lakes, the $\delta^{15}\text{N}$ of calanoid copepods was on average 2.55‰ and 2.44‰ higher than *Daphnia* or *Holopedium*, respectively, whereas the $\delta^{13}\text{C}$ of calanoid copepods was 2.19‰ and 2.23‰ lower than *Daphnia* or *Holopedium*, respectively. If ^{15}N fractionation is similar among species, the differences in $\delta^{15}\text{N}$ suggest that calanoid copepods either feed at a higher trophic position in the food web or they have a consistently higher baseline $\delta^{15}\text{N}$ signature than *Daphnia* or *Holopedium* among lakes. Differences in $\delta^{13}\text{C}$ suggest that zooplankton taxa in the pelagia of lakes have different food sources. We conclude that species composition and feeding behaviors of the zooplankton community should be considered before making among-lake comparisons of food web structure. We show that *Daphnia* is a useful isotopic baseline for organisms that rely on primary production in lakes.

Aquatic ecologists frequently use stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) to measure the food source and trophic position of aquatic consumers and to make inferences about food web structure (Kling et al. 1992; Cabana and Rasmussen 1994; Vander Zanden et al. 1999; Post 2002). Comparisons of food web structure among and within ecosystems rely on a baseline isotopic signature for each system. Without an ecosystem specific isotopic baseline, results do not account for the large among-system variations in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ at the base of food webs (Rounick and Winterbourn 1986; Cabana and Rasmussen 1996; Lake et al. 2001). Recent multiple-lake food web analyses used primary consumers, including pelagic zooplankton, as an isotopic baseline for other members of the lake community (Kling et al. 1992; Cabana and Rasmussen 1994; Vander Zanden and Rasmussen 1999; Post 2002). Each of these studies used a slightly different method of baseline correction that was tailored to address a question of specific ecological interest. Each method, except that of Kling et al. (1992), used a size fraction of pelagic zooplankton to develop the baseline (Vander Zanden and Rasmussen 1999; Post 2002) or as part of the baseline itself (Cabana and Rasmussen 1994).

The substantive goal of a baseline is to reflect the isotopic signature of the primary source of production for the food web (Cabana and Rasmussen 1994; Post 2002). However, choosing and finding an appropriate baseline depends on the spatial and temporal context of the ecological question under consideration. For example, Cabana and Rasmussen (1994) modeled food chain length using a size fraction of zooplankton ($<250\ \mu\text{m}$) as the baseline $\delta^{15}\text{N}$ signature to estimate the trophic position of invertebrate predators, planktivorous fish, and piscivorous fish. A zooplankton size fraction was chosen as a baseline because isotopic signatures of primary consumers are less temporally and spatially variable than primary producers (Cabana and Rasmussen 1996). However, this method assumes that the mixture of different zooplankton taxa within a given size fraction is representative of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the primary food source for the pelagic food web.

An alternative to a zooplankton size fraction would be to use a single taxonomic grouping, with a known feeding behavior, as an isotopic baseline for production in the habitat where it feeds (*sensu* Kling et al. 1992; Post 2002). For example, Kling et al. (1992) used a copepod that was known to be herbivorous as a baseline for an omnivorous copepod. This scenario was ideal because both species, the baseline and the omnivore, were biologically related and likely had similar temporal and spatial integration of food source isotopic signatures. In other cases, researchers have used mussels as a pelagic indicator species to compare among sampling sites and to correct for among-system variation in baseline isotopic signatures (Fry 1999; McKinney et al. 1999; Lake et al. 2001; Post 2002). A recent study by Post (2002) indicated that mussels and snails reflect the isotopic signatures of the pelagic and littoral environment, respectively. In his study, the $\delta^{13}\text{C}$ of mussels was not statistically different from the median of a time series for a size fraction ($>150\ \mu\text{m}$) of bulk pelagic zooplankton (Post 2002).

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Previous attempts to establish a lake-specific isotopic baseline using pelagic zooplankton (Cabana and Rasmussen 1994; Vander Zanden and Rasmussen 1999; Post 2002) relied in part on size fractions of total zooplankton and did not address possible isotopic differences due to species composition. Within a lake, different taxa of pelagic zooplankton can have substantially different $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures (Kling et al. 1992; Grey and Jones 1999). Among-taxa variability not only depends on foraging behavior and trophic interactions (Kling et al. 1992; Meili et al. 1996; Grey and Jones 1999; Jones et al. 1999; Grey et al. 2001) but may also depend on taxon-specific baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures. Regardless of the cause of variation, significant heterogeneity of stable isotopic signatures within a zooplankton size fraction may lead to bias in multiple-lake food web comparisons.

Since the pioneering study by Kling et al. (1992), no study has measured the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of different pelagic zooplankton taxa in multiple lakes to determine whether there are consistent isotopic differences within and among lakes. The goal of this study is to provide better information on the isotopic signatures of zooplankton in order to advance our understanding of baseline determination in the pelagia of lakes. To this end, we quantify among- and within-lake variation in the isotopic signatures of the dominant taxonomic groups of pelagic zooplankton communities for 12 coastal lakes in British Columbia. We also discuss factors that may affect the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of different zooplankton taxa and suggest when *Daphnia* is an appropriate isotopic baseline for organisms that rely on pelagic production.

Methods

Zooplankton collection and analysis—We collected zooplankton samples every 2 or 3 weeks from June to November 2001 from four lakes in the Greater Victoria region in British Columbia: Council Lake (COL), Elk Lake (ELL), Sooke Lake Reservoir (SOL), and Shawnigan Lake (SHL). We also sampled another eight lakes once during the sampling period. Zooplankton were collected with a 64- μm mesh, 50-cm diameter Wisconsin net from the entire water column or to a maximum depth of 30 m. Zooplankton were left overnight at 4°C in filtered lake water (GFF) or deionized water. Within 24 h of collection we sorted live zooplankton into three categories, calanoid copepods (C), *Daphnia* (D), or *Holopedium* (H) and dried each sample at 60°C. Samples consisted of approximately 40–80 *Daphnia*, 80–150 calanoid copepods, or 20–50 *Holopedium*. Each sample of calanoid copepods was a mixture of adult and late-stage calanoid copepodites with a mean body size of >1 mm. For isotopic analysis, our goal was to get ~1 mg of zooplankton tissue for each sample. Five lakes had all three taxa in sufficient abundance for isotopic analysis, three lakes had only calanoid copepods and *Daphnia*, two lakes had only calanoid copepods and *Holopedium*, and two lakes had only *Daphnia* and *Holopedium* (Table 1). Samples were analyzed at the University of Waterloo Environmental Isotope Laboratory (Waterloo, Ontario, Canada) on an Isochrom continuous flow stable isotope ratio mass spectrometer coupled to a Carlo

Erba elemental analyzer. The precision for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was <0.1‰. The samples were analyzed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, percent carbon, and percent nitrogen. The carbon to nitrogen ratio (C:N) is reported as a molar ratio.

The handling time of invertebrates, while unpreserved, can have a significant effect on both the $\delta^{13}\text{C}$ and the $\delta^{15}\text{N}$ within 24 h of sample collection (Kaehler and Pakhomov 2001). To test for an effect of sample handling, we compared the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *Daphnia* left overnight in filtered lake water to *Daphnia* frozen within 4 h of collection. We found no effect of sample handling in any of the three lakes we tested for either $\delta^{13}\text{C}$ (ELL, $F_{1,4} = 0.044$, $p = 0.844$; SHL, $F_{1,12} = 3.383$, $p = 0.091$; SOL, $F_{1,11} = 1.795$, $p = 0.207$) or $\delta^{15}\text{N}$ (ELL, $F_{1,4} = 0.035$, $p = 0.862$; SHL, $F_{1,12} = 2.87$, $p = 0.116$; SOL, $F_{1,11} = 0.557$, $p = 0.471$).

Statistical analysis—We used a random effects nested analysis of variance (ANOVA) to apportion variance of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and C:N ratio of *Daphnia*, *Holopedium*, and calanoid copepods to among- and within-lake differences. We used variance components from this analysis to compare the relative variability of our dependent variables ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and C:N ratio) among and within lakes. This approach allowed us to quantify how much of the total variance is explained by among-lake differences (a lake effect) compared to the variance explained by within-lake differences due to taxonomic grouping (a taxa effect). For this hierarchical analysis, the taxa effect is nested within the main lake effect.

The null expectation of our nested ANOVA was that neither the lake effect nor the effect of taxa nested within lakes would account for a significant component of the total variance in $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, or the C:N ratio of zooplankton. Rejecting the null hypothesis for the lake effect would support the need for baseline correction of isotopic signatures among lakes. Rejecting the null hypothesis for the taxa effect would indicate that zooplankton community composition should be considered for baseline determination. We included the C:N ratio in the analysis because it does not vary much among lakes and, thus, provided a good reference variable to compare with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

We performed this analysis for Council Lake, Elk Lake, Sooke Lake Reservoir, and Shawnigan Lake, which were the four lakes with extensive temporal sampling. Council and Shawnigan Lakes both had *Daphnia*, *Holopedium*, and calanoid copepods, whereas Sooke and Elk Lakes had only *Daphnia* and calanoid copepods (Table 1). Owing to the unbalanced nature of zooplankton community composition in these study lakes, our nested ANOVA was unbalanced, with four lakes as part of the main lake effect and two or three zooplankton taxa making up the taxa effect nested within each lake. To account for this unbalanced analysis, we used the recommended residual maximum-likelihood method to estimate variance components (Robinson 1987; Rusak et al. 2002).

We tested for isotopic homogeneity of zooplankton $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ as per the method of Ponsard and Arditì (2000): $\delta_{\text{taxa}} = \delta_{\text{base}} + \Delta \pm \sigma_{\Delta}$, where σ_{Δ} is the standard deviation of the isotopic enrichment for multiple species. If the ratio of the observed group variance (σ_g^2) to the variance in fractionation (σ_{Δ}^2) was significantly greater than one (using a

Table 1. Sampling strategy for zooplankton collected from each lake. Zooplankton species were grouped as *Daphnia* (D), *Holopedium* (H), or calanoid copepods (C).

Lake (<i>n</i>)*	Lake ID	Zooplankton species	Categories
Council Lake (8)	COL	<i>Leptodiatomus tyrelli</i>	C
		<i>Daphnia pulex</i>	D
		<i>Holopedium gibberum</i>	H
Elk Lake (9)	ELL	<i>Hesperodiatomus franciscanus</i>	C
		<i>Daphnia pulex</i>	D
Sooke Lake Reservoir (11)	SOL	<i>Leptodiatomus tyrelli</i>	C
		<i>Daphnia rosea</i>	D
Shawnigan Lake (11)	SHL	<i>Hesperodiatomus franciscanus</i>	C
		<i>Daphnia pulex</i>	D
		<i>Holopedium gibberum</i>	H
Coquitlam Reservoir (1)	COR	Unidentified calanoid	C
		<i>Daphnia rosea</i>	D
		<i>Holopedium gibberum</i>	H
Lubbe Reservoir (1)	LUL	<i>Holopedium gibberum</i>	H
		<i>Leptodiatomus tyrelli</i>	C
		<i>Daphnia rosea</i>	D
Deception Reservoir (1)	DER	<i>Hesperodiatomus franciscanus</i>	C
		<i>Daphnia middendorffiana</i>	D
Seymour Reservoir (1)	SER	<i>Daphnia rosea</i>	D
		<i>Holopedium gibberum</i>	H
Cusheon Lake (1)	CUL	<i>Daphnia pulex</i>	D
		<i>Holopedium gibberum</i>	H
Butchart Lake (1)	BUT	<i>Leptodiatomus tyrelli</i>	C
		<i>Holopedium gibberum</i>	H
Goldstream Reservoir (1)	GOL	<i>Leptodiatomus tyrelli</i>	C
		<i>Daphnia rosea</i>	D
		<i>Holopedium gibberum</i>	H
Japan Gulch Reservoir (1)	JGR	<i>Epishura nevadensis</i>	C
		<i>Holopedium gibberum</i>	H

**n* = number of dates sampled from June to November 2001.

one-tailed *F* test), then we rejected the null hypothesis of isotopic homogeneity for that group. The values of σ_{Δ} ($\sigma_{\Delta N} = 0.98$, $n = 56$; $\sigma_{\Delta C} = 1.3$, $n = 107$) from Post (2002), when used for a single taxon of zooplankton, are conservative estimates of variation in trophic enrichment. By using this test for a single taxon over time, we are not testing homogeneity of diet, as did Ponsard and Arditì (2000), but rather temporal homogeneity of isotopic variance resulting from changes in diet and baselines. For example, if a group with calanoids and *Daphnia* has a significantly higher σ_g^2 than $\sigma_{\Delta N}^2$, either taxa have different trophic positions but share a common baseline or taxa have different baselines and differences in $\delta^{15}\text{N}$ are not solely a result of trophic variation. Although we did not, and perhaps could not, measure δ_{base} for each taxon, this approach allowed us to determine whether isotopic variation within a group is larger than we would expect based on variable fractionation from a common baseline signature.

We examined among-lake patterns of within-lake differences in the isotopic signatures of *Daphnia*, *Holopedium*, and calanoid copepods. For each lake our dependent variable was the difference between the $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ of two zooplankton taxa present in that lake. From our twelve study lakes, we used eight to compare *Daphnia*–calanoid isotope signatures, seven to compare *Holopedium*–calanoid isotope signatures, and seven to compare *Daphnia*–*Holopedium* iso-

tope signatures. This approach allowed us to quantify within-lake variability of zooplankton taxa independent of among-lake differences in isotopic baselines.

Results

Among- and within-lake variability—In our nested ANOVA the lake effect accounted for 56.4% of the total variance in $\delta^{15}\text{N}$ but did not account for a significant component of the variation in $\delta^{13}\text{C}$ or C:N ratio (Table 2). We found a significant taxa effect for $\delta^{13}\text{C}$ ($p < 0.001$), $\delta^{15}\text{N}$ ($p < 0.001$), and C:N ratio ($p < 0.001$) (Table 2). Within-lake differences due to taxonomic groupings accounted for 36.7% of the variance in $\delta^{15}\text{N}$, 41.7% of the variance in $\delta^{13}\text{C}$, and 62.5% of the variance in C:N ratio (Table 2).

Within-lake variability—The nested ANOVA indicated isotopic differences among taxa within zooplankton communities. To identify the source of these differences for Council Lake (COL), Elk Lake (ELL), Sooke Lake Reservoir (SOL), and Shawnigan Lake (SHL), we ran a one-way ANOVA and Tukey's post hoc tests for each lake (Table 3). In all four lakes, calanoid copepods had the highest mean $\delta^{15}\text{N}$ (Fig. 1). However, in COL, the mean $\delta^{15}\text{N}$ measurements of *Daphnia* and calanoid copepods were not statistically different. The $\delta^{13}\text{C}$ of calanoid copepods was signifi-

Table 2. Nested ANOVA table for among- and within-lake variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for three zooplankton taxa in four lakes. The design is unbalanced because Council and Shawnigan Lake have three taxa and Elk and Sooke Lake have only two. Variance components are estimated using maximum likelihood methods.

Variable	df	MSQ	F statistic	p value	% Variance
$\delta^{13}\text{C}$					
Lake	3	45.47	2.083	0.204	17.0
Taxa (Lake)	6	21.63	10.49	<0.001	41.7
Residual	77	20.62			41.3
$\delta^{15}\text{N}$					
Lake	3	170.73	5.30	0.040	56.4
Taxa (Lake)	6	31.89	47.21	<0.001	36.7
Residual	77	0.676			6.9
C:N					
Lake		22.45	1.380	0.336	0.001
Taxa (Lake)	36	16.118	17.96	<0.001	62.5
Residual	77	0.897			37.5

cantly lower than $\delta^{13}\text{C}$ of *Daphnia* or *Holopedium* in SHL and SOL but was not significantly different from *Daphnia* in COL or ELL. Seasonal variation in $\delta^{13}\text{C}$ was typically small (<3‰) for individual taxa within a lake (Table 4). Only the calanoids in SOL showed a clear temporal trend. In this case, the $\delta^{13}\text{C}$ declined from -34.0‰ to -35.7‰ throughout the sampling season. Seasonal variation in $\delta^{15}\text{N}$ was variable among and within species. The $\delta^{15}\text{N}$ of calanoids increased from June to November in both SOL (4.7–6.6‰) and SHL (7.8–10.7‰). Over the same time period the $\delta^{15}\text{N}$ of *Daphnia* increased in SOL (2.1–3.5‰) and SHL (4.9–7.4‰). The $\delta^{15}\text{N}$ of *Daphnia* and calanoids in Council Lake was lowest in June (3.4‰ for both taxa), increased to a maximum in July (~5.5‰ for both taxa), and then declined through to September (Table 4). The difference in $\delta^{15}\text{N}$ between *Daphnia* and calanoids was seasonally variable in Elk Lake, but the $\delta^{15}\text{N}$ of calanoids was higher than *Daphnia* for all sampling dates.

Diet and baseline homogeneity—The temporal variation in $\delta^{15}\text{N}$ of individual taxa was small and always significantly

less than interspecific variance in trophic fractionation (Table 4). In groups with multiple taxa, we rejected the null hypothesis of isotopic homogeneity for three out of four lakes. In all such groupings, variation in $\delta^{15}\text{N}$ was more heterogeneous than would be expected by variability in Δ_N alone. For $\delta^{13}\text{C}$, the temporal variance of individual taxa was small in all cases except Elk Lake (Table 4). We only rejected the hypothesis of homogeneity of $\delta^{13}\text{C}$ for groups of zooplankton in Elk Lake and Sooke Lake Reservoir.

Among-lake variability of within-lake differences—To place our observations of within-lake differences into a larger regional context, we compared the results from Council Lake, Elk Lake, Sooke Lake Reservoir, and Shawnigan Lake to eight other lakes in the region. In all cases where calanoid copepods were present, they had a higher mean $\delta^{15}\text{N}$ than either *Daphnia* or *Holopedium*, and in all but two lakes, calanoid copepods had a lower $\delta^{13}\text{C}$ than *Daphnia* or *Holopedium* (Fig. 2). For the eight lakes where calanoid copepods and *Daphnia* occurred together, the $\delta^{15}\text{N}$ of calanoid copepods was on average 2.55‰ higher ($t = 5.817$, $df = 7$, $p < 0.001$) and $\delta^{13}\text{C}$ was on average 2.19‰ lower ($t = 3.94$, $df = 7$, $p = 0.006$) than *Daphnia* $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures, respectively (Fig. 3). In the seven lakes where calanoid copepods and *Holopedium* occurred together, the $\delta^{15}\text{N}$ of calanoid copepods was 2.44‰ higher ($t = 11.51$, $df = 6$, $p < 0.001$) and the $\delta^{13}\text{C}$ was 2.23‰ lower ($t = 2.92$, $df = 6$, $p = 0.027$) than $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of *Holopedium*, respectively (Fig. 3). The mean among-lake difference between the $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ of *Daphnia* and *Holopedium* was not significantly different from zero ($\delta^{15}\text{N}$, $t = -0.49$, $df = 6$, $p = 0.644$; $\delta^{13}\text{C}$, $t = -0.467$, $df = 6$, $p = 0.657$) (Fig. 3).

Discussion

Among- and within-lake variability—The results of our nested ANOVA confirm the need for among-system baseline correction of $\delta^{15}\text{N}$, as previously stressed by several studies (Cabana and Rasmussen 1996; McKinney et al. 1999; Vander Zanden et al. 1999; Post 2002). Of the total variance in $\delta^{15}\text{N}$ of zooplankton, 56.4% was accounted for by differences among lakes. In our study lakes, zooplankton $\delta^{15}\text{N}$ varied from 0.72‰ for *Daphnia* in Coquitlam Reservoir to 13.00‰

Table 3. Within-lake variability of zooplankton (a) $\delta^{15}\text{N}$ and (b) $\delta^{13}\text{C}$. ANOVA was performed on seasonal means of different zooplankton taxa; *Daphnia* (D), *Holopedium* (H), and calanoid copepods (C) (Table 2). Underlines group taxa whose seasonal means are not significantly different based on Tukey's post hoc tests ($p < 0.05$).

Lake	F statistic	p value	r ²	Taxa (mean; n)
(a) $\delta^{15}\text{N}$				
Council Lake	$F_{2,17} = 10.4$	0.001	0.55	<u>H(2.88; 5)</u> <u>D(3.89; 7)</u> C(4.70; 8)
Elk Lake	$F_{1,14} = 68.4$	<0.001	0.83	<u>D(8.40; 9)</u> <u>C(13.0; 7)</u>
Shawnigan Lake	$F_{2,26} = 38.6$	<0.001	0.75	<u>H(5.90; 11)</u> <u>D(5.98; 7)</u> <u>C(8.95; 11)</u>
Sooke Lake Reservoir	$F_{1,20} = 123.0$	<0.001	0.85	<u>D(3.14; 11)</u> <u>C(5.71; 11)</u>
(b) $\delta^{13}\text{C}$				
Council Lake	$F_{2,17} = 5.90$	0.011	0.41	<u>D(-34.02; 7)</u> <u>C(-33.62; 8)</u> <u>H(-32.04; 5)</u>
Elk Lake	$F_{1,14} = 1.67$	0.218	0.11	<u>C(-30.57; 7)</u> <u>D(-28.82; 7)</u>
Shawnigan Lake	$F_{2,26} = 15.7$	<0.001	0.55	<u>C(-32.08; 11)</u> <u>H(-30.44; 5)</u> <u>D(-30.29; 11)</u>
Sooke Lake Reservoir	$F_{1,20} = 276.9$	<0.001	0.93	<u>C(-34.60; 11)</u> <u>D(-30.62; 11)</u>

Table 4. Test of isotopic homogeneity of *Daphnia* (D), *Holopedium* (H), and calanoid copepods (C) in four study lakes with temporal sampling. We compared within-taxa temporal variance of isotopic composition (σ_t^2) to the interspecific variance in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ enrichment derived by Post (2002, fig. 6) ($\sigma_{\Delta\text{N}}^2 = 0.960$, $n = 56$; $\sigma_{\Delta\text{C}}^2 = 1.69$, $n = 107$) using a one-tailed F test ($F = \sigma_t^2/\sigma_{\Delta}^2$) (Ponsard and Arditì 2000). We reject the null hypothesis of isotopic homogeneity when F is significantly greater than one. ** $p < 0.01$, * $p < 0.05$, NS = nonsignificant.

Lake	Grouping	$\delta^{15}\text{N}$ F	$\delta^{15}\text{N}$ range (‰)	$\delta^{13}\text{C}$ F	$\delta^{13}\text{C}$ range (‰)	n
Council Lake	D	<1	2.2	<1	2.6	7
	H	<1	1.8	2.035 NS	3.2	5
	C	<1	2.1	<1	2.1	8
	D+H+C	1.02 NS		<1		20
Elk Lake	D	1.72 NS	4.3	2.57*	6.9	9
	C	<1	2.2	6.54**	8.7	7
	D+C	6.97**		4.47**		16
Shawnigan Lake	D	<1	2.5	<1	2.5	11
	H	<1	1.6	<1	2.8	7
	C	1.32 NS	3.1	<1	1.3	11
	D+H+C	3.3**		<1		29
Sooke Lake Reservoir	D	<1	1.3	<1	1.4	11
	C	<1	1.9	<1	1.7	11
	D+C	2.09*		2.63**		22

for calanoid copepods in Elk Lake. This is a large range for basal taxa of the food web but is comparable to previously reported variability in $\delta^{15}\text{N}$ signatures among lakes (Cabana and Rasmussen 1996; Vander Zanden et al. 1999; Lake et al. 2001; Post 2002). In our study, the large among-lake variation of individual zooplankton species and of particulate organic matter (<41 μm) (unpubl. data) is likely related to anthropogenic activity in the watersheds of our study lakes, as previously suggested by other studies (Cabana and Rasmussen 1996; McKinney et al. 1999). However, our study is the first to quantify the importance of zooplankton species composition to the determination of $\delta^{15}\text{N}$ baselines. In our data set, within-lake differences in zooplankton taxa accounted for 36.7% of the total variance in $\delta^{15}\text{N}$, indicating taxon-specific isotopic signatures within zooplankton communities.

Unlike for $\delta^{15}\text{N}$, we found no significant among-lake differences in zooplankton $\delta^{13}\text{C}$ but found large and significant within-lake differences among zooplankton taxa. Only 17% of the total variance was attributed to among-lake variability, whereas 41.7% was accounted for by differences due to taxonomic grouping. Although our data provide no support for among-lake baseline correction of $\delta^{13}\text{C}$, our range in $\delta^{13}\text{C}$ of zooplankton among four lakes is small compared to studies with more lakes (France et al. 1997; Grey et al. 2000; Post 2002). Even among the 10 lakes where *Daphnia* was present (Table 1), the $\delta^{13}\text{C}$ only varied from -34.4‰ to -30.3‰ , whereas *Daphnia middendorffiana* varied from -44.7‰ to -31.5‰ over a year in a single Alaskan lake (Gu et al. 1999). However, our results show large within-lake variability of $\delta^{13}\text{C}$ signature among zooplankton taxa (Fig. 1). The range of $\delta^{13}\text{C}$ within a lake varies from 1.75‰ in Elk

Lake to 3.98‰ in Sooke Lake Reservoir (Table 3). The magnitude of this variation is not surprising, given previous studies of within-lake variation in the $\delta^{13}\text{C}$ of different zooplankton taxa (Grey and Jones 1999) and zooplankton size fractions (Post 2002). However, it highlights the importance of zooplankton taxonomic composition in determining $\delta^{13}\text{C}$ baselines.

Isotopic homogeneity of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ — $\delta^{15}\text{N}$ values: In the four lakes with temporal sampling, the temporal variance of a single taxon was significantly less than the interspecific variance of Δ_{N} . This suggests that either Δ_{N} is overestimated in the literature (Post 2002) or intrataxon temporal variation, resulting from changes in diet, baseline, and fractionation, is small relative to $\sigma_{\Delta\text{N}}^2$. Improved taxon-specific estimates of Δ_{N} would clearly increase the sensitivity of this approach. In three of four lakes, groups with multiple taxa showed isotopic heterogeneity of $\delta^{15}\text{N}$, suggesting that the variation in $\delta^{15}\text{N}$ is significantly larger than we would expect from the interspecific variance of Δ_{N} . This heterogeneity could result from either taxon-specific baseline $\delta^{15}\text{N}$ signatures or different trophic positions on a common baseline.

$\delta^{13}\text{C}$ values: We found few cases where the temporal variation of a single taxon's $\delta^{13}\text{C}$ signatures was significantly larger than interspecific variation in Δ_{C} . In contrast to the results of Ponsard and Arditì (2000), some of our groupings with multiple taxa showed isotopic heterogeneity. The $\delta^{13}\text{C}$ of *Daphnia* and calanoid copepods in Elk Lake is highly variable over time (Table 4), and σ_t^2 is significantly greater than $\sigma_{\Delta\text{C}}^2$. The high temporal variance in Elk Lake zooplankton has interesting implications for baseline determination.

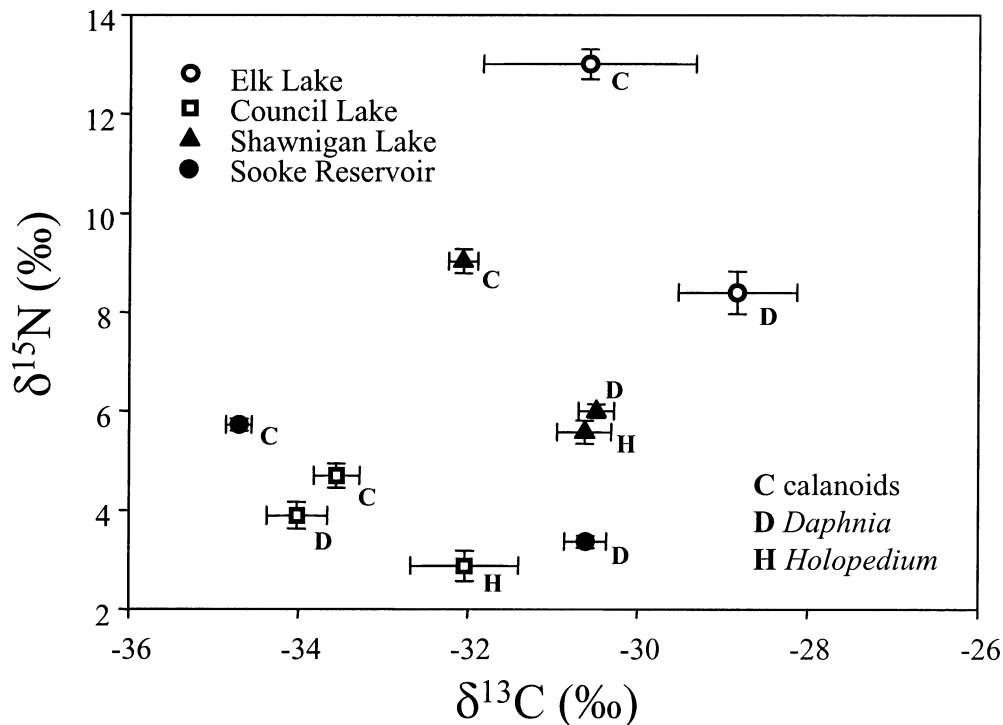


Fig. 1. Pelagic zooplankton food web structure of four lakes: Council Lake (COL), Elk Lake (ELL), Shawnigan Lake (SHL), and Sooke Lake Reservoir (SOL). We interpret the within-lake range in $\delta^{15}\text{N}$ as the maximum amount of error introduced to an estimate of fish trophic position that neglects species composition. Assuming a mean trophic level enrichment of 3.4‰ for $\delta^{15}\text{N}$, the maximum number of trophic levels worth of error in the estimation of fish trophic position is 0.54 for COL, 1.35 for ELL, 0.90 for SHL, and 0.76 for SOL. The mean maximum amount of this error is 0.90 (SE = 0.17, $n = 4$).

Either both taxa have a radically different feeding behavior in Elk Lake, compared to other lakes with the same $\delta^{13}\text{C}$ baseline, or they have a similar feeding behavior and Elk Lake has a variable $\delta^{13}\text{C}$ baseline. Given the low temporal variability of these same taxa in Shawnigan Lake (Table 4), it is more likely that Elk Lake has a seasonally variable baseline.

Given our data, we cannot determine whether among-taxon variability is a result of taxon-specific baselines or variability in feeding behavior. For example, the differences in $\delta^{15}\text{N}$ between *Daphnia* and calanoids could be due to different trophic positions, different fractionations from a common baseline, or different baselines. To help discriminate between these possibilities we consider factors that can affect the within-lake variability of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of different zooplankton taxa.

Within-lake variability of $\delta^{15}\text{N}$ —Trophic variation: Trophic food chain models often consider zooplankton communities as a single trophic level of herbivores connecting algae to fish. However, previous studies have shown that both calanoid copepods and *Daphnia* are omnivores, feeding on nonphotosynthetic prey including bacteria, ciliates, heterotrophic nanoflagellates (HNFs), rotifers, and other microzooplankton (Paul et al. 1995; Sanders et al. 1996; Burns and Schallenberg 2001). Species of both *Daphnia* and calanoid copepods have higher survival and reproductive ca-

pability when their algal diet is supplemented with heterotrophic organisms (Williamson and Butler 1986; Sanders et al. 1996). *Daphnia* and calanoids both consume HNFs, but calanoids are more effective grazers of HNFs, particularly under eutrophic conditions (Burns and Schallenberg 2001). From these previous studies, we know that both *Daphnia* and calanoid copepods can be omnivorous, but to what extent likely depends on lake conditions.

In our study, we used $\delta^{15}\text{N}$ to quantify the relative difference between feeding behaviors of different zooplankton taxa. Without isotopic measurements of the algae, protozoans, or rotifers, we have no evidence for what proportion of a zooplankton's diet is algal versus heterotrophic in origin. However, we hypothesize that the among-taxon variation in $\delta^{15}\text{N}$ is partially a result of calanoid copepods feeding higher in the food chain than the predominantly herbivorous *Daphnia* or *Holopedium* taxa. Among all study lakes, the difference in $\delta^{15}\text{N}$ between calanoid copepods and *Daphnia* or *Holopedium* was 2.55‰ and 2.44‰, respectively (Fig. 3). If we assume an average trophic enrichment of 3.4‰ (Minagawa and Wada 1984; Post 2002) and assume that *Daphnia* and calanoids have the same baseline $\delta^{15}\text{N}$, then calanoids are an average of 0.74 (SE = 0.13, $n = 8$) trophic levels higher than *Daphnia*. However, this estimate of trophic variation is confounded by possible differences in taxon-specific $\delta^{15}\text{N}$ baselines or differences in fractionation from a common baseline.

Within-lake variability of $\delta^{13}\text{C}$ —In 10 of the 12 study lakes, the $\delta^{13}\text{C}$ of calanoid copepods was lower than *Daphnia* or *Holopedium* (Fig. 2a), resulting in a mean difference ($\sim 2.0\text{‰}$) that is significantly greater than zero (Fig. 3b). There are two likely explanations for why calanoid copepods were depleted in ^{13}C relative to *Daphnia* or *Holopedium*. First, lipids are isotopically lighter than other body constituents (Tieszen et al. 1983; Kling et al. 1992), and since copepods can store more lipids than other zooplankton taxa (Arts et al. 1993) they may generally have lighter $\delta^{13}\text{C}$ signatures. Second, calanoid copepods may be feeding on a food source that is isotopically lighter than the food source of other zooplankton, either by feeding more selectively or by feeding deeper in a lake than either *Daphnia* or *Holopedium*.

Lipids—The effect of lipids on the $\delta^{13}\text{C}$ signature of different zooplankton taxa and the corresponding effects on baseline $\delta^{13}\text{C}$ determination are unclear from the current literature. Some studies show that lipids can affect the $\delta^{13}\text{C}$ of zooplankton (Kling et al. 1992; Leggett 1998), while others report no significant effect (France 1995; Campbell et al. 2000). Considering the maximum effect of lipids on $\delta^{13}\text{C}$ may help bound the interpretation of our data. If lipids in calanoid copepods are $\sim 5\text{‰}$ depleted from other body tissue (Kling et al. 1992) and represent upward of 65% of the body tissue (maximum estimate from Arts et al. 1993) then lipids could cause a depletion in calanoid copepods of up to 3.25‰. In our study, the difference between the $\delta^{13}\text{C}$ of calanoid copepods and *Daphnia* or *Holopedium* is an average of $\sim 2.0\text{‰}$ with differences as high as 4.4‰ (Fig. 3). Therefore, if lipids have no effect on *Daphnia* or *Holopedium* $\delta^{13}\text{C}$, the maximum effect of lipids on calanoid copepods cannot fully account for the range in among-taxa $\delta^{13}\text{C}$ variability. Rather, the feeding behavior of calanoid copepods, either by selective feeding or by feeding deeper in the water column than *Daphnia* or *Holopedium*, likely contributes to the discrepancy in $\delta^{13}\text{C}$ signatures among zooplankton taxa.

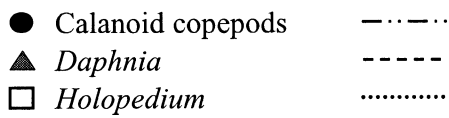
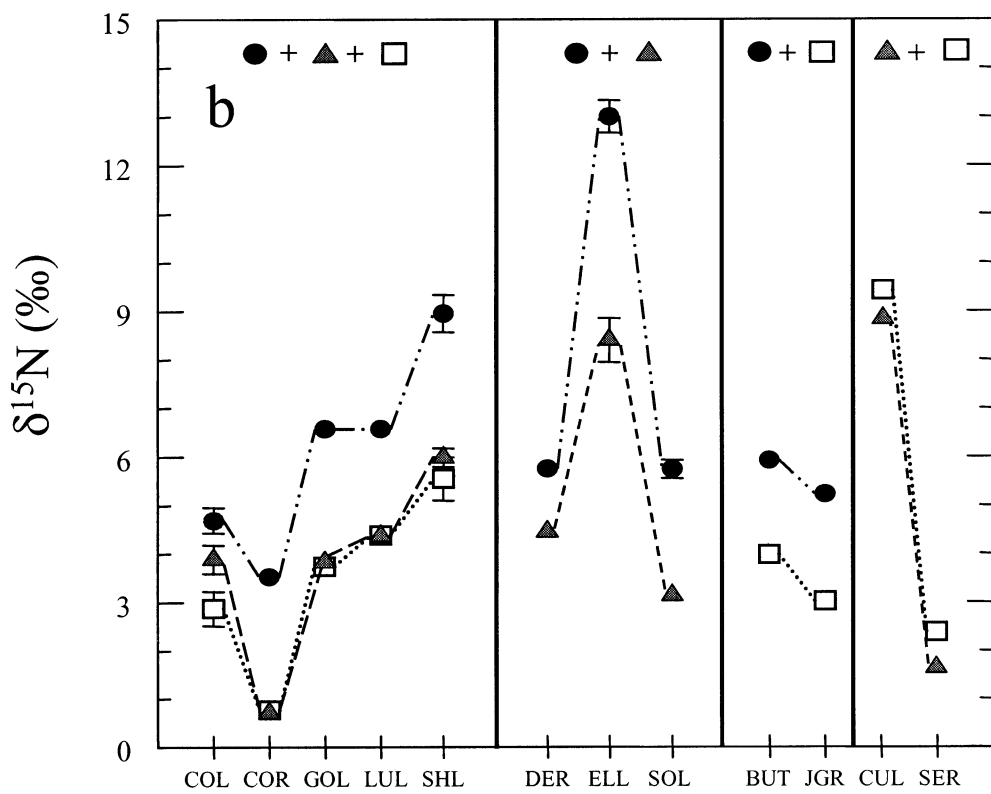
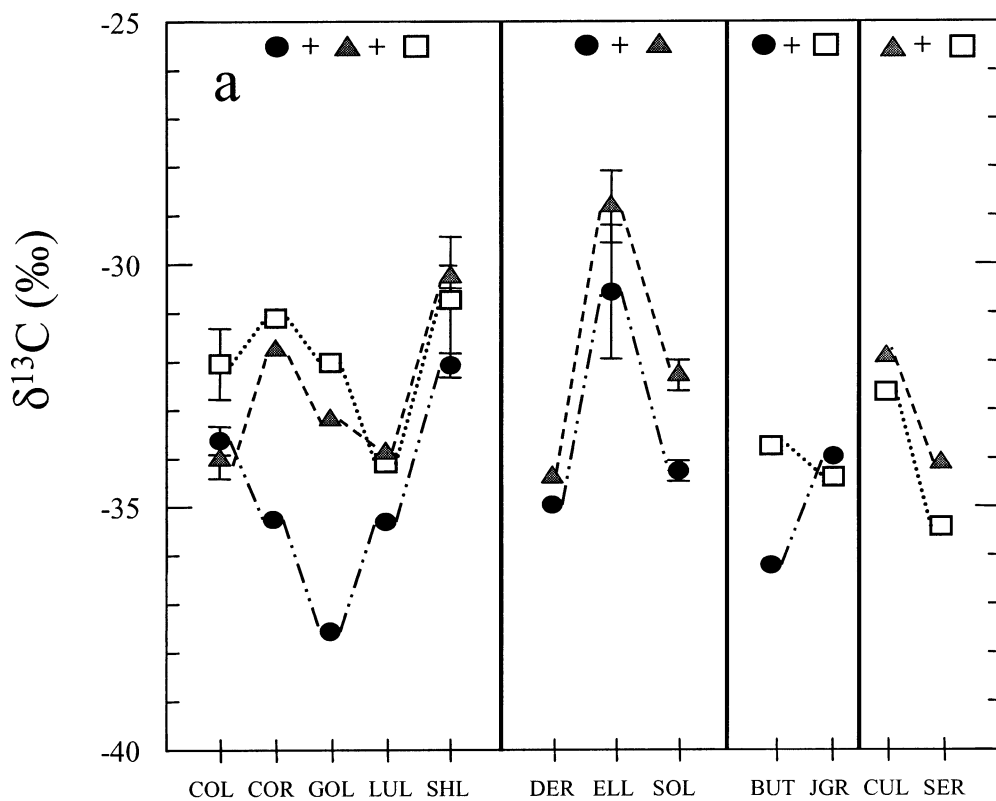
Selective feeding—Among-taxa variability in $\delta^{13}\text{C}$ (Grey and Jones 1999; our study) suggests that a single size fraction of particulate organic matter (POM) is not a suitable baseline for the $\delta^{13}\text{C}$ of multiple zooplankton taxa. Several studies have shown that the $\delta^{13}\text{C}$ of zooplankton is isotopically lighter than size fractions of POM (Kling et al. 1992; Zohary et al. 1994; del Gorgio and France 1996; Meili et al. 1996; Jones et al. 1999; Grey et al. 2000), and some have attributed these differences to the selective feeding behavior of zooplankton (del Gorgio and France 1996; Meili et al. 1996; Jones et al. 1999). POM is a mixture of algae, detritus (allochthonous or autochthonous in origin), bacteria, and small planktonic organisms. Different components within POM can have different $\delta^{13}\text{C}$ signatures (Leggett 1998). For example, a more enriched terrestrial $\delta^{13}\text{C}$ signature may mask a lighter algal $\delta^{13}\text{C}$ signature, especially in lakes with large allochthonous carbon input (Meili et al. 1996; Jones et al. 1999; Grey et al. 2001). In our study, the $\delta^{13}\text{C}$ of POM ($< 41 \mu\text{m}$) varied among lakes in step with zooplankton $\delta^{13}\text{C}$ (unpubl. data). However, since the $\delta^{13}\text{C}$ of a single size fraction of POM does not reflect the $\delta^{13}\text{C}$ of different zooplank-

ton taxa, it may not reflect the $\delta^{13}\text{C}$ of the primary food source that fuels upper trophic levels.

Feeding depth—The $\delta^{13}\text{C}$ signature of zooplankton, and how we establish a pelagic baseline, may depend on where different zooplankton taxa feed in a thermally stratified water column. Respired carbon from heterotrophic metabolism is isotopically lighter than the consumed carbon source (Rau 1978), and, in clear-water lakes, high epilimnetic respiration relative to production combined with hypolimnetic metabolism can result in a depletion of the $\delta^{13}\text{C}$ of dissolved inorganic carbon (DIC) (France et al. 1997). During the period of thermal stratification in lakes, a vertical gradient in the $\delta^{13}\text{C}$ of DIC could lead to a vertical gradient in the $\delta^{13}\text{C}$ of POM. Many of our study lakes are clear-water systems (mean DOC of 2.9 mgC L^{-1}) and have metalimnetic chlorophyll *a* (Chl *a*) maxima throughout much of the summer. In addition, the $\delta^{13}\text{C}$ signature of metalimnetic POM ($< 41 \mu\text{m}$) in our study lakes is depleted by $> 1\text{‰}$ relative to epilimnetic POM (unpubl. data), as commonly reported in other studies (del Gorgio and France 1996; France et al. 1997). If taxa are feeding at different depths in the water column this could affect baseline $\delta^{13}\text{C}$ determination of zooplankton. Unfortunately, we have not quantified the vertical feeding behavior of each taxon in each of our lakes. However, in Council Lake, a fishless lake with abundant invertebrate predation, the *Daphnia* and *Holopedium* populations have peak abundances (both day and night) in the hypolimnion and epilimnion, respectively (unpubl. data). In this lake, the $\delta^{13}\text{C}$ of *Daphnia* is significantly lower than the $\delta^{13}\text{C}$ of *Holopedium* (Table 3). Although perhaps an isolated case, feeding depth could differentially affect the $\delta^{13}\text{C}$ of zooplankton taxa and complicate baseline determination.

A combination of lipids, selective feeding, and vertical feeding behavior in a stratified water column likely influences the $\delta^{13}\text{C}$ of zooplankton in our study lakes. However, these competing hypotheses cannot be resolved with the current data; therefore, we cannot quantify the relative magnitudes of the effect of lipids, depth, and selective feeding on the $\delta^{13}\text{C}$ of different zooplankton taxa and the combined effects on baseline $\delta^{13}\text{C}$ determination.

*Among-lake isotopic variability of the $\delta^{15}\text{N}$ of *Daphnia* and calanoid copepods: different baselines or trophic variation?*—The temporal heterogeneity of $\delta^{15}\text{N}$ in a group of zooplankton taxa can result from different feeding behaviors (namely trophic position) and different baselines. Isotopic homogeneity of $\delta^{15}\text{N}$ for individual taxa suggests that feeding behaviors coupled with temporal baselines can be relatively stable within a lake. Isotopic heterogeneity of $\delta^{15}\text{N}$ for groups of zooplankton suggests that differences among taxa are greater than expected based only on variable fractionation. If this heterogeneity was solely a result of different isotopic baselines, then among lakes we might expect random variation in the difference between the $\delta^{15}\text{N}$ of *Daphnia* and calanoids. However, we found that the $\delta^{15}\text{N}$ of calanoid copepods is higher than *Daphnia* in all eight lakes where they occur together (Fig. 3). Either the baselines are consistently higher for calanoids among lakes or the variation of within-lake taxon-specific baseline $\delta^{15}\text{N}$ is small compared



to trophic variation among taxa. It is also possible that *Daphnia* and calanoids share a common baseline but calanoids have a larger ^{15}N fractionation factor. Although we cannot explicitly quantify among-lake trophic variation due to unknown differences in baselines and fractionation, our data are consistent with the hypothesis that calanoids feed at a higher trophic position than *Daphnia* or *Holopedium*.

Elk Lake (ELL) presents an interesting case where alternate $\delta^{15}\text{N}$ baselines may exist for *Daphnia* and calanoid copepods. The average difference in $\delta^{15}\text{N}$ between *Daphnia* and calanoid copepods is 4.83‰, but this difference is seasonally variable (range = 1.63‰–6.2‰). The $\delta^{15}\text{N}$ of calanoids in ELL follows a similar temporal pattern as in SOL and SHL, but the $\delta^{15}\text{N}$ of *Daphnia* in Elk Lake changes dramatically over the season in response to variable nitrogen dynamics and changes in algal species composition (unpubl. data). At this point, we cannot discriminate between feeding behavior and differences in taxon-specific isotopic baselines; however, several lines of evidence suggest that both are important in determining the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baselines for pelagic production in lakes, and in some cases a single taxa may be a more appropriate baseline for the pelagia of lakes.

Daphnia as an isotopic baseline among and within lakes—Several studies use bulk zooplankton to establish a baseline for the pelagia of lakes (Cabana and Rasmussen 1994; Post 2002). Using bulk zooplankton is methodologically simple but is only suitable if the mixture of taxa reflects the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the primary food source in the pelagia. If fish feed nonselectively on a similar size class of zooplankton that is also collected as the baseline, then the isotopic signature of a bulk zooplankton size fraction could accurately reflect fish diet. However, if fish feed selectively by zooplankton taxa and taxa are isotopically distinct, then using a bulk size fraction of zooplankton could introduce error into the estimate of fish trophic position. To estimate the maximum amount of this error, we calculated a range of zooplankton $\delta^{15}\text{N}$ for each lake (Figs. 1 and 2). For lakes with temporal sampling, the among-lake mean of the maximum amount of error is 0.90 (SE = 0.17, $n = 4$) trophic levels (Fig. 1). For all lakes together, the mean of the maximum error is 0.64 (SE = 0.10, $n = 12$) trophic levels (range = 0.2 to 1.35) (Fig. 2). Consider Elk Lake as an example, which has a maximum error of 1.35 trophic levels. We could achieve this maximum error using two different approaches to baseline determination. If we used a bulk size fraction that was made up of primarily *Daphnia*, then our error would be a maximum if fish fed only on calanoids. Likewise, we could incur maximal error if we used only *Daphnia* as our baseline and fish fed only on calanoids. The actual amount of error for Elk Lake likely varies between 0 and 1.35 trophic levels and ultimately depends on the $\delta^{15}\text{N}$ of the size fraction of bulk zooplankton collected, the zooplankton spe-

cies composition, and the foraging behavior of the fish species of interest.

In this paper we present *Daphnia* as an alternate but complementary method for measuring the baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the pelagia of lakes. *Daphnia*, as a short-lived organism, does not provide the same temporal integration as mussels (Fry 1999; Post 2002) but is better suited for finer scale temporal integration of pelagic $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ signatures. Mussels are commonly used to integrate the temporal variance in the $\delta^{15}\text{N}$ or the $\delta^{13}\text{C}$ of pelagic primary production (McKinney et al. 1999; Post 2002). Mussels are most suitable for the comparison of processes that affect the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ over large temporal scales because they integrate the isotopic signature of the pelagia over a longer period of time than zooplankton (Cabana and Rasmussen 1996; Post 2002). The temporal variation in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *Daphnia* can be large, as in Elk Lake, where it suggests that the pelagic baseline varies throughout the season. This result is both a limitation and strength of using *Daphnia* as a baseline. For example, coarse sampling of a zooplankton taxa with a short tissue turnover time may miss ecologically important sources of production that have substantially different isotopic signatures. This originally motivated the use of long-lived consumers, such as mussels, as pelagic baselines (Cabana and Rasmussen 1996; Post 2002). However, a time series of the $\delta^{15}\text{N}$ of *Daphnia*, with a carefully chosen temporal resolution, may be useful to detect, for example, fine-scale seasonal patterns of anthropogenic activities in recreational or residential lakes. In this case, it is better to use a single species of zooplankton (or multiple species) because changes in species composition will likely increase temporal variability in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of a bulk size fraction of zooplankton.

A potentially significant drawback of using *Daphnia* as a baseline is that the enrichment of ^{15}N per trophic level depends on the C:N ratio of the ingested algae (Adams and Sterner 2000). Further research comparing the $\delta^{15}\text{N}$ of *Daphnia* among lakes with food sources of varying C:N ratios would be valuable for establishing *Daphnia* as a baseline indicator of $\delta^{15}\text{N}$ in the pelagia of lakes. Using zooplankton taxa other than *Daphnia*, such as copepods, may be problematic for two reasons. First, if copepods have high lipid content, $\delta^{13}\text{C}$ may change seasonally or vary among lakes in response to variation in lipid storage. Second, variable calanoid omnivory may complicate the interpretation of $\delta^{15}\text{N}$ among lakes or the temporal pattern of $\delta^{15}\text{N}$ within a lake.

Zooplankton communities are complex, but this complexity is rarely addressed in the context of isotopic baseline determination. Future research should focus on the among-lake variability of individual zooplankton taxa and the primary factors that affect the relative isotopic differences between taxa (see variation in Fig. 3). For example, zooplankton taxa that coexist in the same pelagic environ-

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Fig. 2. (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ of different zooplankton taxa in 12 lakes. Lakes are grouped by different compositions of the zooplankton community. Error bars for the four lakes with temporal coverage are plus or minus one standard error of the seasonal mean. Dashed lines are for clarity of interpretation. The mean maximum number of trophic levels worth of error in the estimation of fish trophic position is 0.64 (SE = 0.10, $n = 12$) (see Fig. 1).

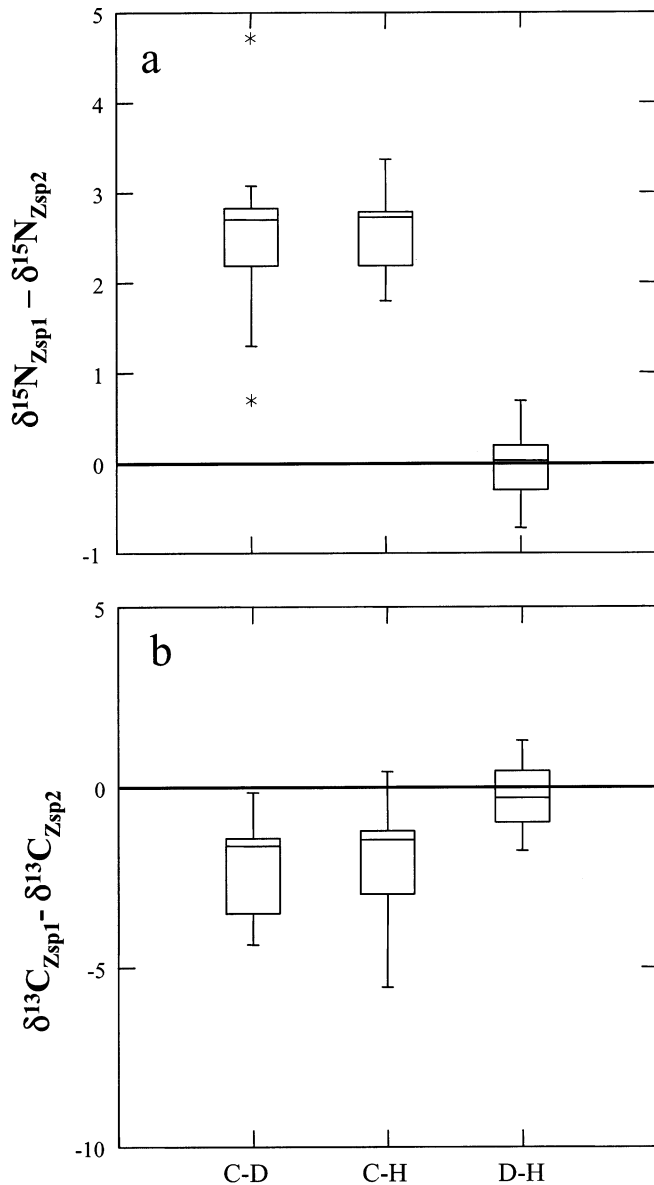


Fig. 3. Boxplots showing the median and quartiles of the differences between two zooplankton taxa. Zooplankton taxa are calanoid copepods (C), *Daphnia* (D), and *Holopedium* (H). Number of lakes denotes the subset of lakes, from all 12 study lakes, where the two zooplankton taxa were present in sufficient abundance for isotopic analysis. (a) Mean calanoid $\delta^{15}\text{N}$ is 2.55‰ higher than *Daphnia* ($t = 5.817$, $df = 7$, $p < 0.001$) and 2.44‰ higher than *Holopedium* ($t = 11.51$, $df = 6$, $p < 0.001$). (b) Mean calanoid $\delta^{13}\text{C}$ is 2.19‰ lighter than *Daphnia* ($t = 3.94$, $df = 7$, $p = 0.006$) and 2.23‰ lighter than *Holopedium* ($t = 2.92$, $df = 6$, $p = 0.027$). Mean difference between *Daphnia* and *Holopedium* $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ is not significantly different from zero ($\delta^{15}\text{N}$, $t = -0.49$, $df = 6$, $p = 0.644$; $\delta^{13}\text{C}$, $t = 0.467$, $df = 6$, $p = 0.657$).

ment may partition food resources either by habitat selection in the water column or by food selectivity on the basis of size or quality. Better consideration of zooplankton trophic structure and food sources could help resolve the causes of

variation in the isotopic signatures at upper trophic levels. This complexity of trophic structure within the pelagic zooplankton community may have larger food web scale consequences. Using stable isotopes, we can determine whether differences at the base of the food chain propagate up the food chain to planktivorous fish and beyond. Pelagic fish are often size or taxa selective when foraging (Kerfoot 1982; Johnston and Mathias 1994) or may switch between prey of different quality (Mazumder et al. 1990). Since different zooplankton taxa have different isotopic signatures, this may help us track the diet of fish. If zooplankton are used appropriately as a baseline, the variation in upper trophic levels can more accurately reflect variation in the isotopic signature of zooplankton. If used poorly, then variation in zooplankton trophic structure (or baselines) will propagate as error in estimates of trophic position and food source.

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