

STABLE ISOTOPES AND PLANKTONIC TROPHIC STRUCTURE IN ARCTIC LAKES¹

GEORGE W. KLING² AND BRIAN FRY

The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543 USA

W. JOHN O'BRIEN

Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66044 USA

Abstract: Actual food-web structure or function is difficult to determine based on visual observation, gut analyses, or the feeding interactions expected from a given list of species. We used C and N stable-isotope distributions to define food-web structure in arctic lakes, and we compared that structure with results based on more traditional analyses. Although zooplankton species composition was similar across the eight lakes studied, the food-web structure varied greatly. In some lakes the copepod predator *Heterocope* fed on the herbivorous copepod *Diaptomus* as expected in a conventional food web. In most lakes, however, $\delta^{15}\text{N}$ data were consistent with *Heterocope* functioning as an herbivore rather than a predator. These inferences were supported by evidence from carbon isotopes and energy-flow data. Our study indicates that only two or three trophic levels exist in the macrozooplankton of these lakes, in comparison to five or six trophic levels reported in temperate lakes. Isotope analyses showed that actual food-web structure is poorly predicted from simple consideration of species lists and potential trophic interactions.

Key words: Arctic lakes; copepod predation; energy flow; food webs; omnivory; realized vs. potential food web; stable isotopes; trophic structure; zooplankton.

INTRODUCTION

Observations of predator–prey relationships, feeding strategies, and trophic energetics are often summarized in food-web diagrams (Pimm 1982). Such diagrams have been criticized as subjective constructs, strongly biased by our inability to observe the relevant taxonomic, spatial, and temporal variations in trophic interactions (Paine 1988). For example, many trophic interactions cannot be visually observed, and gut analysis is misleading if the gut contents are not assimilated. Some approaches measure potential trophic interactions derived from species lists or from observations of feeding in one system extrapolated to another. A “potential” food-web diagram shows all possible trophic interactions among species, whereas a “realized” food-web diagram connects organisms to their important food resources in a way that reflects actual resource use (Fig. 1). The realized food web is of more practical interest, but is difficult to measure. Because of these inherent difficulties, there is a need to combine several lines of evidence to clarify trophic relationships and distinguish actual trophic links from those potentially possible.

One little-used approach to this problem is to combine feeding observations and energy flow data with stable isotope measurements. The strength of stable-isotope analyses is that they measure actual assimila-

tion integrated over the time scale of tissue turnover in the organism. Because consumers generally have carbon and sulfur isotope compositions similar to their foods, these measurements place constraints on the importance of potential food sources. Nitrogen isotope measurements can be used to define trophic level because there is a consistent increase in the ^{15}N content of consumers with increasing trophic level (Miyake and Wada 1967, Owens 1987). Stable-isotope measurements of carbon, nitrogen, and sulfur have been helpful in determining the strength of food-web connections in marine and terrestrial systems (DeNiro and Epstein 1978, Rau et al. 1983, Schell 1983, Peterson and Fry 1987). In freshwaters, however, very few published studies have used multiple isotopes to analyze trophic structure (Estep and Vigg 1985, Fry 1986). To date no study has separated zooplankton species and combined isotope measurements with energy flow data.

In this study we report on planktonic food-web structure in eight arctic lakes as determined by isotope values of algae and individual zooplankton species. These arctic systems are well known and have relatively simple planktonic food webs. Our objective is to illustrate the differences in food-web structure based on isotope analyses compared to what is expected given traditional analyses, and to discuss the strengths and problems of using stable isotopes in freshwater ecology.

SITE DESCRIPTION AND METHODS

Toolik Lake (68°38' N, 149°35' W) is a complex kettle lake and one of the largest and deepest [150 ha, maximum depth (Z_{max}) = 22 m] of a group of nearby

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² Present address: Department of Biology, University of Michigan, Ann Arbor, Michigan 48109-1048 USA.

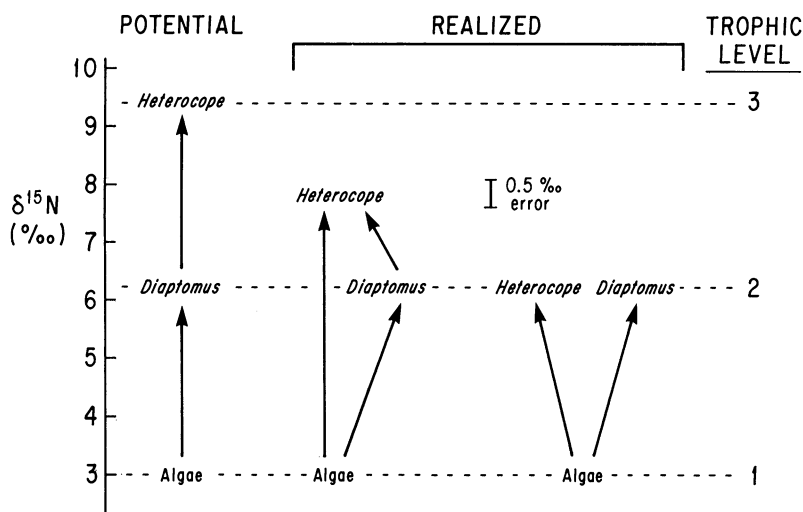


FIG. 1. Illustration of "potential" vs. "realized" trophic structure in a simple planktonic community as deduced by ratios of stable nitrogen isotopes. Dashed lines indicate primary (lowest line), secondary, and tertiary trophic levels. In the middle diagram *Heterocope* is an omnivore, feeding on both *Diaptomus* and algae. The error bar represents the typically observed deviation between two replicate analyses of the same population within a lake (50–200 individuals per sample).

lakes studied from 1987 to 1989 on the North Slope of Alaska. The other lakes studied were Itigaknit (153 ha, 6 m), N-1 (4.4 ha, 18 m), Galbraith (422 ha, 6 m), Anne (8.5 ha, 2 m), George (7.3 ha, 2 m), Camp (0.2 ha, 0.7 m), and Dam (0.1 ha, 1 m). In general, these lakes are oligo- to ultraoligotrophic (Miller et al. 1986).

The dominant zooplankters are the herbivorous copepod *Diaptomus pribilofensis* and the large predaceous copepod *Heterocope septentrionalis*. *Diaptomus* is exclusively herbivorous, and feeding studies in these lakes show that if *Diaptomus* is present it will be eaten by *Heterocope* (Luecke and O'Brien 1983). Other potential prey for *Heterocope* include the herbivores *Daphnia longiremis* and *Bosmina longirostris*, which occur only in Toolik Lake, and the copepod *Cyclops scutifer*, which occurs in all lakes. It is unclear whether *Cyclops* functions as an herbivore, a predator, or both in these food webs. *Daphnia middendorffiana* occurs in all eight lakes but as an adult is too large to be prey for *Heterocope*. Where they occur, these four species are usually less important numerically than *Diaptomus* (O'Brien et al. 1979). Microheterotrophs such as ciliates and rotifers were not analyzed. Only lakes N-1, Toolik, and Itigaknit contain fish.

Particulate organic matter (POM) was collected by filtration of open lake water onto Whatman QM-A quartz fiber filters (effective wet pore size: $\approx 1.0 \mu\text{m}$). The POM is considered to be mainly phytoplankton, although some microheterotrophs and terrestrial detritus will be retained by the filters. Zooplankton were collected from vertical or oblique tows with a 100- or 240- μm mesh net, and the adults of major species were separated by hand. Zooplankton samples for isotope analysis were composites of 50–200 individuals. Such population samples are less sensitive to variations in

isotope composition than are samples of individuals, and replicate isotope analyses of composite samples collected at different locations within a lake varied in this study by no more than 0.5‰ (error bar on Fig. 1). All isotope samples were dried at 60°C.

Lipids may be depleted in ^{13}C , and substantial lipid storage may affect ecological interpretations based on whole-animal $\delta^{13}\text{C}$ values (Parker 1964, McConnaughey and McRoy 1979). We tested the magnitude of lipid storage effects in several fish and zooplankton samples by extracting lipids (Folch et al. 1956). Up to 1.0 g of dry animal tissue was diluted to 20 mL with 2:1 (volume : volume) chloroform : methanol and heated for 15 min in a water bath at 60°C. This homogenate was filtered through Whatman GF/C glass fiber filters into centrifuge tubes and mixed with 0.2 times its volume of 50 mmol/L NaCl. The mixture was then allowed to separate cleanly into two phases, after which the upper phase was removed. A mixture of 3:48:47 (volume : volume : volume) chloroform : methanol : water was used to rinse the inside tube wall and the rinse was then removed. The lower phase, containing lipids, was evaporated at $< 60^\circ\text{C}$ to dryness. Isotopic mass balances were calculated using measurements of the whole animal, the lipids, and the lipid-extracted components.

Measurements of carbon and nitrogen stable-isotope ratios were made using a Finnigan MAT 251 or Delta S isotope-ratio mass spectrometer. Results are reported as comparisons with atmospheric nitrogen or Peedee Belemnite (PDB) carbon as standards and calculated as:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} (\text{‰}) = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 10^3,$$

TABLE 1. Nitrogen and carbon isotope values for particulate organic matter (POM, algae) and zooplankton in the eight arctic study lakes. Values for Toolik are given as means \pm 1 SE, $N = 6$.

| Lake | | POM | <i>Diaptomus</i> | <i>Heterocope</i> |
|-----------|----------------------------------|-----------------|------------------|-------------------|
| Toolik | $\delta^{15}\text{N}$ (‰) | 3.2 ± 0.2 | 6.4 | 7.9 |
| | $\delta^{13}\text{C}$ (‰) | -32.0 ± 0.8 | -33.0 | -33.8 |
| N-1 | $\delta^{15}\text{N}$ (‰) Aug 87 | 2.5 | 6.3 | 8.1 |
| | $\delta^{13}\text{C}$ (‰) | -29.6 | -33.7 | -33.4 |
| | $\delta^{15}\text{N}$ (‰) Jul 89 | 1.8 | 3.7 | 5.8 |
| | $\delta^{13}\text{C}$ (‰) | -30.4 | -33.1 | -33.7 |
| Anne | $\delta^{15}\text{N}$ (‰) | 2.0 | 5.3 | 9.9 |
| | $\delta^{13}\text{C}$ (‰) | -28.6 | -30.5 | -31.3 |
| Itigaknit | $\delta^{15}\text{N}$ (‰) Aug 87 | ... | 5.9 | 6.1 |
| | $\delta^{13}\text{C}$ (‰) | ... | -26.4 | -26.5 |
| | $\delta^{15}\text{N}$ (‰) Jun 88 | 2.6 | 5.9 | 6.9 |
| | $\delta^{13}\text{C}$ (‰) | -27.6 | -30.1 | -30.3 |
| Dam | $\delta^{15}\text{N}$ (‰) | 2.5 | 5.5 | 6.2 |
| | $\delta^{13}\text{C}$ (‰) | -29.7 | -32.8 | -32.4 |
| Camp | $\delta^{15}\text{N}$ (‰) | 1.6 | 5.5 | 6.3 |
| | $\delta^{13}\text{C}$ (‰) | -21.6 | -28.9 | -26.2 |
| Galbraith | $\delta^{15}\text{N}$ (‰) | ... | 6.6 | 7.4 |
| | $\delta^{13}\text{C}$ (‰) | -29.9 | -34.6 | -32.7 |
| George | $\delta^{15}\text{N}$ (‰) | ... | 8.7 | 9.4 |
| | $\delta^{13}\text{C}$ (‰) | -27.3 | -29.9 | -30.6 |

where R is ($^{15}\text{N}/^{14}\text{N}$) or ($^{13}\text{C}/^{12}\text{C}$). Duplicate determinations on the same sample usually differed by $<0.2\%$.

RESULTS AND DISCUSSION

Because ^{15}N content increases with trophic level in consumers, the $\delta^{15}\text{N}$ values define the realized trophic level occupied by an organism. This increase results from preferential excretion of the lighter ^{14}N as a by-product of protein synthesis, leaving the animal enriched in ^{15}N compared with its diet. The general enrichment of predator relative to prey averages 3.4% across a variety of systems (Minagawa and Wada 1984). There are fewer published enrichment factors specific to zooplankton; Montoya et al. (1990) found average enrichment values between POM and marine zooplankton of 3.3 and 4.2‰ during different seasons, and our results indicate an average enrichment of $3.2 \pm 0.3\%$ ($X \pm 1$ SE) between POM and *Diaptomus* in arctic lakes (Table 1). Our calculated enrichment between the first two trophic levels is based on the assumption that POM is mainly phytoplankton and not terrestrial peat (molar C-to-N ratios of POM ranged from 5 to 10). It is not possible to determine the importance of phytoplankton and terrestrial food sources in this system using natural abundance $\delta^{15}\text{N}$ values, because the average measured values of POM and terrestrial peat are similar ($2.3 \pm 0.2\%$, $N = 7$ vs. $1.1 \pm 0.3\%$, $N = 9$). The relative enrichment between predatory zooplankton and their prey is not well known, and in natural systems it will depend on the extent of omnivory by the organism. For example, the relative enrichment will be large if the organism is a strict pred-

ator, intermediate if the organism feeds on foods at different trophic levels, and small if the organism is a strict herbivore (Fig. 1). It is these relative enrichments in the isotopic values between organisms that we are studying. The absolute isotopic values vary among systems depending on the value at the base of the food web (Table 1). This value is difficult to estimate, in part because the POM is a mixture of food sources, and different foods such as species of algae are known to have different isotopic compositions (Montoya 1990). Determination of these compositions at the molecular level is now possible for biochemicals such as pigments and lignin (Benner et al. 1987, Freeman et al. 1990, Bidigare et al. 1991), and will be required to understand that fraction of the POM is most important to consumer nutrition.

In some of the study lakes the measured enrichments of ^{15}N indicate that the planktonic food web is structured very much as one would expect based on the potential trophic relationships (Table 1). *Diaptomus* had $\delta^{15}\text{N}$ values that were $\approx 3\%$ enriched compared to POM. Similar ^{15}N enrichment continued up the food chain to the predator *Heterocope*. Thus some lakes, like Anne and N-1, contain three well-defined planktonic trophic levels (excluding fish and microheterotrophs)—POM, *Diaptomus*, and *Heterocope*. There was, however, a continuum of relative enrichments of ^{15}N between *Heterocope* and *Diaptomus*, which indicates that the realized trophic interactions varied among lakes. In lakes Itigaknit, Dam, Camp, Galbraith, and George the $\delta^{15}\text{N}$ values of *Heterocope* were relatively low and very similar to those of *Diaptomus* (Fig. 2).

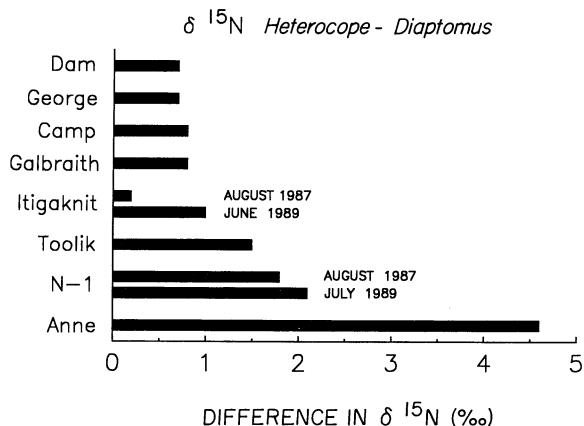


Fig. 2. Relative differences in $\delta^{15}\text{N}$ value between *Heterocope* and *Diaptomus* in the eight arctic study lakes. Based on the variability of isotope values in replicate samples and the seasonal and annual variation in values within a single lake, we consider that a difference $>1\text{‰}$ between lakes has ecological significance. A difference of zero indicates that the two zooplankters occupy the same realized trophic level and probably feed on algae, and excludes predation by *Heterocope* on *Diaptomus*. Increasing differences indicate greater predation and omnivory in the *Heterocope* diet.

This means that in these lakes *Heterocope* must be feeding less on herbivorous zooplankton like *Diaptomus* or *Daphnia* and more on a food lower in the trophic chain such as algae. There is also evidence for some omnivory in the *Heterocope* diet because their $\delta^{15}\text{N}$ values are slightly but significantly higher than those of *Diaptomus* (null hypothesis of similar means between species, $F = 35.2$, $P = .002$, $N = 5$ lakes). The ability to quantify the degree of omnivory is important for developing matrix models of food webs, because the use of different parameter values for such interactions can lead to opposite results (Yodzis 1981, Pimm 1982). For the macrozooplankton of these five lakes, then, the realized food web has only slightly more than two trophic levels, less than that found in lakes Anne and N-1.

Pimm (1982, Pimm et al. 1991) summarized the arguments that most food webs will have three to four trophic levels. In contrast, recent field studies in temperate lakes suggest that five to six potential trophic levels typically occur in planktonic food webs, excluding fish and microheterotrophs (Sprules and Bowerman 1988). The existence of these longer planktonic food webs may be due to increased omnivory (Sprules and Bowerman 1988). Our data indicate that the comparable number of potential trophic levels in arctic lakes is three or four, and the number of realized trophic levels is only two or three. It is apparent that resolving such disparities in the number of trophic levels is, at present, hampered by too little detailed information on realized trophic interactions in most systems.

We examined the seasonal and annual variation of isotopic values in Toolik, N-1, and Itigaknit (Table 1).

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of POM from Toolik Lake on 7 August 1987, 13 July 1988, and 4, 11, 18, and 25 July 1989 ranged from 2.8 to 3.9‰ and from -29 to -34.7‰ , respectively. There were no obvious patterns over time. In Lake N-1 the absolute $\delta^{15}\text{N}$ values of zooplankton varied by $\approx 2\text{‰}$ between 1987 and 1989, but the relative enrichments between different trophic levels remained more or less constant ($<0.3\text{‰}$ difference; Fig. 2). In zooplankton from Itigaknit both the absolute isotopic values and the enrichments between organisms were similar in two different years.

There are several hypotheses to explain this variability in trophic structure among lakes, and the shift from three to two trophic levels in the planktonic invertebrate food chain. The first, and we believe the most robust, is that *Heterocope* relied heavily on POM for nutrition rather than on *Diaptomus* or another zooplankton. It is important to note that the *Heterocope* analyzed were adults and not herbivorous nauplii, and that other copepods generally considered as predaceous can subsist as herbivores (Hutchinson 1967, N. E. Grossnickle and R. W. Nero, *personal communication*). There is also evidence from gut analyses that *Heterocope* adults feed on diatoms in these arctic lakes (C. Luecke, *personal communication*). The absence of preferred prey species such as small cladocerans (e.g., *Daphnia longiremis*) from lakes other than Toolik may contribute as well to the greater reliance of *Heterocope* on algae.

It is also possible that the zooplankton in these lakes feed on terrestrial detritus, which has $\delta^{15}\text{N}$ values similar to POM. For example, Hessen et al. (1990) found that in some high-latitude, humic lakes terrestrial detritus is the most important carbon source for zooplankton. The importance of new algal production vs. terrestrial detritus as food for zooplankton was tested in Lake N-2, next to Toolik Lake. Lake N-2 has been divided into fertilized and control halves since 1985. In the control side of the lake, G. W. Kling (*unpublished manuscript*) found, by labeling only the phytoplankton with $^{15}\text{NH}_4$ additions, that terrestrial detritus was an unimportant source of nutrition for *Diaptomus* and *Daphnia*.

We also examined whether algal productivity in these oligotrophic lakes was in general sufficient to support *Heterocope* growth and abundance. The carbon requirement of growing *Heterocope* is $\approx 2.3 \mu\text{g} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ in arctic lakes (Stross et al. 1980), and 1987 summer abundances in Toolik were at most 0.1 animals/L. Assuming zooplankton movement through the epilimnion (7 m deep) in Toolik and a 10% assimilation efficiency, *Heterocope* require $16 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ of carbon for growth. Summer primary carbon productivity in Toolik averages $100 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ (Miller et al. 1986), and so in terms of energy it is reasonable that *Heterocope* can survive on a diet of algae.

The second possible reason for *Heterocope* and *Diaptomus* to have similar nitrogen isotope ratios is that

the fraction of *Diaptomus* assimilated by *Heterocope* has a lighter $\delta^{15}\text{N}$ composition than that of the entire animal. Although chitin can be isotopically lighter than muscle in arthropods (Schimmelmann 1985), it is improbable that *Heterocope* would assimilate only chitin, and observation shows that predaceous copepods choose soft body parts of their prey. Because isotopic composition is integrated over the time scale of tissue turnover, and arctic *Heterocope* are monovoltine, the results presented here are probably due to sustained herbivory rather than to short-term fluctuations in diet.

The final possibility is that *Heterocope* feeds on animals lower in the food chain, such as microheterotrophs, with $\delta^{15}\text{N}$ values similar to POM. There are three trophic-chain scenarios in the lakes where *Heterocope* and *Diaptomus* have similar $\delta^{15}\text{N}$ values: (1) *Heterocope* feeds on microheterotrophs that feed on algae, (2) *Heterocope* feeds on microheterotrophs that feed on bacteria, or (3) *Heterocope* feeds on algae. The first scenario is improbable because in these lakes microheterotrophs graze mostly bacteria not algae (Hobbie and Helfrich 1988; P. Rublee, *personal communication*). The second scenario is also unlikely given that the bacterial production of carbon in the epilimnion of Toolik averages only $15 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ (Hobbie and Helfrich 1988). Assuming a 10% efficient carbon transfer leaves $1.5 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ available to microheterotrophs. If microheterotroph net production does not exceed this value, *Heterocope* could not depend solely on microheterotrophs for nutrition. This is consistent with our hypothesis that in these lakes *Heterocope* are feeding mainly on algae.

The carbon isotope measurements independently support the proposed dietary links between zooplankton and algae. In every lake studied the $\delta^{13}\text{C}$ values of *Heterocope* and *Diaptomus* were similar to each other and were slightly lower than values for POM by 2–6‰ (Table 1). Part of this difference may be due to lipid storage (Table 2). Absolute deviations in $\delta^{13}\text{C}$ between whole animals and lipid-extracted material were up to 1.2‰ for the zooplankton with high lipid content (Table 2). Thus lipid storage may account for one sixth to one half of the $\delta^{13}\text{C}$ difference between zooplankton and POM.

Another part of the $\delta^{13}\text{C}$ difference may be explained by the allochthonous component of analyzed POM. Measured $\delta^{13}\text{C}$ values of possible allochthonous inputs, peat (–28‰) and *Carex* leaves (–27‰), were less negative than POM, meaning that the autochthonous phytoplankton component of POM would be more negative isotopically and thus more similar to the zooplankton. LaZerte (1983) found similar isotopic values for allochthonous inputs to Lake Memphremagog, and a much more negative autochthonous phytoplankton component (–33‰ average). Rau (1980) reported strongly negative $\delta^{13}\text{C}$ values in animals from a lake where ^{13}C -depleted, dissolved inorganic carbon (DIC) was produced by respiration, but we have not

TABLE 2. Carbon isotope values of whole animals, lipids, and lipid-extracted (LE) components of lake trout (*Salvelinus*) and zooplankton from various lakes.*

| Sample | % lipid | $\delta^{13}\text{C}$ (‰) | | | |
|-------------------|---------|---------------------------|-------|-------|----------|
| | | Lipid | Whole | LE | Whole-LE |
| <i>Diaptomus</i> | | | | | |
| Toolik Lake | 14.6 | –37.7 | –33.0 | –31.8 | –1.2 |
| <i>Heterocope</i> | | | | | |
| Toolik Lake | 8.6 | –35.5 | –33.8 | –32.6 | –1.2 |
| <i>Salvelinus</i> | | | | | |
| Toolik Lake | 5.4 | –36.6 | –30.0 | –29.8 | –0.2 |
| Toolik Lake | 4.9 | –36.6 | –30.2 | –30.0 | –0.2 |
| Itigaknit Lake | 5.6 | –31.3 | –25.5 | –25.4 | –0.1 |
| N-1 Lake | 4.9 | –32.1 | –27.5 | –27.4 | –0.1 |

* Isotopic mass balance was calculated as: ‰ difference from ideal balance = [(lipid mass) × ($\delta^{13}\text{C}$ lipid)] + [(lipid extracted mass) × ($\delta^{13}\text{C}$ LE)] / (total mass). These differences from ideal balance were small, ranging from 0.1 to –1.0‰ (mean absolute difference = 0.3‰), which indicates that all components were conserved during sample processing.

found such ^{13}C -depleted DIC in lakes in the Toolik region (G. W. Kling and B. Fry, *unpublished data*).

CONCLUSIONS

The potential trophic interactions between predatory and grazing zooplankton were realized in only some of the eight study lakes. In the other lakes there were several intermediate situations where the predator *Heterocope* fed more or less on phytoplankton rather than on other zooplankton. In fact *Heterocope* rarely functioned as a strict predator in these lakes. These interactions were easily identified using stable isotopes of nitrogen, and possible alternatives were constrained using evidence from carbon isotopes, direct observation, and energy flow data. This approach raised a new question as well—why are there different food-web structures in similar lakes containing the same species? Our results add a new dimension to a recent analysis of omnivory and planktonic food webs in lakes (Sprules and Bowerman 1988), and highlight that theories in trophic ecology are based too often on incomplete or inaccurate data collection (see Pimm et al. 1991). Paine (1988) argued that in fact food-web theory is well ahead of the data. The use of stable isotopes can efficiently and in some cases uniquely determine the strength of trophic interactions and thus trace the flow of energy through an ecosystem. Applied to trophic ecology, and combined with traditional analyses, stable isotope measures should allow better evaluations of theoretical models and lead to more accurate pictures of food-web structure and function.

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