

**Foodweb characteristics based on stable isotopic analyses of carbon and
nitrogen from streams in the central and upper Noatak River basin:
Gates of the Arctic Park and Preserve and the Noatak National
Preserve, Alaska**

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SUMMARY

1. We used stable isotope analyses of the organic matter components of 32, 1st-3rd order, open-canopy, arctic streams in the Noatak National Preserve, Alaska, to determine the trophic structure of the stream food-webs and the relative importance of terrestrial and aquatic organic matter to stream consumers during two field seasons (2005 and 2006).
2. Noatak streams are simple systems with low taxonomic richness (≤ 10 taxa/site) and 2-4 trophic levels. The mean number of trophic positions was similar across streams and years. In 2005, the mean number of trophic positions was 2.1 and in 2006 was 2.5. The highest trophic positions, 3.5 and 3.6, were occupied by fish species in both years of the study.
3. We used the stable isotope ratio of carbon ($\delta^{13}\text{C}$) in macroinvertebrate taxa that are known to be grazers, to infer epilithic algal $\delta^{13}\text{C}$ and compared these estimates with the $\delta^{13}\text{C}$ values of terrestrial detritus in each stream. We determined that the stable isotopic composition of autochthonous food resources were highly variable across sites (-10 to $+14\text{‰}$ $\delta^{15}\text{N}$, -40 to -30‰ $\delta^{13}\text{C}$) and were much more variable than allochthonous sources as reflected by *Salix* spp. (-5 to $+1\text{‰}$ $\delta^{15}\text{N}$, -30 to -26‰ $\delta^{13}\text{C}$).
4. Because baseline isotopic values varied widely among streams we used a site-specific approach to determine that epilithic algae formed the majority of the energy base of 24 out of 32 of the stream food-webs. Moreover, a two-source mixing model showed that 4 of the 5 consumer taxa in 2005 and 9 of the 12 consumer taxa in 2006 were comprised of $>50\%$ autochthonous carbon. This is consistent with streams draining unforested watersheds that have open-canopies.
5. Autochthonous and allochthonous resource use varied among functional feeding groups across sites and years. Variable isotopic compositions of consumers relative to terrestrial and aquatic end-members suggests that some macroinvertebrates occupy broad ecological niche spaces. We interpret this as opportunistic generalism that is a result of a low diversity of food resources in these arctic streams.

Introduction

The structure and function of stream ecosystems may change in response to anthropogenic impacts such as pollution, habitat degradation, and greenhouse gas emissions that cause climate change. The effects of climate change are of particular importance in arctic regions that have, over the past three decades, warmed faster than their temperate and tropical counterparts (i.e. about 2°C per decade) (Overpeck *et al.*, 1997; Serreze *et al.*, 2000; Hassol, 2004). Recent evidence suggests that streams in the arctic are already being exposed to rapid shifts in local conditions such as: increases in temperature and precipitation, earlier break-up and later freeze, the increasing incidence of thermokarst events (Bowden *et al.*, 2008), and range expansion of shrub vegetation along water tracks and riparian corridors (Hassol, 2004; Magnusson *et al.*, 2000; Tape *et al.*, 2006). It also seems likely that arctic streams may serve as indicators of climate change and help predict future ecological trends, because they integrate chemical, physical, and biological changes occurring at the watershed scale. However, predicting their response is difficult given the lack of large scale studies to better understand arctic stream ecology.

Most studies of stream ecosystems have focused on temperate and tropical, forested and grassland streams that have experienced anthropogenic alteration. Studies of unimpacted streams are far fewer, with the majority conducted at high elevation or latitude or in remote tropical forests (citations). Previous studies in Alaska (Parker & Huryn, 2006, Craig & McCart, 1975), show that arctic streams have simple food-webs with 2-4 trophic levels comprised of few species. However, most of these studies are small scale and focus on one or two streams, which limits generalizations about the relative importance of terrestrial and algal carbon sources for food-webs of unaltered streams. Thus, it is imperative to document the natural condition of arctic streams, which will allow us to know the extent to which they have been anthropogenically altered.

Empirical data from temperate streams gave rise to the River Continuum Concept (RCC) which predicts that as the form of particulate organic matter available in streams varies longitudinally, so will the functional feeding groups (FFG) of benthic macroinvertebrates (Vannote *et al.*, 1980). For example, temperate headwater streams draining forested catchments tend to be shaded due to their close proximity to woody riparian vegetation and their food-webs are subsidized by inputs of coarse particulate organic matter in the form of woody debris and leaf litter. As a result they tend to be heterotrophic (i.e. production/respiration <1) and are dominated by consumers that can use terrestrial food resources, such as shredders and collectors. Due to low levels of shading, leaf litter inputs, and the absence of retentive mechanisms such as woody debris dams, consumers in arctic streams may depend more on algal production. Thus, low to mid-order arctic streams are thought to be structurally and functionally more similar to intermediate-sized temperate streams with open canopies.

Stable isotope analyses are widely used to identify the carbon and nitrogen sources that support production at different trophic levels within stream food-webs (Fry, 1991, Peterson *et al.*, 1993a, Huryn *et al.*, 2001). This approach is most successful when the stable isotope signatures of aquatic and terrestrial organic matter are distinct and food-webs are simple. The assumption that stable isotope ratios ($^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$) of aquatic consumers reflect their diet is implicit in this approach and has been well

established (Peterson & Fry, 1987). The approach has several advantages over more traditional methods such as gut-content analysis (Hershey & Peterson, 1996). One advantage is attributed to the fact that the stable isotope ratios of proteins in consumer tissue vary predictably with those in the diet (Hobson & Clark, 1992; Hobson, 1999). For example, $^{15}\text{N}:^{14}\text{N}$, expressed in $\delta^{15}\text{N}$ (‰), generally increases incrementally with each trophic level and therefore the $\delta^{15}\text{N}$ values of consumer tissues tend to be between 2‰ and 5‰ more enriched than those of their diets (DeNiro & Epstein 1981; Hobson & Clark 1992; Bearhop *et al.* 2002). As a result of this stepwise enrichment, $^{15}\text{N}:^{14}\text{N}$ in consumer tissues can be used to estimate the trophic positions of organisms in a food-web. On the other hand, carbon isotopes ($\delta^{13}\text{C}$) change little with trophic level (0-1‰), but vary considerably among primary producers with different photosynthetic pathways (e.g., C₃ vs. C₄ plants). While carbon fixed by terrestrial C₃ plants typically has $\delta^{13}\text{C}$ values around -28‰ (O’Leary, 1988), carbon fixed by aquatic plants has a much wider range of values (-50‰ -10‰) (Doucett *et al.*, 1996a). Therefore, $\delta^{13}\text{C}$ can be used to determine site-specific sources of dietary carbon (DeNiro & Epstein, 1981; Peterson & Fry, 1987; Post 2002b). When presented in tandem, stable isotopes of carbon and nitrogen create an isotopic niche space (termed “ δ -space” as in Newsome *et al.*, 2006) which provides quantitative information that can be used to define ecological niche space. Lastly, stable isotope signatures provide a time-integrated measure of the food resources that are assimilated by individual consumers rather than those prey items that have been recently ingested. As a result, stable isotope signatures can be used to document omnivory (Cabana & Rasmussen, 1994; Evans-White, 2001) and to track the flow of energy or mass through food-webs (Peterson & Fry, 1987; Kling *et al.*, 1992).

Our study tested the assumption that arctic streams rely on autotrophic production using large scale stream surveys conducted as part of a National Park Service project to inventory and monitor the aquatic biodiversity, community composition, and ecosystem processes in freshwater systems throughout Gates of the Arctic Park and Preserve (GAAR) and the Noatak National Preserve (NOAT). Specifically, we used stable isotope analyses to examine the relative contribution of terrestrial and aquatic organic matter to stream consumers. Our objectives were to determine baseline values of stable isotopes in each stream for future reference, to identify the organic matter sources most important for stream consumers, and to develop a first level assessment of trophic structure including estimates of the number of trophic levels represented in each stream collection. We anticipated that the lack of a forested riparian zone would result in Noatak streams being supported by algal production. Because of the oligotrophic nature of arctic streams, we predicted that the Noatak streams would have low species richness and simple trophic structure with 2-4 trophic levels per site.

Methods

Study Sites

The Noatak River is located north of the Arctic circle in northwestern Alaska. The Noatak is nationally designated a wild and scenic river and its surrounding watershed (area=30,352 km²) was internationally recognized in 1976 as a Biosphere Reserve by UNESCO. The river itself is over 644 kilometers long and is contained within two adjacent national parks; GAAR and the NOAT (Figure 1).

The river's headwaters begin in GAAR and are fed primarily by annual snowmelt with small contributions from groundwater and glacial melt (Elias 1999). Its headwaters are located well within the Brooks Range and from there it flows westward through an unaltered, mountain-ringed basin to Kotzebue Sound, and empties into the Chukchi Sea (Milner 2005). The Noatak River basin is characterized by long, cold winters and short, cool summers. Mean temperatures for July and February are approximately 11°C and -25°C, respectively (Bartlein et al. 1994). As a result of harsh, variable climatic conditions, streams in this region have numerous high latitude characteristics that distinguish them from their temperate analogues. Arctic streams are characterized by a seasonal freeze-thaw cycle and with the exception of spring streams, they experience little or no flow during the winter months. In stark contrast, the icebound period is followed by major flooding in the spring as snowmelt inundates the stream channels. As a result, abiotic controls play a major role in structuring the ecology of arctic streams. Aside from a few isolated studies (Young, 1974; O'Brien, 1975; Binkley *et al.*, 1994; and Oswald *et al.*, 1999), very little baseline data exists on the tributaries of the Noatak River due to its remote location.

Sampling Noatak Streams

We collected samples on July 14-24, 2005 and July 7-23, 2006 from thirty-two tributary and headwater streams throughout the Noatak Basin. In 2005, we floated the mainstem of the Noatak River with inflatable rafts from 12-Mile Creek to Lake Matcharak in the western region of GAAR (Figure 1). We sampled 20 tributaries at the confluence of the Noatak River in the upper Noatak River Basin in GAAR and NOAT and 15 of those sites were included in the stable isotope analysis.

During the 2006 field season, we measured the same indicators in 17 streams, but revised our sampling methodology to collect baseline data from streams on contrasting carbonate and ultramafic lithologies in an area around Feniak Lake in the central part of NOAT (Figure 1). We accessed streams in this area using a Robinson 44 II helicopter. This sampling strategy allowed us to sample low order streams draining a single lithology type farther from the Noatak River mainstem and thus provide a more representative ecological baseline for future monitoring.

Methods and Analyses

At each stream reach, 6 components of the aquatic food-web and potential terrestrial food resources were sampled when present: 1) coarse benthic organic matter (CBOM),

including leaves and wood, 2) live riparian vegetation, 3) aquatic macroalgae, 4) bryophytes, 5) macroinvertebrate consumers, and 6) fish. CBOM, aquatic macroalgae, and bryophytes were sampled qualitatively by hand when present. CBOM was sub-sorted into leaf litter and woody debris components for stable isotope analysis. Live foliage from each of the selected riparian vegetation species was hand-collected from several individuals to obtain a representative sample and placed into a brown paper bag. Qualitative kicknet and quantitative Surber samples (0.09 m² frame with 250µm mesh) were taken from riffles and dominant macroinvertebrates were selected and stored in plastic scintillation vials. All taxa were allowed to clear their guts for 12-24 hours prior to preservation by drying. Adipose fin clips were taken from fish species collected by active gill netting and angling and the fish were returned to the stream from which they were collected.

All samples were air-dried in the field and subsequently placed in a drying oven at 60°C for 36-48 hours in the lab. Terrestrial vegetation, aquatic macroalgae, and bryophyte samples were ground into a fine, homogenous powder using a ball mill and stored in pre-ashed, glass scintillation vials until analysis. Macroinvertebrate samples were dried in the original scintillation vials and were homogenized when sufficient material was present (1-2 mg) or analyzed whole when there was too little sample. Since 1-2 mg of dried tissue was required for analysis of macroinvertebrates, those samples often contained more than one individual. Fish fins were dried and analyzed whole.

All samples were weighed using a microbalance, packed into 5x9mm tin capsules, and analyzed for total carbon, total nitrogen, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on a continuous flow isotope ratio mass spectrometer (PDZ Europa “20-20”) at the Marine Biological Laboratory’s stable isotope facility at the Ecosystems Center in Woods Hole, Massachusetts. Carbon and nitrogen isotope ratios are written in ‘permil’ notation (‰), which is calculated using the following equation:

$$\delta^{13}\text{C} \text{ and } \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where R_{sample} is the $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ of the sample and R_{standard} is the $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ of the standard (Peedee belemnite carbonate for ^{13}C and atmospheric N for ^{15}N).

Particle size of substrate was measured by pebble count method where a gravelometer was used to randomly measure at least one hundred particles selected at random per stream and a median grain size (D_{50}) was calculated.

Identification of food resources

To assess the trophic base of these streams, we first determined the isotopic composition of the dominant autochthonous and allochthonous food resources at each site and then used a linear isotope mixing model to determine the relative contribution of each food resource to each macroinvertebrate taxon. To identify the autochthonous resources at each site in 2005, we established an isotopic baseline by using *Baetis* sp. (Ephemeroptera: Baetidae) as an indicator of the ^{13}C and ^{15}N of autochthonous resources. Using *Baetis* sp. as an indicator of the ^{13}C and ^{15}N of autotrophic resources appeared to be a good choice for two reasons: 1. previous studies indicate *Baetis* tracks autotrophic

resources closely in arctic streams (Peterson *et al.*, 1993a; Peterson *et al.*, 1993b; Wolheim *et al.*, 1999; Parker & Huryn, 2006) and 2. because the isotopic signature of *Baetis* samples was the most distinct from the allochthonous resource end-member in each stream. No other consumer we collected provided a closer estimate of the autochthonous resource. This method was necessary because epilithic biofilms consist of a mixture of diatoms, other algae, bacteria, and detritus and so it is usually not possible in the field to obtain pure algal samples. The caveat of this approach is that by using *Baetis* to define the autochthonous end member, the importance of this end-member will be overestimated to the extent that *Baetis* is less than 100% autochthonous.

In 2006 the thaw season was late and so at most sites no *Baetis* were collected because the larvae were too small to be sampled. To establish the autochthonous baseline in 2006 we developed a linear regression between the $\delta^{13}\text{C}$ in *Baetis* *sp.* and the $\delta^{13}\text{C}$ of non-predaceous chironomids where both were collected together in 2005 (Figure 2a). A similar regression was developed for the $\delta^{15}\text{N}$ of these two groups (Figure 2b). These regressions were then used to predict the presumed autochthonous baseline in 2006, based on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in chironomid samples, which could be reliably found at all sites. In both years we assumed that willow, *Salix* *sp.*, represented the allochthonous end-member at each site because it was the most abundant streamside vegetation type.

The linear mixing model used to calculate the relative contribution of autochthonous and allochthonous organic matter to consumers at each site was based on the following equations:

$$a = \sqrt{(A_x - C_x)^2 + (A_y - C_y)^2}$$

$$b = \sqrt{(B_x - C_x)^2 + (B_y - C_y)^2}$$

$$c = \sqrt{(B_x - A_x)^2 + (B_y - A_y)^2};$$

where A is the autochthonous end-member, B is the allochthonous end-member, and C is the sample or mixture (Liu *et al.* 2004). The mean proportion (p) of source a and b in the mixture c can be calculated (Balesdent and Mariotti 1996) using the following equations:

$$p_a = (\delta_c - \delta_b) / (\delta_a - \delta_b)$$

$$p_b = (\delta_c - \delta_a) / (\delta_b - \delta_a);$$

where δ_a , δ_b , and δ_c represent the mean isotopic signatures (e.g. $\delta^{13}\text{C}$) for sources a and b and the mixture c , respectively, and p_a and p_b are the proportions of a and b in c . By normalizing to common end members, this approach converts data from δ -space to p -space, where “ p ” is the proportion of each food source in the consumer’s diet. Thus, we are able to measure variation independently of the absolute value of isotopic signatures and these values can be compared to other estimates of niche space (Newsome *et al.* 2006).

Convex hull diagrams were constructed to show the variability of isotopic values for autochthonous and allochthonous food resources in Noatak streams in 2005 and 2006 (Figures 5a and b). The convex hull of a set of points, e.g. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of autochthonous resources in 2005, is the smallest convex set containing or bounding all those points (<http://www.wolfram.com>). All convex hulls were calculated using R.

Determination of trophic position

Trophic positions of higher consumers can be estimated from the site-specific analysis of stable isotope data. The methods we used assign primary producers to trophic level 1, then by analyzing their stable isotope values, consumers are assigned site-specific trophic positions at each stream by:

$$\text{TP} = \lambda + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}) / 3$$

where TP is the trophic position of the consumer, λ is the trophic position of the organism used to estimate $\delta^{15}\text{N}_{\text{baseline}}$, $\delta^{15}\text{N}_{\text{consumer}}$ is measured directly, and 3 is the $\delta^{15}\text{N}$ enrichment per trophic level (Post *et al.*, 2002). To calculate the site-specific trophic position of macroinvertebrate consumers, we assumed a trophic enrichment of 3‰ for all $\delta^{15}\text{N}$ values (Peterson *et al.*, 1993a) and no change in the $\delta^{13}\text{C}$ values. For example, the epilithic food resource was calculated to be equal to the $\delta^{13}\text{C}$ content of *Baetis* and 3‰ less enriched in ^{15}N . In our case *Baetis* is by our procedural assignment a trophic level 2 consumer.

In previous studies, a difference has been made between the term ‘trophic level’ and ‘trophic position,’ where a level is a discrete, integer unit (e.g. 1, 2, 3, ...etc.) and position is based on stable isotope values and therefore can be a non-integer value. The terms are often used interchangeably, but the latter can reveal habitat-specific variation (e.g. omnivory or adaptable feeding behavior) in the diet of consumers that may be overlooked with static trophic level designations.

Results

Stream Reach Characteristics

The majority of the streams sampled were 1st-3rd order and characterized by a riffle-pool morphology and cobble substrate (2005 D_{50} = 54.1 and 2006 D_{50} = 65.9). The stream reaches ranged from 100-300m in length and had varying amounts of riparian tussock grass, sedge, and shrub vegetation and in general, were not heavily shaded. The cobble substrate was generally colonized by a biofilm of epilithic diatoms and bacteria, and rarely with filamentous algae or bryophytes. These streams were oligotrophic and were characterized by low algal and macroinvertebrate biomasses. All streams had on average fewer than 10 macroinvertebrate taxa. It is not known how much allochthonous organic matter enters these streams, but visual estimates from this study suggest that little organic matter was retained.

Stable isotope composition of stream consumers and their putative food resources

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic compositions of riparian vegetation were somewhat variable, but the isotopic compositions of macroinvertebrates were highly variable in both C and N stable isotopes across sites and years (Figures 3 and 4). The unusually large variation in the isotopic composition of the consumers means that any detailed analysis of the importance of food resources or of trophic structure must be conducted on a site by site basis or alternatively all consumer isotopic ratios could be normalized for variation in end-members.

Through this procedure, we determined that autochthonous food resources (a reflection of grazer ratios) were highly variable across sites (-10 to $+14\text{‰}$ $\delta^{15}\text{N}$, -40 to -30‰ $\delta^{13}\text{C}$) and much more variable than allochthonous sources as reflected by *Salix sp.* (-5 to $+1\text{‰}$ $\delta^{15}\text{N}$, -30 to -26‰ $\delta^{13}\text{C}$) (Figure 5a and b).

Based on results of the site specific analyses, we determined that there were not more than 3.6 trophic positions represented in these stream collections. In our case *Baetis* is by our procedural assignment a trophic level 2 consumer. The other insects are all very close to the same trophic position on average, with non-predaceous chironomids (2005), oligochaeta (aquatic worms) and Hydrachnidae (aquatic mites) (2006) slightly higher. In 2006 streams, tanypods (predatory chironomids) occupy trophic position 2, which is contrary to their traditional FFG designation as predators (Table 1). Larger predatory insects were not common at most sites and thus trophic position 3 insects (i.e. secondary consumers) were not abundant enough to be included in the isotopic analysis. The highest trophic positions were occupied by fish species in both years of the study. Slimy sculpin, *Cottus cognatus*, collected in 2005, from the only 2 sites where they might reflect the local food resources, were assessed at trophic position 3.5 indicating a diet of stream insects as expected. In 2006, arctic grayling, *Thymallus arcticus*, were collected at 10 sites and were also identified as being a third trophic level consumer (TP = 3.6, Table 1).

The mean number of trophic positions in streams sampled in 2005 was 2.1 ($n = 15$) and 2006 was 2.4 ($n=17$). The presence of oligochaetes and mites in 2006 may have been responsible for the higher mean number of trophic positions we observed in that year.

End-member mixing analyses of macroinvertebrates and fish indicated a broad range of autochthonous resource use for individual taxa and that on average 61% of the secondary production of these tributaries was supported by autochthonous carbon (Table 1). Switching of functional feeding roles by consumer taxa is evident in the large standard errors associated with the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Figures 3a and b) and the mean autochthonous resource use (Table 1). For example, at site SCS09 in 2006, the nemourid stonefly, *Nemoura*, which is typically classified as a facultative shredder, was more depleted in $\delta^{13}\text{C}$ than *Heptagenia sp.*, a grazer (Figure 6). Macroinvertebrate taxa throughout the Noatak stream collections showed similar feeding plasticity, which is apparent in the ranges of autochthonous resource use of most taxa in Table 1. Comparing

taxon-specific autochthonous resource confirmed that oligochaetes, simuliids, and tipulids relied more on allochthonous carbon than other taxa (Table 1).

Fish were not collected at most tributaries in 2005, with the exception of *C. cognatus* at 4 sites. At sites 7 and 8, *C. cognatus* were depleted in ^{13}C and had low ^{15}N values, which suggests that these individuals may have been feeding previously in another area. *C. cognatus* collected at sites 17 and 19 had isotope values that indicated they were feeding on local resources or at an isotopically similar site, so these sites were used in the stable isotope analysis. In 2006, *T. arcticus* was the only fish species collected in the Noatak streams. Overall, grayling were characterized by isotope values that indicated they were eating local macroinvertebrates even though they are summer transients and may have recently migrated to the stream reaches (Figure 4).

To develop a generalized food-web structure of Noatak tributaries, we combined the information from site-specific trophic analyses with the results of end-member mixing analyses (e.g. Figure 6). This approach relies on the fact that there were strong isotope differences of the end-members and the trophic structure of these streams was simple. Results of this analysis underscored the slightly greater importance of autochthonous resources to the stream food-webs, but also indicated that some taxa rely more on allochthonous resources. The site-specific analysis revealed that many taxa were generalist and able to switch between resources types.

Discussion

Our research shows that the streams in the Noatak Basin that we sampled are characterized by low taxonomic richness and simple food-webs that are supported by autochthonous production. On average, the streams have 10 or fewer macroinvertebrate taxa, 1 or 2 fish species, and between 2 and 4 trophic levels. The invertebrate communities of these streams were remarkably similar across time and space; approximately 90% of the dominant macroinvertebrate taxa were similar in both years. Our results are consistent with a previous study of arctic mountain and spring streams on the North Slope of Alaska, which reported small inter-stream differences in macroinvertebrate community composition (Parker and Huryn 2006). The same study found food-webs consisted of 4-5 trophic levels, which is slightly higher than we found for the streams we sampled in the Noatak River basin. This is due in part to fewer predatory macroinvertebrates in our collections. It is also attributable to the absence of bird predators such as *Cinclus mexicanus*, which was observed at the spring stream studied by Parker & Huryn (2006). The highest mean trophic positions (TP = 3.5 and 3.6) in the Noatak streams are occupied by fish species, *C. cognatus* or *T. arcticus*, whose isotopic values indicate they typically feed on local macroinvertebrates. However, at sites 7 and 8 in 2005, *C. cognatus* were depleted in ^{13}C and had low ^{15}N values relative to the local food resources. While this may indicate they were exploiting a different geographical foraging area or are recent migrants into the reach, a study in agricultural streams found that site-specific isotopic signatures suggest that *C. cognatus* have high site fidelity and incorporate their signatures over a narrow spatial scale (Gray *et al.*,

2004). It is not possible from our study of arctic streams to attribute the divergent isotopic values of *C. cognatus* to foraging or migration.

Most macroinvertebrate consumers are very close to the same trophic position on average, with non-predaceous chironomids (2005), oligochaeta (aquatic worms) and Hydrachnidae (aquatic mites) (2006) slightly higher. Since chironomids are a mixture of different, non-predaceous species and oligochaetes are known to exploit a wide variety of food resources, it is not possible to judge what significance might be attached to their elevated $\delta^{15}\text{N}$ values. Hydrachnidae are aquatic parasites, which may explain their elevated $\delta^{15}\text{N}$ values.

Recently some concern has been expressed about pooling $\delta^{13}\text{C}$ data from many locations (France 1995) versus site-specific analyses (Doucett *et al.*, 1996b) to discriminate between autochthonous and allochthonous organic matter in freshwater ecosystems. A well-documented pattern of highly variable autochthonous carbon sources was used by Doucett (1996b) to promote site-specific stable isotope analysis. In the streams that we sampled, autochthonous food resources as reflected by grazer ratios were highly variable across sites and much more variable than allochthonous sources such as *Salix sp.*. The high degree of variability observed in both years of the study (Figures 3a and b) necessitates the site-specific approach we used to establish the energy base of the stream food-webs. The variability in $\delta^{13}\text{C}$ values among the autochthonous food resources could be from a variety of likely sources including variation in respiratory CO_2 concentrations, turbulence, and further fractionation by algae during carbon uptake, all of which can affect the carbon isotope ratios in algae (Finlay *et al.*, 1999; Fry, 2006). Another explanation may result from the fact that biofilm is a complex matrix consisting of both autotrophic and heterotrophic components (Haack & McFeters, 1982). The heterotrophic components include bacteria and fungi that may incorporate dissolved and particulate forms of terrestrial organic matter thus shifting the $\delta^{13}\text{C}$ value toward that of allochthonous material. While some macroinvertebrate taxa can selectively feed on epilithic diatoms in the biofilm matrix, others likely assimilate both heterotrophic and autotrophic components. Although direct measurements of biofilm were not made in this study, it seems plausible that this could explain some of the variability we observed from our inferred values among sites and between years. The source of the variability in $\delta^{15}\text{N}$ is potentially due to either variation in the ratios in dissolved inorganic nitrogen or to fractionation in uptake by algae (Finlay *et al.*, 1999; Fry 2006). The reason for these extreme source variations deserves further investigation.

Several lines of evidence indicate the importance of algae when compared to allochthonous resources in Noatak streams. First, using a site-specific approach, we determined that aquatic primary production formed the dominant energy base for 24 out of 32 of the stream food-webs. This finding seems reasonable given the low level of shading and absence of leaf litter; factors that should favor autochthonous production. Another line of evidence supporting autochthony is based on results of the two-source mixing model analysis that we used to transform δ -space to p -space. These results show that 4 of the 5 consumer taxa in 2005 and 9 of the 12 consumer taxa in 2006 were comprised of >50% autochthonous carbon (Table 1). However, the designation of *Baetis*

as the autochthonous end-member creates a bias that will overestimate the importance of autochthonous resources to the extent that *Baetis* is less than 100% autochthonous. Consideration of this bias reveals food-webs in which autochthonous resources are of slightly greater importance and in some cases may be nearly equal to allochthonous resources.

In stream systems, generalism is common among macroinvertebrates and has been documented recently using stable isotope data (McCutchan & Lewis, 2002). Variable isotopic compositions of macroinvertebrate consumers in Noatak streams relative to source end-members suggest that most taxa are generalists and few subsist exclusively on algal or terrestrial organic matter. Moreover, some taxa thought to be obligate specialists (e.g. the shredder, Tipulidae) use different feeding strategies among sites. Switching of functional feeding roles by consumer taxa (e.g. a shredder consuming algae) was also observed in southern Ontario streams (Rosenfeld & Roff, 1992) and at Ten Mile Creek (Finlay, 1999; *unpublished data*). The pattern of utilizing different food resources is shown by the large standard errors associated with the mean autochthonous resource use (Table 1). For example in Figure 6, the obligate shredder, Tipulidae, has $\delta^{13}\text{C}$ values that indicate a mixed diet. This suggests it is exploiting a larger ecological niche than would be expected based on the traditional functional feeding designation of a shredder organism. At the same site, Nemouridae, considered a facultative shredder, derived most of its carbon from autochthonous resources, which shows it occupies a general ecological niche. This result agrees with the finding that nemourids may also feed as collector-gatherers (Harper & Stewart, 1984). We documented a similar pattern in most of the streams we sampled which leads us to conclude that adaptable feeding behavior and generalist taxa are favored in these systems due to limited food resources. This finding is potentially important for arctic streams as climate changes (i.e. as shrubs colonize riparian corridors) because it implies that some taxa are likely to respond to shifts in basal resources (e.g. increases in leaf litter) by changing their feeding behavior rather than being extirpated. This adaptable behavior may buffer the loss of taxonomic diversity that is predicted as climate changes.

The slightly greater importance of autochthonous carbon is expected in oligotrophic tributaries of the Noatak and this finding is consistent with previous studies in low to mid-order arctic and alpine streams with open canopies (Parker & Huryn, 2006; Fureder *et al.*, 2003; Peterson *et al.*, 1993a). It also supports the RCC-based assumption that these streams are more comparable to their intermediate-sized, temperate counterparts. Results from our large-scale survey of Noatak streams provide an important baseline for documenting future changes in arctic stream ecosystem structure and function.

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Table 1 Autochthonous resource utilization of consumers in Noatak tributaries during 2005 and 2006.

Taxonomic Group	n (# of sites analyzed in SIA ¹)	Range of autochthonous resource use (%)	Mean of autochthonous resource use (% +/- SE)	Range of trophic position (#)	Mean trophic position (# +/- SE)
Hydrachnidae*	3	42-72	53.6 +/- 9.2	3.0-3.1	3.0 +/- 0.04
Baetidae	9	52-100	91.2 +/- 0.08	2.12-2.14	2.1 +/- 0.004
Brachycentridae*	3	37-76	58.6 +/- 11.5	1.1-2.6	1.9 +/- 0.8
Heptageniidae*	2	84-88	85.9 +/- 1.8	1.1-2.1	1.6 +/- 0.5
Capniidae	20	0-100	56.5 +/- 7.1	1.2-3.9	2.2 +/- 0.2
Chironomidae (non-predaceous)	18	49-100	84.2 +/- 4.1	1.2-3.0	2.2 +/- 0.1
Nemouridae	25	52-100	75.9 +/- 3.8	1.2-2.9	2.1 +/- 0.2
Orthoclaadiinae (subfamily of Chironomidae)*	10	39-99	72.9 +/- 6.6	1.5-2.5	2.1 +/- 0.1
Oligochaeta*	11	0-78	13.4 +/- 7.0	2.0-4.3	2.9 +/- 0.2
Tanypodinae (subfamily of Chironomidae)*	2	53-79	65.9 +/- 0.13	1.8-2.1	2.0 +/- 0.1
Tipulidae*	9	0-71	44.9 +/- 7.3	1.0-3.8	2.0 +/- 0.3
Simuliidae*	13	0-66	41.8 +/- 4.7	2.4-3.2	2.7 +/- 0.1
<i>Cottus cognatus</i> **	2	44-56	49.9 +/- 5.9	3.1-3.9	3.5 +/- 0.4
<i>Thymallus arcticus</i>	9	0-38	16.7 +/- 5.2	3.2-4.4	3.7 +/- 0.1

¹ SIA is stable isotope analysis

*Indicates presence at only 2006 sites

** Sculpin was present at 4 sites, but at 2 sites depleted ¹³C and low ¹⁵N values suggest a recent migration into the tributary rather than a signature indicative of predation on local food resources

Figure 1 Map of study area; ▨Noatak National Park and ▩Gates of the Arctic National Park, and sampling sites in 2005 (▲) and 2006 (■)

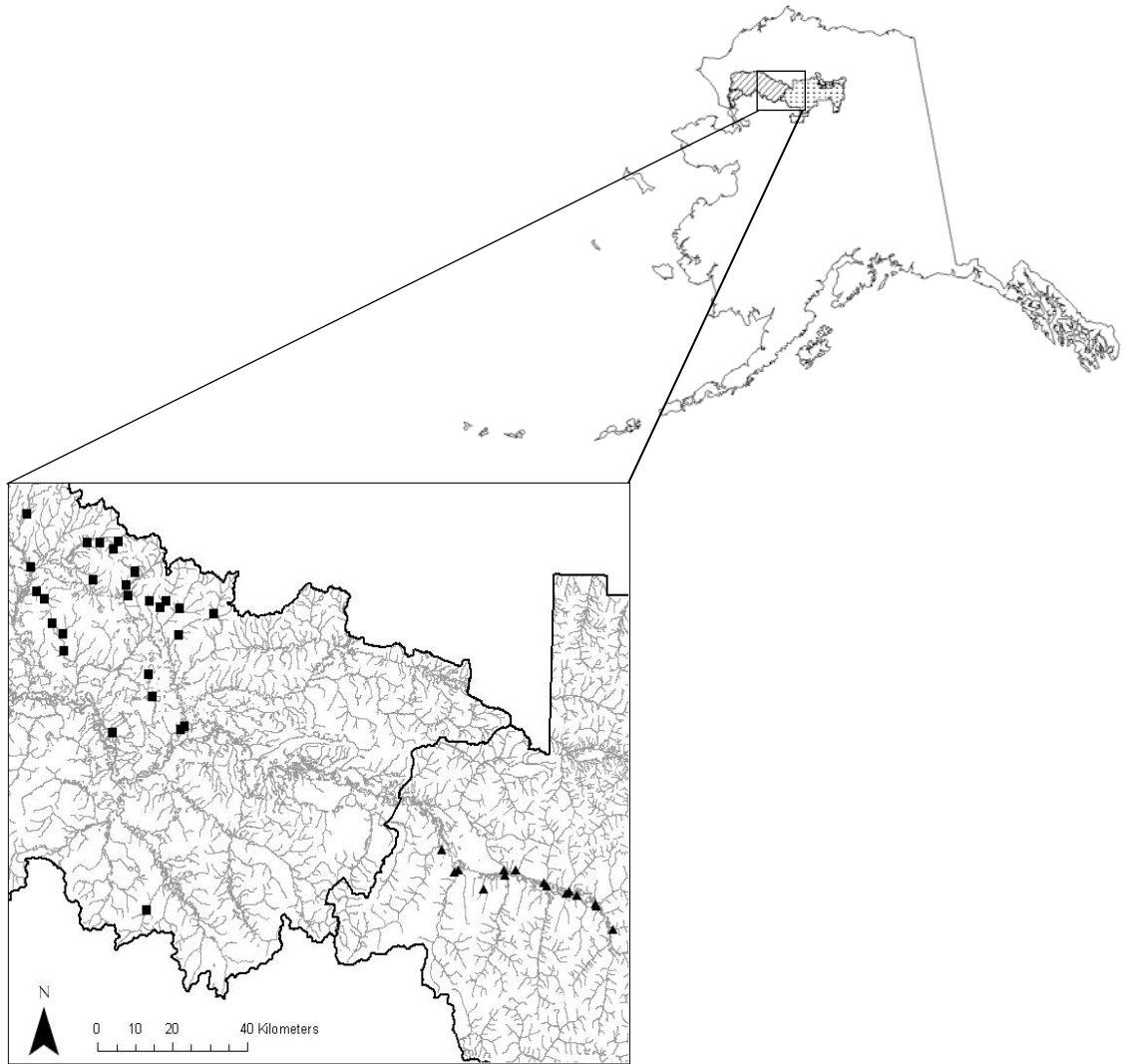
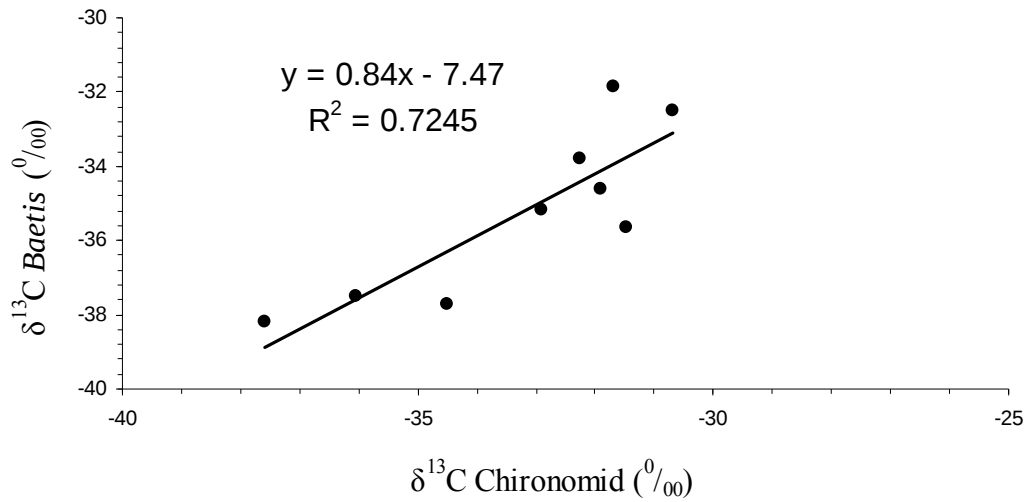


Figure 2 Linear relationship of C and N isotope values of *Baetis sp.* and non-predaceous chironomids in 2005. Strong correlations suggest they are exploiting similar food resources.

a)



b)

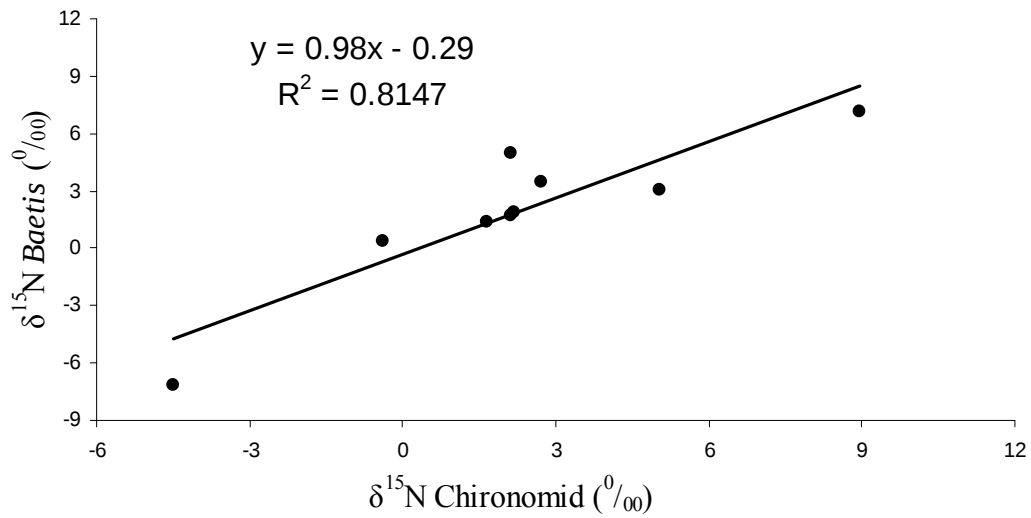
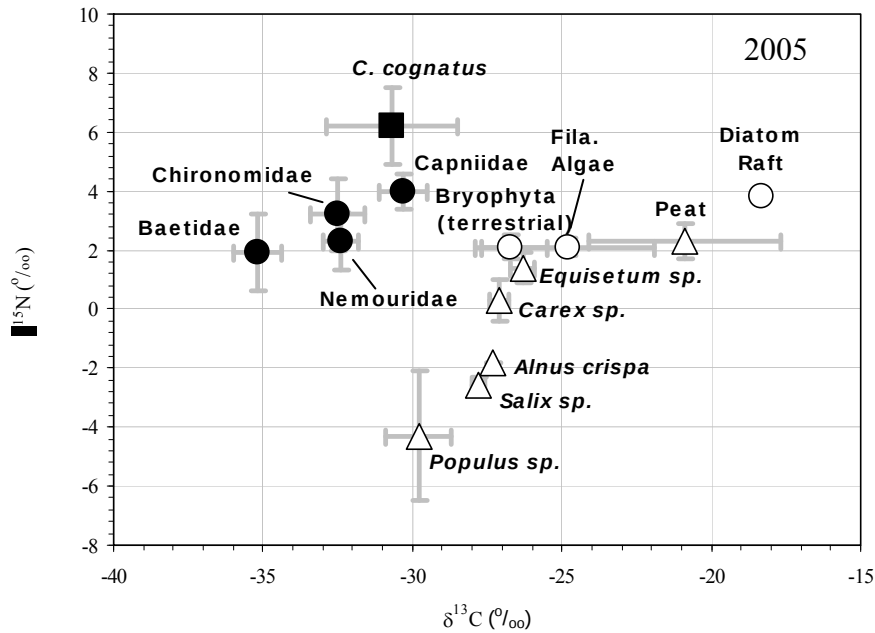


Figure 3 Distribution of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) for dominant vegetation, macroinvertebrates, and fish sampled in headwater and tributary streams of the Noatak River in 2005 and 2006. ■ = fish species, ● = macroinvertebrate consumers, △ = riparian vegetation, ○ = aquatic primary producers, and CBOM = coarse benthic organic matter.

a)



b)

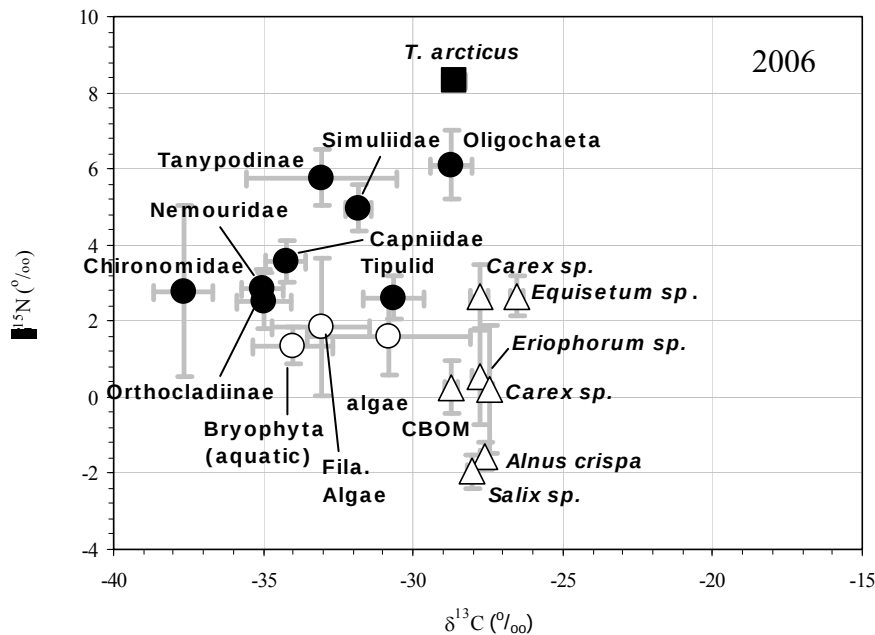


Figure 4 Ranges of isotopic compositions of dominant vegetation, macroinvertebrates, and fish in headwater and tributary streams of the Noatak River in 2005 and 2006. CBOM = coarse benthic organic matter

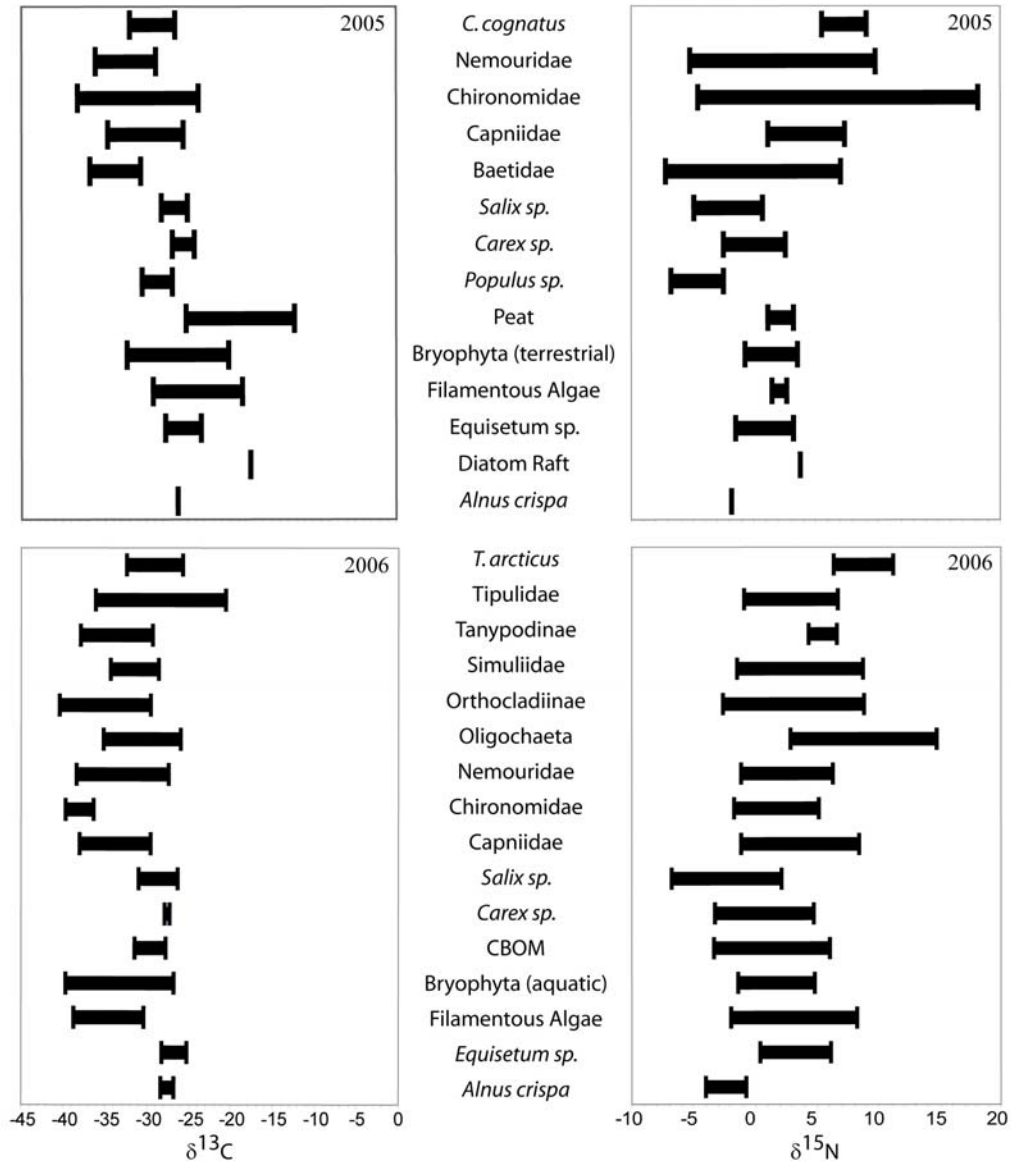
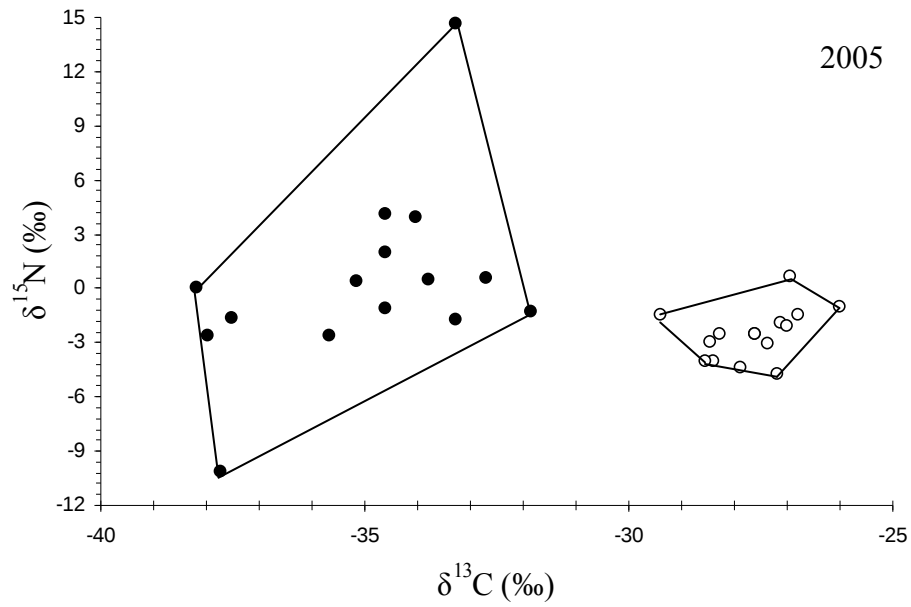


Figure 5 Convex hull diagrams show the variability of isotopic values for autochthonous (●) and allochthonous (○) food resources in Noatak streams in 2005 and 2006.

a)



b)

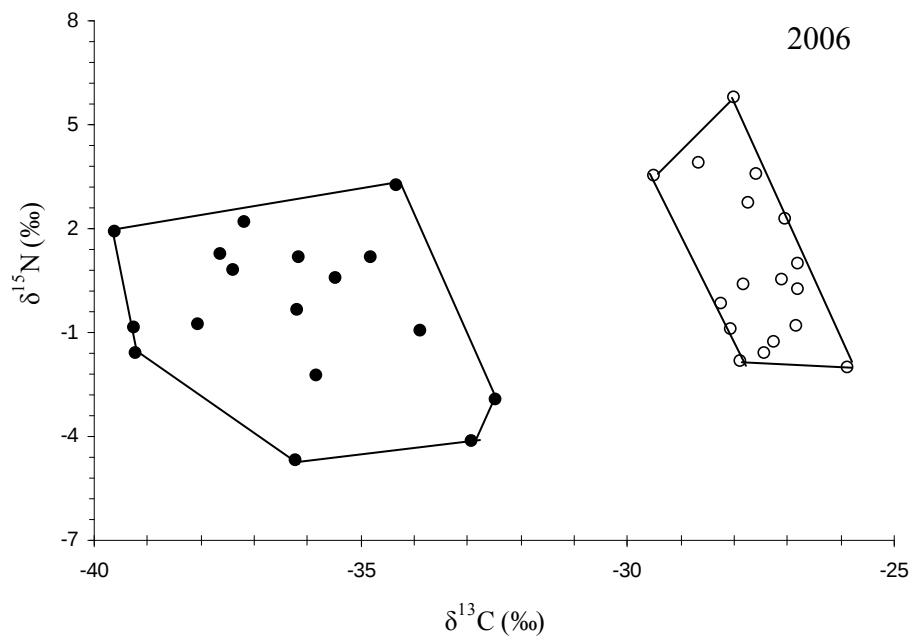


Figure 6 ^{13}C and ^{15}N Isotope Values at Site SCS09 in 2006. Note the location of Tipulidae and Nemouridae, obligate and facultative shredders, respectively, relative to autochthonous (○) and allochthonous (i.e. *Salix sp.* (△)) end-members.

