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Resident fish community impacts on stocked rainbow trout ecology in 15 eastern Washington lakes

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**RESIDENT FISH COMMUNITY IMPACTS ON
STOCKED RAINBOW TROUT ECOLOGY
IN 15 EASTERN WASHINGTON LAKES**

**A Thesis Presented to
Eastern Washington University
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MASTER'S THESIS

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ABSTRACT

The principal purpose of this research was to analyze the effects of resident fish communities and lake habitat on energy source use and trophic position of stocked rainbow trout. Stable isotope analysis was used to accomplish this goal, with stable carbon isotope ratios indicating the source of carbon, pelagic or littoral, in each species' diet and stable nitrogen isotope ratios determining species' relative trophic positions. The research was conducted in 15 eastern Washington State lakes, all stocked with rainbow trout for sport fishing purposes. I found wide confidence intervals around the % estimated littoral carbon in most of the lakes. However, the estimate of percent littoral carbon used by stocked rainbow trout could be predicted by several factors including the complexity of the resident fish community, amount of littoral vegetation present, and the presence of other resident trout and brown bullhead. In addition, significant negative correlations were detected between rainbow trout $\delta^{15}\text{N}$ and resident fish community complexity and the presence of other resident trout. As a consequence, alteration of rainbow trout stocking densities is recommended in aquatic systems containing complex resident fish communities and/or resident trout and/or brown bullhead, as the presence of those specific constituents negatively correlated to stocked rainbow trout littoral carbon use and/or trophic position. Despite these findings, stable isotope analysis does have limitations and difficulties, as seen in this research. Based on poor confidence intervals for estimated percent littoral carbon use, the diet of sampled organisms was difficult to assess. In addition, a more specific analysis of each sampled species' relative trophic position could not be done because I did not have clear baseline $\delta^{15}\text{N}$ for littoral primary consumers in several of the lakes. As a result, conclusions should be considered

preliminary and tentative. An extensive sampling regimen is recommended for similar future studies to avoid these issues.

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INTRODUCTION

Rainbow trout (*Oncorhynchus mykiss*) is a highly desirable sport fish stocked in many lakes across eastern Washington State. However, little is known about how the composition of a lake's fish community impacts stocked rainbow trout feeding ecology in this region. The goal of this project was to examine the impact that resident fish populations have on stocked rainbow trout trophic position and relative use of energy derived from pelagic versus littoral zones.

I used stable isotope analysis to examine the impact that resident fish communities have on stocked rainbow trout feeding ecology. Stable isotope analysis can be used to map the structure of aquatic food webs and has the potential to identify factors that influence the stocking success of rainbow trout in an aquatic system. In this study, stable carbon isotope ratios indicated the source of carbon, pelagic or littoral, in each species' diet and stable nitrogen isotope ratios were used to determine species' relative trophic positions. I then compared inferred energy sources and trophic positions to physical characteristics of the lakes and composition of resident fish communities. In addition, I used stable isotope results to examine whether ontogenetic shifts were occurring in the feeding behavior of stocked rainbow trout. Ontogenetic shifts can be defined as behavioral changes resulting in shifting trophic positions and/or resource use as fish age. The research was conducted in 15 eastern Washington State lakes, all stocked with rainbow trout for sport fishing purposes.

Hatchery-reared rainbow trout play an important role in Washington's lake fisheries, but stocking in aquatic systems containing resident fish communities has been difficult and largely unsuccessful. Maintaining put-and-take fisheries in fishless lakes,

streams, and reservoirs is a widely accepted use of hatchery rainbow trout (Utter 1994, Epifanio and Nickum 1997). However, few eastern Washington State lakes are void of resident fish. Thus, fisheries managers are forced to attempt to successfully stock rainbow trout into aquatic systems containing resident fish communities.

Stocking of rainbow trout in aquatic systems containing resident fish communities, wild rainbow trout included, has been determined to be largely unproductive. This study did not specifically focus on stocking success of rainbow trout, as all study site lakes have some degree of stocking success. However, by elucidating the resources used by stocked rainbow trout in systems with resident fish, and how resource use changes in response to resident species, this study may provide managers with information on the resources needed to successfully stock rainbow trout in lakes containing resident fish, and the conditions under which those resources are likely to be available. For example, stocked rainbow trout may be able to switch between littoral and pelagic feeding to reduce competition or predation, but only in lakes where the alternate resource is adequately abundant.

This study examined the effects of resident fish populations upon the use of dietary resources by stocked rainbow trout, and under what conditions those resources were available. In a similar study, Juncos et al. (2011) analyzed the effects on rainbow trout growth by food web structure and prey quality in four Patagonian lakes. Using gut content analysis paired with a bioenergetics model, they determined a strong correlation between energetically high-quality prey and high growth of rainbow trout. Furthermore, rainbow trout density, production, and biomass were highest in larger, more structurally complex lakes, although smaller lakes were comparable. Food web structure was also

found to influence rainbow trout growth. In general, native fish species, most notably creole perch (*Percichthys trucha*), were found to be primarily littoral consumers and rainbow trout were mainly piscivorous. However, in one lake that did not contain creole perch, rainbow trout were able to incorporate substantial proportions of littoral invertebrates in their diet. This study demonstrated that rainbow trout growth is highly plastic, allowing the species to successfully colonize a variety of aquatic systems where prey and prey-quality greatly vary.

There is considerable evidence for the negative impact of resident fish on rainbow trout stocking success in the northwestern U.S., due to predation or competition. For example, Miller (1958) and Needham (1959) determined immediate and heavy mortality on stocked rainbow trout in streams containing resident trout. Kerr and Lasenby (2000) reviewed factors that influence the success of rainbow trout stocking in an aquatic systems. They identified predation, prey availability, and competition, as the most important factors. Minor factors that influenced the stocking success of rainbow trout included: water quality, habitat, disease, stocking practices, and post–stocking weather conditions. Predation and competition are the result of resident fish communities, and the severity of these effects will depend on the abundance and composition of the resident community. Competition can further reduce the stocking success by reducing prey availability (Kerr and Lasenby 2000). Below I will address other studies, including studies specific to the U.S. northwest, demonstrating the effects of predation and competition on rainbow trout stocking success.

Of the primary factors influencing stocking success of rainbow trout, Kerr and Lasenby (2000) determined that predation was the single greatest source of mortality.

This finding concurred with previous research conducted by Johnson and Hasler (1954), who determined that post-stocking mortality on rainbow trout in Wisconsin and Michigan lakes was almost entirely predator dependent. Predator dependent mortality rates in the study lakes were particularly high for 1+ rainbow trout, 32% – 60%. In Idaho, wild rainbow trout have higher abundance and growth rate in streams and lakes with stocked rainbow trout, most likely due to predation upon the stocked fish (High 2008). Net-reared rainbow trout in Flaming Gorge Reservoir (UT & WY) appeared to be heavily preyed upon by lake trout (*Salvelinus namaycush*) (Budy and Haddix 2005). Christensen and Moore (2010) determined that largemouth bass (*Micropterus salmoides*) were partially to blame for high mortality rates of stocked rainbow trout in South Twin Lake, Washington. Using gut content analysis and a bioenergetics model, they determined that largemouth bass consumed approximately 6.3% of total fall stocked rainbow trout in the lake. Although this percentage consumed appears low at first glance, of the approximately 98,000 stocked rainbow trout in South Twin Lake, 77,000 of those were stocked in the fall. Therefore, largemouth bass consumed approximately 5,000 stocked rainbow trout. Interestingly, in North Twin Lake, where rainbow trout were also stocked, largemouth bass preyed primarily on golden shiner (*Notemigonus crysoleucas*). Differences in macrophyte distribution, bathymetry, temperature, and/or predator-prey demographics likely caused the variability between the two lakes. Lake Roosevelt, Idaho stocked rainbow trout were found to be limited by top down impacts, primarily predation by walleye (*Stizostedion vitreum*) (Baldwin and Polacek 2002).

Considerable previous research has also shown that stocking success is poor in lakes with significant competition among resident fish communities and hatchery

rainbow trout (Clark 1959, Murphy 1962, Soldwedel 1974, Stuber et al. 1985, Gipson and Hubert 1991). Miller (1958, 1962) concluded that stocking hatchery trout in streams already containing wild trout populations made little sense because hatchery rainbow trout could not effectively compete. Donald (1987) determined that the presence of interspecific competition from mountain whitefish (*Prosopium williamsoni*), longnose sucker (*Catostomus catostomus*), and lake trout (*Salvelinus namaycush*) prevented successful stocking of rainbow trout in lakes within the Canadian mountain national parks. Fraser (1972) identified an inverse relationship between the complexity of the resident fish community and the success of stocked salmonids, rainbow trout included. Competition, either intraspecific or interspecific, may result in decreased prey availability and further decrease stocking success (Kerr and Lasenby 2000). Although rainbow trout are opportunistic feeders and have a diverse diet (Kerr and Lasenby 2000), prey availability heavily influences growth and survival, especially in juvenile rainbow trout (Johnson and Hasler 1954, Kerr and Grant 2000). This was illustrated by Schmuck and Petersen (2005), when they determined that Fish Lake, Washington rainbow trout were competing with yellow perch for forage, resulting in smaller than average juvenile fish at the time of the survey.

Not all effects of resident fish are deleterious to rainbow trout, however. Scheuerell et al. (2007) observed positive effects of anadromous sockeye salmon (*Oncorhynchus arcticus*) on the trophic ecology of rainbow trout in the Bristol Bay region of southwest Alaska. By comparing ration size and energy intake for rainbow trout before and after sockeye salmon returned to their spawning grounds, the research determined that both measures increased by 480 – 620% following the salmon's return.

Presumably, this is due to a dietary switch to salmon eggs, flesh, and blowflies that colonize salmon carcasses. In addition, following spawning, delta (δ) ^{15}N increased for rainbow trout, indicating an increase in higher trophic level food in the diet.

Although the ultimate goal of this study is to provide information useful in improving stocking success, this study directly examined dietary resources used by surviving stocked rainbow trout. Dietary flexibility may allow stocked rainbow trout to partially compensate for predation or competition by feeding in habitats where resident fish predators and/or competitors are less abundant. Many studies have demonstrated that trout are opportunistic feeders whose diet varies from water body to water body. Warner and Quinn (1995) tracked Lake Washington (WA) stocked rainbow trout with ultrasonic transmitters and determined by analyzing depth distribution and movement patterns that rainbow trout primarily fed on zooplankton in both littoral and pelagic areas, and supplemented their diet with benthic prey. Predation on pelagic planktivorous fishes was unlikely because the trout spent little time in the same habitats as these fish. Interestingly, Nowak et al. (2000) determined that cutthroat trout in Lake Washington become increasingly piscivorous and tend to occupy the pelagic zone after they reach approximately 250 mm fork length. In contrast, Flaming Gorge Reservoir (UT & WY) stocked rainbow trout fed primarily on aquatic macroinvertebrates, although zooplankton were abundant. Similarly to Lake Washington, stocked rainbow trout rarely switched to piscivory in later age classes in Flaming Gorge Reservoir (Budy and Haddix 2005). Verhey and Mueller (2001) determined in Pine Lake, Washington that littoral carbon not only provides a valuable energy source for fish, including stocked rainbow trout, but also provides crucial refugia for smaller fish to decrease the possibility of predation. These

findings were also supported in four British Columbia Lakes, where juvenile rainbow trout were found in both pelagic and littoral zones in predator-free lakes, but were restricted to littoral zones in lakes where predators were present (Biro et. al, 2003). The importance of pelagic versus littoral carbon sources may also fluctuate temporally. Baldwin et.al (2000) determined that although both *Daphnia* and macroinvertebrates are important to stocked rainbow trout in Strawberry Reservoir, Utah, demand for *Daphnia* in late winter increased and actually exceeded *Daphnia* biomass, resulting in a bottleneck in prey supply during that time of year. As a result, changes to stocking strategies of rainbow trout were recommended. In Lake Oahe, South Dakota, stocked rainbow trout were opportunistic feeders whose diet shifted over time and varied among size classes (Lynott et al. 1995). Based on diet analysis, zooplankton had the greatest relative importance index (RI) to the diet of Lake Oahe trout during May, July, and August. Terrestrial invertebrates had the greatest RI values during June and September. Overall, zooplankton and terrestrial invertebrate prey categories had the greatest RI values, and aquatic macroinvertebrates and rainbow trout smelt were less important prey. Zooplankton were the most important prey for young rainbow trout (< 330 mm) and decreased in importance as fish grew. Terrestrial invertebrates were the predominant prey item for rainbow trout between 330 mm and 459 mm. Rainbow trout smelt were then incorporated into the diet of rainbow trout between 201 mm and 330 mm and became the dominant prey for fish larger than 460 mm. This trend indicates a significant ontogenetic shift in prey type as rainbow trout grow.

Niche shifts during ontogeny are widespread among aquatic organisms (Mittelbach et al. 1988), including stocked rainbow trout. Ontogenetic niche shifts occur

when species change their habitat use, feeding, or other behavior as they grow. For example, many piscivorous fish, including rainbow trout, feed primarily on zooplankton during early life stages (Werner 1986). Thus, rainbow trout both compete with (during early life stages) and consume (during later life stages) species of planktivorous fishes that remain planktivores throughout their lives (Werner and Gilliam 1984). If ontogenetic niche shifts occur within stocked rainbow trout in eastern WA, this may have important consequences for their interactions with resident populations of fish in these lakes. Competition between early life stages and resident fish may limit initial stocking success, while competition between later life stages and resident fish could limit growth to larger sizes preferred by fishermen. These potential consequences are supported by the effects of ontogenetic niche shifts by trout in Midwestern food webs; as a result of competition among planktivores interactions, there may be bottlenecks in recruitment of rainbow trout to later, piscivorous stages (Werner and Gilliam 1984). These bottlenecks may prevent piscivore biomass from increasing in response to increased production of its prey, ultimately leading to a negative correlation between resources and consumers (Bystrom et al. 1998). This is a counterintuitive result that may be important to consider in stocking management, as one would otherwise expect stocking success to increase with resource availability.

Developing a clearer understanding of rainbow trout feeding ecology could improve the management and stocking success of the species in eastern Washington lakes. However, accomplishing this goal is labor-intensive with traditional field techniques. Gut content analyses provides dietary information for a single snapshot in time and requires extensive laboratory work to identify contents. To understand diets

over a longer period using this technique, diets must be sampled multiple times, increasing both labor and expense. This study used stable isotope analysis to infer rainbow trout dietary information. Stable isotope analysis integrates information about diet over time within a single sample, requires minimal laboratory work, and provides information on the overall energy sources (e.g. littoral versus pelagic primary production) and trophic position of the animal, rather than its specific prey items. Because it is less labor-intensive, it is an inexpensive alternative to dietary analyses, and provides broader-scale ecological information. Vinson and Budy (2009) compared sources of variability and cost between stable isotope analysis and gut content analysis in three salmonid species during a four-year study. Gut content analysis determined high dietary overlap between brown trout, rainbow trout, and mountain whitefish at the study sites. However, stable isotope analysis showed little overlap and species, year, and size effects were significantly different, implying that although these species consumed similar prey items, they did so in very different proportions. Stable isotope samples cost \$12 (US) to process. Gut content analysis samples cost between \$1.50 for an empty stomach to \$291.50 for a stomach with an array of prey items, with the mean cost per sample equaling \$25.49. However, in many cases, both isotope analysis and direct examination of diets provide useful complimentary information.

Stable isotope analysis can be used to construct the food web structure of aquatic communities and has the potential to identify factors that influence the stocking success of rainbow trout. Over the past twenty-five years, stable isotope analyses have been applied to construct food webs in a wide diversity of aquatic habitats. Studies by Fry and Sherr (1984) were among the earliest examples. These studies used carbon stable isotope

ratios of dissolved nutrients, aquatic plants, and animals to establish a chemical outline of the aquatic food web. A dual-isotope approach is often used in aquatic food web studies. For example, nitrogen isotopes are commonly used to indicate trophic level, whereas carbon isotopes are used for determining which energy sources are being used by consumers (Peterson and Fry 1987).

Isotopic compositions change in predictable ways as they are cycled through the biosphere. Applications of stable isotope analysis throughout the environmental sciences employ the ratio of heavy to light stable isotopes (Keough et al. 1996). The heavy to light stable isotope ratio of carbon, $^{13}\text{C}:^{12}\text{C}$, and nitrogen, $^{15}\text{N}:^{14}\text{N}$, is determined by analyzing the isotopic ratio of an organism's tissue using a mass spectrometer. Stable isotopic compositions are reported as a δ value, which is the difference (parts per thousand – ‰) in isotopic composition between a sample and standard. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are calculated using the following equation:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}}) \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$. For example, $\delta^{13}\text{C} = (^{13}\text{C}:^{12}\text{C}_{\text{sample}}/^{13}\text{C}:^{12}\text{C}_{\text{standard}}) \times 1000$. The standard reference materials are PeeDee limestone for carbon and atmospheric nitrogen (Peterson and Fry 1987). An increase in δ denotes an increase in the heavy isotope concentration and, conversely, a decrease in the light isotope concentration.

In food webs, carbon and nitrogen isotope ratios behave in predictable ways during trophic transfers of organic molecules between predators and prey (Minegawa and

Wada 1984, DeNiro and Epstein 1978). During assimilation of prey molecules into consumer tissue, heavy isotopes of carbon and nitrogen preferentially incorporated, leading to fractionation, or an increase in concentration of the heavy isotope. The fractionation between prey and predator is 0 – 2 ‰ $\delta^{13}\text{C}$ and 3 – 4 ‰ $\delta^{15}\text{N}$ (DeNiro and Epstein 1981, Peterson and Fry 1987). Due to the relatively small change of $\delta^{13}\text{C}$ as it moves through the food web, stable carbon isotope values are typically used to evaluate the ultimate source of carbon for an organism when the isotopic signatures of the sources are different (Post 2002). As a result of $\delta^{15}\text{N}$ enrichment with each successive trophic transfer (Peterson and Fry 1987), stable nitrogen isotopes are typically used to examine the trophic position of an organism (DeNiro and Epstein 1981, Minagawa and Wada 1984, Peterson and Fry 1987).

This study used stable carbon isotope ratios to determine the predominant carbon source, littoral or pelagic, used by stocked rainbow trout and other fish resident in the study lakes. Littoral carbon can be distinguished from pelagic carbon due to the significant enrichment in $\delta^{13}\text{C}$ in periphyton (littoral algae) in comparison to phytoplankton (planktonic algae) (France 1995). The $\delta^{13}\text{C}$ enrichment of periphyton compared to phytoplankton is due to the high diffusion resistance of CO_2 in water. Plants with well-defined boundary layers will become carbon limited due to slow CO_2 diffusion and assimilate more ^{13}C , which is normally discriminated against during photosynthetic carbon uptake (France 1995). In littoral zone conditions, with decreased water turbulence and thicker boundary layers around photosynthetic organisms, periphyton will become more enriched in ^{13}C relative to ^{12}C , resulting in a higher $\delta^{13}\text{C}$ (Osmond et al. 1981). Phytoplankton experiences less carbon limitation, resulting in increased discrimination

against ^{13}C and a lower $\delta^{13}\text{C}$. Based upon global primary consumer stable isotope data, periphyton is enriched in ^{13}C by approximately 7‰ in comparison to phytoplankton (France 1995). A primary consumer species' $\delta^{13}\text{C}$ value reflects the stable carbon isotope ratios of its food, and can be used to determine if that food includes littoral or pelagic primary production, or both (DeNiro and Epstein 1978, Peterson and Fry 1987). A secondary consumer species' $\delta^{13}\text{C}$ will reflect its prey species within 0 – 2‰ and, in turn, its carbon source (Peterson and Fry 1987).

This study used stable nitrogen isotope ratios to infer relative trophic positions of fish within each lake's food web. Increases in $\delta^{15}\text{N}$ correspond with increasing trophic status (Minagawa and Wada 1984, Peterson and Fry 1987, Post 2002). Trophic status of each lake constituent can be obtained by detecting the stepwise increase of 3 – 4‰ in $\delta^{15}\text{N}$ values between prey and predator (DeNiro and Epstein 1981). Post (2002) demonstrated that this 3 – 4‰ stepwise increase is consistent among different trophic guilds of fishes including herbivores, carnivores, and detritivores. $\delta^{15}\text{N}$ enrichment with trophic transfer within food webs is due to preferential excretion of the light isotope, ^{14}N , resulting in concentration of ^{15}N with each successive trophic transfer (Peterson and Fry 1987). Because most consumers feed at more than one trophic level, isotope studies rarely yield integer trophic position values (e.g. 2.0 or 3.0) for consumers corresponding to classic trophic position descriptions (primary consumer, secondary consumer, etc.) (Jones and Waldron 2003).

Stable nitrogen and carbon isotope ratios are often plotted together to illustrate aquatic food webs, including carbon sources and trophic positions of the consumers. A hypothetical dual carbon-nitrogen stable isotope plot is presented in Figure 1.

Several recent studies using carbon and nitrogen isotope ratios illustrate their potential value in understanding lake food webs. Using stable carbon and nitrogen ratios, Black et al. (2003) determined most littoral aquatic species, including rainbow trout, inhabiting Lake Roosevelt, Washington, where annual water fluctuation limits littoral productivity, draw primarily from pelagic carbon sources. Similarly, Beaudoin et al. (2001) investigated lake food webs in Canada's Boreal Plain by using stable carbon and nitrogen isotopes. Food webs in the lake spanned a range of four to five trophic levels, with many organisms feeding on mixed trophic level diets. Northern pike (*Esox lucius*) and fathead minnows (*Pimephales promelas*) occupied the top predator position in most lakes despite obvious large differences in body size and morphology. The relative importance of external (terrestrial) and internal carbon sources was determined for each system.

Keough et al. (1996) used stable isotope ratios to determine the carbon source (wetland versus pelagic) for coastal Lake Superior consumers. In addition, ontogenetic shifts were detected for rainbow smelt (*Osmerus mordax*) and walleye (*Stizostedion vitreum*), shifting from a wetland isotopic signature for young-of-the-year (YOY) to pelagic isotopic signatures in juveniles and adults, indicating a trend that as rainbow smelt and walleye grew they relied more heavily on pelagic carbon in their diet. Linear regression of yellow perch (*Perca flavescens*) length versus $\delta^{15}\text{N}$ indicated a trend that as yellow perch trout grew they relied more heavily on higher trophic level prey in their diet. Harvey and Kitchell (2000) examined spatial heterogeneity of a Lake Superior food web using stable isotope analysis. Interestingly, they found previously implied trophic linkages by gut content analysis were only somewhat supported by stable isotope

analysis. Assuming the nearby cities of Duluth, Minnesota and Superior, Wisconsin were the source of ^{15}N , they were able to analyze spatial heterogeneity of sampled species. Slimy sculpin (*Cottus cognatus*) were found to be the most sedentary, with ^{15}N levels enriched in the Deluth-Superior site relative to other sites. Rainbow smelt (*Osmerus mordax*) were found to have the highest vagility, showing no differences in ^{15}N at any sites.

Browne and Rasmussen (2009) determined using stable isotope analysis and gut content analysis that brook trout (*Salvelinus fontinalis*) compete for resources and interact as prey and predator with yellow perch in three Algonquin Provincial Park, Ontario, Canada lakes. Moreover, they determined that brook trout littoral carbon use differed between lakes containing perch (10 – 70%) and lakes void of perch (50 – 100%). Brook trout in lakes containing perch fed primarily on pelagic prey, which contrasted in lakes without perch where they feed on a mixture of littoral and pelagic prey items. This study showed the value of stable isotope analysis in comparing pelagic and littoral resource use in lakes with varying fish community constituents.

Using stable isotope analysis and gut content analysis, Christensen and Moore (2009), analyzed dietary niches within Twin Lakes, Washington. The researched determined successive enrichment in $\delta^{15}\text{N}$ for largemouth bass (*Micropterus salmoides*), suggesting an ontogenetic shift to higher trophic level prey items as fish grew. An intermediary isotopic signature for golden shiner (*Notemigonus crysoleucas*), combined with gut content data, suggesting horizontal diel migration, feeding on pelagic, nocturnal phantom midges at night and littoral damselflies during the day. Stable isotope analysis

also determined stocked rainbow trout fed primarily on pelagic zooplankton and showed the least amount of dietary variability.

Studying Lake Pend Oreille, Idaho piscivores, rainbow trout included, Clarke et al. (2005) were able to compare the effectiveness of stable isotope analysis versus gut content analysis in determining dietary information. Large rainbow trout (> 500 mm total length) were piscivorous, feeding mainly on kokanee salmon (*Oncorhynchus nerka*), confirmed by both gut content analysis and stable isotope analysis. The diet of small rainbow trout and cutthroat trout (*Oncorhynchus clarkii*) (< 400 mm total length) overlapped and were comprised mainly of littoral invertebrates, again confirmed by both gut content analysis and stable isotope analysis. However, stable isotope analysis predicted kokanee consumption for 400 – 500 mm rainbow trout, large cutthroat trout, and small lake trout (*Salvelinus namaycush*), but no kokanee were identified in gut content samples for any of the species. This study again demonstrated that the value of pairing gut content analysis with stable isotope analysis to determine diets of sample species.

As shown by the research above, stable isotope analysis is a powerful tool that can be used to understand the organization of aquatic communities, and identify the resources that are spatially and temporally important to consumers, such as rainbow trout, that are being actively managed. The purpose of the research was to examine the impact that resident fish communities have upon stocked rainbow trout trophic position and relative use of energy from pelagic and littoral zones of a lake. I hypothesized that rainbow trout use of littoral carbon and consequently, their stable carbon ratios, would be negatively associated with the presence of resident fish and to increasing resident fish

community complexity, due to competition for littoral resources. I hypothesized that extent of lake littoral vegetation and lake size would also predict stocked rainbow trout littoral carbon use. Furthermore, I hypothesized that YOY and 1+ rainbow trout would primarily use pelagic carbon sources due to competition, both interspecific and intraspecific, and switch to littoral carbon as age increased. Stable nitrogen isotope signatures were used to determine the species' trophic positions. My hypothesis was that stocked rainbow trout stable nitrogen isotope signatures would be negatively correlated to resident fish presence and the complexity of the resident fish community, due to stocked rainbow trout shifting their diet to avoid predation by piscivorous fish, thereby, occupying lower trophic level positions relative to rainbow trout in systems with little to no predation. Lastly, I hypothesized a positive correlation between rainbow trout size and $\delta^{13}\text{C}$, indicating a shift towards greater use of littoral resources as fish grow, and a positive correlation between size and $\delta^{15}\text{N}$, indicating that larger rainbow trout occupy a higher trophic position.

METHODS AND MATERIALS

Study Sites: Research was conducted in fifteen study lakes across the eastern Washington State lake landscape. The origin of eastern Washington lakes, including the study sites, fall into two general categories: glacial-formed lakes, otherwise known as kettle lakes; and plunge basin lakes (Wolcott, 1973). The latter were formed from the breaking of the Lake Missoula ice dam and subsequent cataclysmic floods across eastern Washington approximately 15,000 years ago (Allen et al, 2009).

All study site lakes were stocked with rainbow trout and managed for sport fishing by the Washington Department of Fish and Wildlife. Study sites lakes were chosen to represent a wide distribution of lakes across eastern Washington, as well as encompass a variety of resident fish constituents. Washington Department of Fish and Wildlife hatchery trout stocking plans (2002 – 2007) for study site lakes are presented in Table 1. Study sites were stocked with rainbow trout fry and/or “catchables” at varying year intervals. For the purpose of this study, no distinction was made between stocked triploid rainbow trout and diploid rainbow trout. The majority of lakes contained existing resident fish populations, introduced by intentional or unintentional stocking. Only two lakes contained solely stocked rainbow trout. Historically, most eastern Washington lakes were fishless. However, some lakes contained a variety of native fish species (Wolcott, 1973), none of which were included in this study. I attempted to collect all fish community members. However, limitations in sample collection techniques prevented this at some study sites and some fish community members were not obtained. Littoral vegetation in the lakes was variable, including, but not limited to, common elodea (*Elodea canadensis*), northern water milfoil (*Myriophyllum sibiricum*), yellow water-lily (*Nuphar polysepala*), hardstem bulrush (*Schoenoplectus acutus*), reed canary grass (*Phalaris arundinacea*), and cat-tail (*Typha* sp.) (Aquatic Plant Monitoring, ecy.wa.gov). Where present, littoral zone constituents included a wide variety of taxa, including, but not limited to, Ephemeroptera, Gastropoda, and Amphipoda. Surrounding watersheds included pasture and rangeland, woodland, scabland, and/or forest. A map of study site locations across eastern Washington State is presented in Figure 2. Study site data,

including size, location, and maximum and average depth for each lake is presented in Table 2.

Sample Collection and Processing: During autumn of 2006 and spring of 2007, fish tissue samples were collected from five individuals per age class per representative species. Gill nets, creel surveys, and hook and line were used to collect fish. Resident fish species were collected if they could be readily obtained by these methods. Muscle tissue samples, filleted from dorsal section or caudal peduncle, were collected from each fish. If too small for field filleting, fish were collected whole and then later filleted in the lab. Samples were immediately placed on ice and preserved in a freezer at -15 °C.

Pelagic and littoral invertebrate species were collected in spring 2007. Conical zooplankton nets (253µm) and D-ring dip nets were used to collect pelagic invertebrates (zooplankton) and littoral invertebrates, respectively. In addition, chironomids were collected from profundal sediment in three study sites using an Eckman dredge. A 740µm screen was used to filter the lake sediment samples, allowing chironomids to be removed by hand. Invertebrate species were kept alive in 20L carboys until the following day when they were sorted taxonomically. *Daphnia* were separated from other zooplankton constituents using mesh sieves (450µm – 850µm). Individual pelagic and littoral invertebrates were pooled with individuals of the same order and frozen in plastic vials. *Daphnia* were sampled from each site, as they were readily available in all lakes. One representative littoral herbivore, such as Ephemeroptera, Gastropoda, or Amphipoda, was also collected from each study site. Invertebrates were classified to family and/or

genus. Since primary producers show a great deal of variation in isotopic ratios (Zohary et. al 1994), they were not collected for analysis.

Individual fish and invertebrate samples, excluding shells if applicable, were prepared by rinsing with deionized water, drying at 60°C, grinding to homogeneity, and storing in glass vials (Black et al. 2003). Samples were then weighed to 1mg \pm 0.2mg and enclosed in tin capsules. For fish samples, where 1mg could be obtained from a single individual, one individual per sample was used. For pelagic and littoral invertebrate species, where 1mg could not be obtained, individuals were pooled and a single sample was prepared. Finished prepared samples were shipped to University of California Davis Isotope Facility (Department of Agronomy) and analyzed with a PDZ Europa ANCA–GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

Data Analysis: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and associated standard deviation (SD) were determined for each sampled species, per age class if applicable. These values were used in mixing models to assess percent littoral carbon in tissues of higher consumers and to assess trophic level of sampled species. *Daphnia* were used as a base reference for the pelagic zone, and Ephemeroptera, Gastropoda, or Amphipoda were initially used as the base reference for pelagic the littoral zone. *Daphnia* and Gastropoda have been utilized as base reference organisms in previous studies (Black et. al 2003). However, after analyzing higher trophic level consumers' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, it became apparent that base littoral herbivores' isotope values were not always exclusively representative of the lake's littoral zone or primary consumer trophic level. As a result, trophic level was not

calculated and, instead, generalizations were made about each lake's food web based on the stepwise increase of 3 – 4‰ in $\delta^{15}\text{N}$ values between prey and predator (DeNiro and Epstein 1981).

Instead of relying on littoral herbivores collected as part of this study, littoral zone base reference $\delta^{13}\text{C}$ values were assumed to be enriched 7‰ from the pelagic $\delta^{13}\text{C}$ base reference (*Daphnia*) for each lake. This assumption was based upon periphyton $\delta^{13}\text{C}$ enrichment by approximately 7‰ (standard deviation equal to 3.00‰) in comparison to phytoplankton, as determined by an assessment of global primary consumer stable isotope data (France 1995). For application to mixing models, standard deviation of $\delta^{13}\text{C}$ for the pelagic base reference, *Daphnia*, was determined by compiling *Daphnia* $\delta^{13}\text{C}$ from all study sites and calculating the associated standard deviation. For inclusion in mixing models, standard deviation of the littoral base was adjusted to account for both the standard deviation in the pelagic base and the standard deviation in the difference between pelagic and littoral base $\delta^{13}\text{C}$ using standard error propagation, resulting in a standard deviation of 5.72‰ for littoral base estimates. For each species sampled (except *Daphnia*), the percent carbon derived from littoral primary production was estimated using the IsoSource two-source mixing model calculator for Excel provided by Phillips and Gregg (2001). This model allows calculation of confidence intervals around estimates of percent contributions by specific sources.

Estimates of percent littoral carbon in rainbow trout tissues from mixing models were compared with lake characteristics to assess factors that might explain variability in trout reliance on littoral productivity. Statistical tests for each comparison were selected based on the independent variable type and whether data fit assumptions for parametric

tests. The Wilcoxon/Kruskal-Wallis test was used to analyze the relationship between lake littoral class and rainbow trout estimated littoral carbon use. Lake littoral class was determined by assigning each a rank based on estimated percent littoral zone present (1 = $\leq 10\%$, 2 = 10 – 30%, 3 = $\geq 30\%$). Lake littoral class for each study site is presented in Table 2. Linear regression was used to analyze rainbow trout estimated littoral carbon use and lake size. ANOVA (with age class as the independent variable) and linear regression were used to analyze the relationship between rainbow trout size and estimated littoral carbon use. A t-test was used to analyze the relationship between resident fish community (with “yes” or “no” for resident fish presence as the independent variable) and rainbow trout estimated littoral carbon use, $\delta^{13}\text{C}$, or $\delta^{15}\text{N}$. ANOVA was used to analyze the correlation between rainbow trout estimated littoral carbon use, $\delta^{13}\text{C}$, or $\delta^{15}\text{N}$ and resident fish community complexity, the latter measured by the number of resident fish age classes present.

Ontogenetic shifts, or changes in community structure in different age classes of fish species, were examined using linear regression. A significant linear regression $\delta^{13}\text{C}$ versus fish length indicates a possible ontogenetic shift in littoral versus pelagic carbon utilization. For example, a significant increase in $\delta^{13}\text{C}$ with an increase in length would indicate that as fish grew they relied more heavily on littoral carbon in their diet. Linear regression analysis of length versus $\delta^{15}\text{N}$ indicates a possible ontogenetic shift in trophic position. For example, an increase in $\delta^{15}\text{N}$ with an increase in length would indicate that as fish grew they relied more heavily on higher trophic position prey in their diet.

Calculated using Bonferroni correction for multiple comparisons, the α for assessing

ontogenetic niche shifts in rainbow trout was 0.004. For all other fish species, α equaled 0.05.

Where applicable, proportional data was transformed using the arcsine square-root transformation. Statistical analysis of data was conducted using JMP, SAS Institute, 2006, version 6.0.3 software.

RESULTS

In this research, stable isotope analysis was used to assess the impact of lake physical characteristics and fish community composition on the relative use of littoral and pelagic energy sources and trophic position of stocked rainbow trout. More specifically, I determined whether estimated percent littoral carbon in stocked rainbow trout tissue could be significantly explained by independent variables related to lake habitat and fish community composition. However, based on poor confidence intervals for estimated percent littoral carbon utilization, the diet of sampled organisms was difficult to assess. In addition, I assessed whether the same independent variables predicted $\delta^{15}\text{N}$ in stocked rainbow trout tissue. A more specific analysis of each sampled species' relative trophic position could not be done because I did not have clear baseline $\delta^{15}\text{N}$ for littoral primary consumers in several of the lakes, and could not calculate trophic position.

For each lake, the species collected, age classes (if applicable), sample sizes, mean $\delta^{13}\text{C}$ (& SD), mean $\delta^{15}\text{N}$ (& SD), and percent littoral carbon use (& 95% confidence interval) are presented in Tables 3 – 17. In addition, dual isotope plots for each lake with organisms' mean $\delta^{13}\text{C}$ and mean $\delta^{15}\text{N}$ are presented in Figures 3 – 17.

I estimated the percent littoral carbon in stocked rainbow trout of each age class in each lake using the IsoSource two-source mixing model calculator for Excel provided by Phillips and Gregg (2001). Estimated percent littoral carbon ranged from 0.57% (Dusty Lake 3+ rainbow trout) to 100% (Amber Lake 2+ and 3+, Fishtrap Lake 2+, Hog Lake 2+, Lower Hampton Lake 2+, Spectacle Lake 2+ and 3+ rainbow trout); however the confidence intervals for these estimates were very large, in most cases including both 0% and 100%, indicating little confidence in dietary information. These estimates were based on using *Daphnia* data from each lake as the pelagic base for that lake; *Daphnia* $\delta^{13}\text{C}$ ranged from -25.08‰ (Dry Falls Lake) to -41.25‰ (Hog Lake). As a single composited *Daphnia* sample was collected & processed from each lake, the standard deviation for *Daphnia* $\delta^{13}\text{C}$ was calculated by compiling *Daphnia* $\delta^{13}\text{C}$ values from all lakes, and equaled 4.88‰. The littoral base reference $\delta^{13}\text{C}$ for each lake was assumed to equal the pelagic base reference $\delta^{13}\text{C}$ value minus 7‰ (SD \pm 5.72‰).

Estimated percent littoral carbon use was compared to two aspects of lake habitat, littoral vegetation and lake size. As rainbow trout from 2+ or 3+ age classes were present in all lakes, those age classes were used for estimated littoral carbon use. Where both 2+ and 3+ age classes were present, an average of their estimated littoral carbon use was calculated. These 2+ and 3+ age class data were used for all subsequent tests relating rainbow trout isotope data to fish community composition described in this results section. The Wilcoxon/Kruskal-Wallis test was used to analyze the relationship between lake littoral class and rainbow trout estimated littoral carbon use. Lake littoral class was determined by assigning each lake a rank based on estimated percent littoral zone present (1 = \leq 10%, 2 = 10 – 30%, 3 = \geq 30 %). According to the Wilcoxon/Kruskal-Wallis, test

lake littoral class does predict rainbow trout estimated littoral carbon use (chi-square = 16.032, $p = 0.0003$, d.f. = 2). Linear regression was used to analyze rainbow trout estimated littoral carbon use and lake size. Linear regression indicated that lake size does not predict rainbow trout estimated littoral carbon use ($R^2 = 0.129$, F-ratio = 1.938, $p = 0.187$).

A t-test was used to analyze the relationship between resident fish community (with “yes” or “no” for resident fish presence as the independent variable) and rainbow trout estimated littoral carbon use. No significant relationship was found between rainbow trout estimated littoral carbon use and the presence of resident fish ($p = 0.366$, d.f. = 4.520, $t = 1.005$). T-test results indicated a significant relationship between rainbow trout estimated littoral carbon use and the presence of other resident trout ($p = 0.014$, d.f. = 13.369, $t = 2.816$) and the presence of brown bullhead ($p = 0.028$, d.f. = 12.152, $t = 2.501$), where stocked rainbow trout used less littoral carbon in both cases. No significant relationship was found between rainbow trout estimated littoral carbon use and the presence of centrarchids ($p = 0.082$, d.f. = 28.854, $t = 1.803$).

Because of the uncertainty associated with estimated % littoral carbon use, it seemed useful to also directly test the affects of fish communities on $\delta^{13}\text{C}$. The relationship between resident fish community (with “yes” or “no” for resident fish presence as the independent variable) and 2+ and 3+ rainbow trout $\delta^{13}\text{C}$ was analyzed using a t-test. No significant relationship was found between rainbow trout $\delta^{13}\text{C}$ and the presence of resident fish ($p = 0.255$, d.f. = 5.353, $t = 1.274$). According to t-test, rainbow trout $\delta^{13}\text{C}$ is not predicted by the presence of other resident trout ($p = 0.337$, d.f. = 9.828, $t = 1.009$) or centrarchids ($p = 0.56$, d.f. = 22.949, $t = 0.587$). T-test results indicated the

presence of brown bullhead predict rainbow trout $\delta^{13}\text{C}$ ($p = 0.045$, $d.f. = 12.819$, $t = 2.226$), with $\delta^{13}\text{C}$ becoming less enriched in systems containing brown bullhead.

A t-test was used to analyze the relationship between resident fish community (with “yes” or “no” for resident fish presence as the independent variable) and 2+ and 3+ rainbow trout $\delta^{15}\text{N}$. No significant relationship was found between rainbow trout $\delta^{15}\text{N}$ and the presence of resident fish ($p = 0.085$, $d.f. = 26.188$, $t = 1.789$). T-test results indicated a significant relationship between rainbow trout $\delta^{15}\text{N}$ and the presence of other resident trout ($p = 0.043$, $d.f. = 10.097$, $t = 2.310$), where stocked rainbow trout $\delta^{15}\text{N}$ was significantly lower in lakes containing resident trout. No significant relationship was found between rainbow trout $\delta^{15}\text{N}$ and the presence of brown bullhead ($p = 0.055$, $d.f. = 7.541$, $t = 2.261$) or the presence of centrarchids ($p = 0.104$, $d.f. = 16.636$, $t = 1.723$).

ANOVA was used to analyze the correlation between rainbow trout estimated littoral carbon use, $\delta^{13}\text{C}$, or $\delta^{15}\text{N}$ and resident fish community complexity, the latter measured by the number of resident fish age classes present. According to ANOVA, resident fish community complexity does predict rainbow trout estimated littoral carbon use, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ (ANOVA results are presented in Tables 18A and 18B), with all three measures decreasing with increasing resident fish community complexity.

Ontogenetic niche shifts, or changes in habitat used and feeding behavior as fish grow, were examined using linear regression and ANOVA. I used both age class and fish length as independent variables for these comparisons. ANOVA was used to analyze the relationship between rainbow trout age class and estimated littoral carbon use. According to ANOVA, rainbow trout age class does not predict rainbow trout estimated littoral carbon use (ANOVA results are presented in Table 19). I used linear regression

to relate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to fish length for both stocked rainbow trout and other fish species present in multiple age classes in sampled lakes. Calculated using Bonferroni correction for multiple comparisons, α for rainbow trout regressions was 0.004. For all other fish species, $\alpha = 0.05$. A significant positive correlation was detected between rainbow trout length and $\delta^{13}\text{C}$ in Fishtrap, Spectacle, West Medical, and Williams Lakes and yellow perch length and $\delta^{13}\text{C}$ in Williams Lake. These results indicate that as fish in these lakes grew they relied more heavily on littoral carbon in their diet. A significant positive correlation was detected between $\delta^{15}\text{N}$ and Fishtrap and West Medical Lake rainbow trout length and Rat Lake brown trout. These results indicate that as fish in these lakes grew they relied more heavily on higher trophic position prey in their diet. All linear regression results of fish length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the fifteen study sites are presented in Tables 20A and 20B, respectively.

In this research, I used stable isotope analysis techniques to obtain the primary goal of analyzing the impacts that lake habitat and fish community composition have upon energy source use and trophic position of stocked rainbow trout. Significant correlations between rainbow trout percent littoral carbon utilization and lake littoral class, presence of other resident trout and brown bullhead, and resident fish community complexity were detected. In addition, a significant correlation was detected between rainbow trout $\delta^{13}\text{C}$ and resident fish community complexity and the presence of brown bullhead. I also compared fish $\delta^{15}\text{N}$ to lake habitat and community composition variables to determine whether relative trophic position appeared to respond to these variables. A significant correlation was detected between rainbow trout $\delta^{15}\text{N}$ and resident fish community complexity and the presence of other resident trout. Several ontogenetic

shifts were detected including a significant positive correlation between rainbow trout length and $\delta^{13}\text{C}$ in Fishtrap, Spectacle, West Medical, and Williams Lakes and yellow perch length and $\delta^{13}\text{C}$ in Williams Lake, and a significant positive correlation between $\delta^{15}\text{N}$ and Fishtrap and West Medical Lake rainbow trout length and Rat Lake brown trout.

DISCUSSION

The goal of this project was to examine the impact that resident fish populations have on stocked rainbow trout trophic position and relative use of energy derived from pelagic versus littoral zones of a lake using stable isotope analysis. Research was conducted in 15 eastern Washington lakes, all popular rainbow trout sport fishing destinations and therefore stocked for that purpose.

To examine the impact that resident fish populations have on stocked rainbow trout relative use of energy derived from pelagic versus littoral zones of a lake, rainbow trout estimated littoral carbon use was compared with a host of ecological independent variables. I hypothesized that rainbow trout percent littoral carbon use and stable carbon ratios would be negatively correlated with the presence of specific resident fish, and with increasing resident fish community complexity. A significant relationship was detected between rainbow trout estimated littoral carbon use and the presence of other resident trout and brown bullhead, as indicated by significantly lower littoral carbon percentages in lakes containing other resident trout and/or brown bullhead. Furthermore, the presence of brown bullhead predicted rainbow trout $\delta^{13}\text{C}$. These findings are most likely due to competition. Despite high zooplankton abundance in many of the lakes, stocked rainbow

trout appeared to feed primarily on littoral macroinvertebrates,. Competition with other trout species (mainly brown trout and tiger trout), and brown bullhead may have reduced the ability of stocked rainbow trout to use littoral food sources and shifted their diets toward pelagic carbon sources, as shown by significantly lower estimated percent littoral carbon use and $\delta^{13}\text{C}$ values in lakes containing those species. Although brown bullhead appear ecologically different from rainbow trout, Kline and Wood (1996) determined high electivity for littoral and benthic prey items by brown bullhead in Perch Lake, New York. Among the 27 prey items identified in brown bullhead diet, chironomid larvae and pupae and Amphipoda were found to have the highest electivity. If brown bullhead have similar diets in Eastern Washington lakes, they would likely be competitors with stocked rainbow trout for littoral prey items.

These findings were concurrent with a previous research conducted (Clark 1959, Donald 1987, Fraser 1972, Gipson and Hubert 1991, Miller 1958, Miller 1962, Murphy 1962, Needham 1959, Soldwedel 1974, Stuber et al. 1985) that determined that hatchery-reared rainbow trout experience heavy competition when stocked in systems containing resident fish communities, therefore, making such stocking practices largely ineffective. Moreover, a significant relationship was detected between resident fish community complexity and rainbow trout estimated littoral carbon use and $\delta^{13}\text{C}$. As the complexity of resident fish communities increased, rainbow trout estimated littoral carbon use and $\delta^{13}\text{C}$ decreased. These findings were also supported by previous research that determined that an inverse relationship exists between the complexity of the resident fish community and the success of stocked salmonids, rainbow trout included (Fraser 1972). Again, this is most likely due to increased competition as complexity of the resident fish

communities increases. No significant relationship was found between rainbow trout estimated littoral carbon use and the presence of resident fish or the presence of centrarchids. Only two lakes did not contain resident fish, so statistical power to test for effects of the presence/absence of resident fish was weak. In this data set, relationships with the complexity of the resident fish community are more likely to be indicative of the overall effect of resident fish on rainbow trout niche. No significant relationship was found between rainbow trout $\delta^{13}\text{C}$ and the presence of resident fish, presence of other resident trout, or centrarchids. It should be noted that confidence intervals for estimated percent littoral carbon were very large, in most cases including both 0% and 100%, indicating little confidence in dietary information. More precise dietary information may have revealed additional relationships between ecological parameters and stocked rainbow trout feeding.

Although the above results appear to suggest that competition associated with the presence of resident trout and brown bullhead and increasing fish community complexity is correlated to a decrease in rainbow trout estimated littoral carbon use and $\delta^{13}\text{C}$, alternative explanations are possible. Further studies are needed to determine if alternative hypothesis are in fact the reason for the negative correlation. For example, predation on stocked rainbow trout, not competition, may drive them to pelagic carbon sources, resulting in a decrease in estimated littoral carbon use and $\delta^{13}\text{C}$. Alternatively, the presence of other fish species may be correlated with some physical component of lake habitat that was not explicitly evaluated in this study.

Estimated percent littoral carbon use was compared to two aspects of lake habitat, littoral vegetation and lake size. Rainbow trout are opportunistic feeders whose diet

varies from water body to water body. I hypothesized that lake littoral class (based on estimated percent littoral zone present) could predict rainbow trout estimated littoral carbon use. Data collected supported this hypothesis. As estimated percent littoral zone present increased, so did rainbow trout estimated littoral carbon use, indicating a high relative importance of littoral carbon sources in stocked rainbow trout diet. Secondly, I hypothesized that lake size could predict rainbow trout estimated littoral carbon. This hypothesis was not supported by stable isotope data. This is most likely due to a small sample size, making such generalizations difficult. However, further research is needed sufficiently make this determination. Other characteristics of the lakes, such as differences in macrophyte distribution, bathymetry, temperature, and/or predator-prey demographics may be more important than size in explaining stocked rainbow trout diet.

Finally, I hypothesized that juvenile rainbow trout (YOY and 1+) would primarily use pelagic carbon sources. This hypothesis was not supported by stable isotope data, as 1+ fish in many of the lakes appeared to use primarily littoral carbon, and variation among lakes was much higher than variation among age classes. These findings indicate that, like previous research has suggested, rainbow trout do indeed have a diverse diet that varies from one aquatic system to the next. For example, a several studies have determined that stocked rainbow trout use primarily pelagic carbon (Yoshioka et al. 1994, Lynott et al. 1995). Alternatively, littoral carbon has been found to a primary energy source for rainbow trout in other systems (Herwig et al. 2004, Budy and Haddix 2005, Warner and Quinn 1995). Thus, previous research seems to indicate that both littoral and pelagic carbon are energy sources in aquatic systems, whose relative importance to rainbow trout varies from water body to water body. My research suggests that extent of

littoral vegetation and resident fish community structure are two predictors of the importance of littoral resources to rainbow trout in a particular lake system.

I also used $\delta^{15}\text{N}$ of fish tissue to assess relative trophic position of stocked rainbow trout to a similar set of independent variables. I could not estimate specific, quantitative trophic positions of stocked rainbow trout because I did not have clear baseline $\delta^{15}\text{N}$ for littoral primary consumers in several of the lakes. I hypothesized that stocked rainbow trout stable nitrogen isotope ratios would be negatively correlated to resident fish presence, both overall and species specific. In addition, I hypothesized that stocked rainbow trout stable nitrogen isotope ratios would be negatively correlated to increasing complexity of resident fish community. No significant relationship was found between rainbow trout stable nitrogen isotope signatures and the presence of resident fish. However, results did indicate a significant relationship between rainbow trout $\delta^{15}\text{N}$ and the presence of other resident trout. Similarly, according to data analysis, resident fish community complexity does predict rainbow trout $\delta^{15}\text{N}$. These findings indicate that, first of all, resident trout, mainly brown trout and/or tiger trout, force stocked rainbow trout to shift their diet to avoid predation, thereby, occupying lower trophic level positions relative to rainbow trout in systems with little to no predation, and, secondly, stocked rainbow trout occupy lower trophic levels in large, complex fish communities. Kerr and Lasenby (2000), Johnson and Hasler (1954), Budy and Haddix (2005), and High (2008) determined similar findings of predation on stocked rainbow trout by select resident fish species. Other species-specific correlations (presence of brown bullhead or the presence of centrarchids) to rainbow trout stable nitrogen isotope signatures were not

found to be significant in my research however, indicating that rainbow trout diet consists of similar trophic level prey and piscivory is unlikely.

Ontogenetic shifts, or behavioral changes resulting in shifting trophic positions and/or energy sources as fish age, were also assessed. I hypothesized that a positive correlation exists between rainbow trout length and $\delta^{13}\text{C}$ and a positive correlation between length and $\delta^{15}\text{N}$, both due to ontogenetic shifts resulting in increased use of littoral carbon and increased trophic level as fish grow. This hypothesis was supported by collected data in some of the study lakes. A significant positive correlation was detected between rainbow trout length and $\delta^{13}\text{C}$ in Fishtrap, Spectacle, West Medical, and Williams Lakes and yellow perch length and $\delta^{13}\text{C}$ in Williams Lake. These results indicate that as fish in these lakes grew they relied more heavily on littoral carbon in their diet. A significant positive correlation was detected between $\delta^{15}\text{N}$ and Fishtrap and West Medical Lake rainbow trout length and Rat Lake brown trout length. These results indicate that as fish in these lakes grew they relied more heavily on higher trophic position prey in their diet, most likely planktivorous fish. Again however, this trend seems to vary widely from water body to water body. Previous research has also shown variation in whether stocked rainbow trout switch to piscivory in later age classes. Lynott et al. (1995) found that rainbow trout smelt were readily incorporated into the diet of rainbow trout between 201 mm and 330 mm and became the dominant prey for fish larger than 460 mm. Budy and Haddix (2005) found the opposite; stocked rainbow trout rarely switched to piscivory in later age classes in Flaming Gorge Reservoir.

This research demonstrated the applicability of stable isotope analysis techniques to manage rainbow trout in eastern Washington lakes and to identify aquatic

constituencies' ecological roles. Stable isotope analysis has several advantages over gut content analysis for this purpose. Gut content analysis provides information from a single snapshot in time, unless samples are collected repeatedly. Even with a large sample size, gut content analysis can be difficult to interpret due to differing digestion rates of prey items. Conversely, stable isotope analysis requires only a small sample size due to temporally integrated assimilation of a consumer's diet into muscle tissue.

Yet, stable isotope analysis does have limitations and difficulties, as seen in this research. Based on poor confidence intervals for estimated percent littoral carbon use, the diet of sampled organisms was difficult to assess. In addition, a more specific analysis of each sampled species' relative trophic position could not be done because I did not have clear baseline $\delta^{15}\text{N}$ for littoral primary consumers in several of the lakes. Obtaining baseline primary consumers for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, exclusively representative of each lake zone, is crucial in assessing lake constituent diet and trophic level. As shown in this research, obtaining a representative species for the pelagic zone is not difficult, as zooplankton are plentiful and easy to obtain. However, obtaining a representative organism for the littoral zone is difficult, as numerous species are present in the littoral zone, but may not be exclusively representative. Initially, it was assumed that Gastropoda would be exclusively representative of the littoral zone and, as a result, was the primary littoral taxon collected, although Amphipoda and Ephemeroptera were also collected in some water bodies. After analyzing isotope signatures, it was apparent that no single taxon was exclusively representative of the littoral zone, including Gastropoda, as initially assumed. An extensive sampling regime that incorporates all littoral primary consumers is recommended, as the baseline littoral primary consumer may vary from

water body to water body. A base reference organism, exclusively representative of the lake's littoral zone, may have been determined if more littoral organisms had been included in sampling and calculating base organism values using enrichment assumptions could have been avoided. Confidence intervals would also have been much lower if replicate pelagic baseline samples had been collected from each lake. Variability among pelagic samples from the same lake would likely have been much lower than the SD calculated from variability among lakes, and would have allowed improved resolution of food webs within each lake. Despite uncertainty in data, it should be noted that most significant correlations for estimated percent littoral use were also found in direct analysis of $\delta^{13}\text{C}$. Large confidence intervals are more likely to obscure patterns in food web interactions than to cause spurious significant statistical results. However, all conclusions regarding estimated percent littoral carbon use should be considered provisional and tentative given the uncertainty in the data.

In conclusion, the principal purpose of this research was to analyze the effect(s) that the composition of resident fish communities and lake habitat have upon energy source use and trophic position of stocked rainbow trout. Stable isotope analysis was used to accomplish this goal. I found the amount of littoral carbon used by stocked rainbow trout could be predicted by several factors including the complexity of the resident fish community, amount of littoral vegetation present, and the presence of other resident trout and brown bullhead. In addition, significant negative correlations were detected between rainbow trout $\delta^{15}\text{N}$ and resident fish community complexity and the presence of other resident trout. Several ontogenetic shifts were also detected in several study sites, indicating that as fish in those systems grow, they shifted to a diet

incorporating more littoral carbon and higher trophic level prey. This study provided a unique opportunity to collect stable isotope data from 15 eastern Washington State lakes, which, in turn, enhanced knowledge of the effect that the lakes' animal constituency have upon stocked rainbow trout ecology. Collecting this data from 15 lakes provided insight into the structure of aquatic communities across the eastern Washington lake landscape. Such knowledge may be used by Washington Department of Fish and Wildlife (WDFW) to permit targeted management of individual lakes and thereby improve sport fishing of this important resource. Following this study, WDFW managers were made aware of the energy sources used and trophic position held by stocked rainbow trout within each lake. As a consequence, WDFW will be able to adjust stocking densities of this crucial resource, especially in those aquatic systems containing complex resident fish communities and/or resident trout and/or brown bullhead, as the presence of those specific constituents negatively correlated to stocked rainbow trout littoral carbon use and/or trophic position.

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TABLES

Table 1. **Washington Department of Fish and Wildlife Hatchery Trout Stocking 2002 – 2007** plan, including year, species, number fry plants, number 8-12 inches stocked, number 14 inches or larger stocked, and approximate time stocked. RBT = Rainbow trout. BT = Brown trout. TRB = Triploid rainbow trout. TT = Tiger trout. CT = Cutthroat trout. EB = Brook trout.

Lake	Year	Species	Number fry plants	Number 8-12 inches stocked	Number over 14 inches stocked	Approximate time stocked
Alta Lake	2002	RBT	36,800			Spring, fall
	2004	RBT	35,008			Spring, fall
	2005	RBT	36,720			Spring, fall
	2006	RBT	33,105			Spring, fall
	2007	RBT	55,055			Spring, fall
Amber Lake	2002	RBT	2,500			Spring, fall
	2003	CT	1,490			Spring, fall
		RBT	997			Spring, fall
	2004	RBT	2,692			Spring, fall
		CT	1,500			Spring, fall
	2005	RBT	9,990			Spring, fall
2007	CT	999			Spring, fall	
	RBT	12,786			Spring, fall	
Burke Lake	2002	RBT	21,011		7,000	March
	2003	RBT	20,930			Spring, fall
	2004	RBT	20,013	5,000		March
	2005	RBT	21,080	9,917		October
	2006	RBT	20,995	5,000		February
	2007	RBT	35,084			Spring, fall
Corral Lake	2002	RBT	31,054			Spring, fall
	2003	RBT	29,998			Spring, fall
	2004	RBT	29,990			Spring, fall
	2005	RBT	35,083			Spring, fall
	2006	RBT	30,000			Spring, fall
	2007	RBT	27,320			Spring, fall

Lake	Year	Species	Number fry plants	Number 8-12 inches stocked	Number over 14 inches stocked	Approximate time stocked	
Dry Falls Lake	2002	RBT	5,005			Spring, fall	
		TRB	5,00			Spring, fall	
		TT	1,003			Spring, fall	
	2003	BT	1,007			Spring, fall	
		RBT	5,040			Spring, fall	
		TRB	5,000			Spring, fall	
	2004	TT	1,000			Spring, fall	
		RBT	4,998			Spring, fall	
	2005	BT	2,483			Spring, fall	
		BT	1,000			Spring, fall	
	2006	RBT	5,002			Spring, fall	
		TT	1,001			Spring, fall	
	2007	BT	2,000			Spring, fall	
		RBT	10,008			Spring, fall	
		BT	3,092			Spring, fall	
Dusty Lake	2005	RBT	8,029			Spring, fall	
		TT	1,079			Spring, fall	
	2006	BT	2,000			Spring, fall	
		TT	795			Spring, fall	
	2007	RBT	8,008			Spring, fall	
		BT	1,500			Spring, fall	
		RBT	8,304			Spring, fall	
	Fishtrap Lake	2002	TT	801			Spring, fall
			RBT	100,000			Spring, fall
2003		TRB			1,848	April	
		RBT	123,246			Spring, fall	
2004		RBT		25,000	300	March, April	
		TRB			1,800	April	
2005		RBT	97,303	10,000	100	March, April	
		TRB			1,977	April	
2006	RBT		10,000	400	March, April		
	TRB			1,615	April		
2007	RBT	98,140	15,000		March, April		
	TRB			1,615	April		

Lake	Year	Species	Number fry plants	Number 8-12 inches stocked	Number over 14 inches stocked	Approximate time stocked
Hog Lake	2002	RBT	22,000	10,000		March, April
	2003	RBT	22,040	10,000		March, April
	2004	RBT		12,000		March, April
	2005	RBT		8,000		March, April
	2006	RBT		5,000		March, April
	2007	RBT	53,058	10,000		March, April
Lower Hampton Lake	2002	RBT	8,000			Spring, fall
	2003	RBT	8,052			Spring, fall
	2004	RBT	8,057			Spring, fall
	2005	RBT	4,048			Spring, fall
	2006	RBT	8,037			Spring, fall
	2007	RBT	6,723			Spring, fall
Quincy Lake	2002	RBT	19,095		6,000	March
	2003	RBT	19,000			Spring, fall
	2004	RBT	19,012			Spring, fall
	2005	RBT	19,040	11,207		October
	2006	RBT		5,000		February
	2007	RBT	22,017			Spring, fall
Rat Lake	2002	BT	2,095			Spring, fall
		RBT	8,066			Spring, fall
	2003	RBT	8,928			Spring, fall
	2004	RBT	8,236			Spring, fall
		BT	2,070			Spring, fall
	2005	RBT	8,068			Spring, fall
	2006	BT	3,890			Spring, fall
		RBT	12,497			Spring, fall
2007	BT	2,591			Spring, fall	
	RBT	10,500			Spring, fall	
Spectacle Lake	2002	RBT		30,000		April, May
		TRB			2,400	April
	2003	RBT	26,450	18,000		April, May
		TRB			2,200	April
	2004	RBT	31,133	27,000		April, May
		TRB			1,350	April
	2005	RBT		25,000		March, May
		TRB			1,590	May
2006	RBT		32,000		March, May	
	TRB			958	April	

Lake	Year	Species	Number fry plants	Number 8-12 inches stocked	Number over 14 inches stocked	Approximate time stocked
Spectacle Lake continued...	2007	BT	3,531			Spring, fall
		EB	500			Spring, fall
		RBT	155,000			Spring, fall
West Medical Lake	2002	RBT	136,000	11,000	1,500	March, April
		TRB			2,500	April
	2003	TRB			1,915	March, April
		RBT	117,182			Spring, fall
	2004	TRB			1,250	April
		RBT	135,350			Spring, fall
		BT	9,999	1,000		March, April
	2005	TRB			1,484	April
		BT		1,000		March, April
		RBT	130,000			Spring, fall
		TT	10,101			Spring, fall
	2006	RBT	15,017	5,000	400	March, April
		TRB			1,214	April
		TT	10,012			Spring, fall
	2007	RBT	200,132	10,000		March, April
TRB				1,214	April	
Williams Lake	2002	RBT	18,000			Spring, fall
	2003	RBT		8,000		March, April
	2004	RBT	13,056		200	March, April
	2005	RBT	18,018			Spring, fall
	2006	RBT	18,060			Spring, fall
	2007	RBT	17,995			Spring, fall
Z Lake	2006	RBT	5,000			Spring, fall
	2007	RBT	3,274			Spring, fall

Table 2. **Study Site** descriptions, including location (county, section, township, and range), size (ha), maximum depth (Z_{\max} , m), mean depth (Z_{mean} , m), date(s) sampled, and lake littoral class. Lake littoral class was determined by assigning each study site a rank based on estimated percent littoral zone present (1 = $\leq 10\%$, 2 = 10 – 30%, 3 = $\geq 30\%$).

Lake	County	Section	Township	Range	Size	Z_{\max}	Z_{mean}	Date(s) Sampled	Lake Littoral Class
Alta Lake	Okanogan	10-15	29N	23E	60.72	22.86	11.97	2007	2
Amber Lake	Spokane	26	22N	40E	46.96	12.19	5.64	2007	3
Burke Lake	Grant	15	19N	23E	28.35	11	NA	2007	2
Corral Lake	Grant	15-16	17N	28E	31.57	18	NA	2007	1
Dry Fall Lake	Grant	6	24N	28E	40.24	9.14	2.99	2007	2
Dusty Lake	Grant	16	19N	23E	33.60	41	NA	2007	1
Fishtrap Lake	Lincoln and Spokane	1, 12	21N	39E	79.35	9.14	6.15	2006, 2007	3
Hog Lake	Spokane	19, 30	22N	40E	21.45	3.96	1.62	2006, 2007	3
Lower Hampton Lake	Grant	30	17N	29E	6.07	15	NA	2007	2
Quincy Lake	Grant	15	19N	23E	25.50	8	NA	2007	2
Rat Lake	Okanogan	15	31N	24E	28.74	24	NA	2007	2
Spectacle Lake	Okanogan	2, 4, 9-11	38N	26E	124.24	9.14	0.08	2006, 2007	2
West Medical Lake	Spokane	12, 13, 24	24N	40E	95.14	10.67	6.88	2007	2
Williams Lake	Stevens	36	38N	38E	15.38	14	NA	2006, 2007	2
Z Lake	Lincoln	4-5	24N	35E	12.14	3	NA	2007	2

Table 3. **Alta Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -29.95 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -22.95 (SD = 5.72). Linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated no significant ontogenetic shift of energy source utilization or trophic position as rainbow trout grew ($p = 0.08$ and 0.68).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	2+	4	-25.66	0.66	10.20	0.20	61.28	0 – 100
Rainbow Trout	3+	3	-24.95	1.29	10.34	0.58	71.40	0 – 100
<i>Daphnia</i>	NA	NA	-29.95	NA	6.48	NA	0.00	NA
<i>Gastropoda</i>	NA	NA	-26.92	NA	8.03	NA	43.20	NA

Table 4. **Amber Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -35.37 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -28.37 (SD = 5.72). Cutthroat trout (*Oncorhynchus clarkii*) were stocked in Amber Lake in 2003, 2004, and 2007, but were unable to be collected and included in this study. No significant ontogenetic shift of energy source utilization or trophic position as rainbow trout grew was detected using linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($p = 0.07$ and 0.38).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	2+	5	-28.26	2.43	10.81	0.64	100	0 – 100
Rainbow Trout	3+	5	-26.66	1.22	10.83	0.33	100	0 – 100
Rainbow Trout	4+	5	-26.04	1.72	10.60	0.24	100	0 – 100
<i>Daphnia</i>	NA	NA	-35.37	NA	8.48	NA	0.00	NA
<i>Chironomidae</i>	NA	NA	-30.73	NA	1.99	NA	66.30	NA
<i>Amphipoda</i>	NA	NA	-27.01	NA	6.42	NA	100	NA

Table 5. **Burke Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -30.95 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -23.95 (SD = 5.72). Linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated no significant ontogenetic shift of energy source utilization or trophic position as rainbow trout grew ($p = 0.20$ and 0.07).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	3+	5	-25.6	1.58	9.04	0.33	76.40	0 – 100
Rainbow Trout	4+	4	-24.66	1.68	9.64	0.64	89.90	0 – 100
Black Crappie	1+	5	-22.35	1.34	7.18	0.51	100	0 – 100
<i>Daphnia</i>	NA	NA	-30.95	NA	4.36	NA	0.00	NA
<i>Ephemeroptera</i>	NA	NA	-28.66	NA	6.18	NA	32.71	NA
<i>Gastropoda</i>	NA	NA	-26.83	NA	5.97	NA	58.86	NA

Table 6. **Corral Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -30.10 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -23.10 (SD = 5.72). *Ephemeroptera* was collected from Corral Lake, however, sample size equaled one (n = 1) and, thus, data was excluded from this research.

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	3+	4	-28.73	0.58	10.97	0.33	19.57	0 – 92
Pumpkinseed	1+	5	-28.11	0.84	9.35	0.64	28.06	0 – 89
<i>Daphnia</i>	NA	NA	-30.10	NA	6.91	NA	0.00	NA

Table 7. **Dry Falls Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -25.08 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -18.08 (SD = 5.72). Linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated no significant ontogenetic shift of energy source utilization or trophic position as rainbow trout grew ($p = 0.03$ and 0.052).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	1+	5	-23.13	1.90	10.90	0.56	27.86	0 – 92
Rainbow Trout	3+	5	-22.61	1.63	11.84	0.60	35.28	0 – 94
Brown Trout	3+	4	-20.56	0.74	12.51	0.46	64.57	0 – 100
Tiger Trout	3+	3	-22.04	1.00	12.00	0.17	43.42	0 – 100
<i>Daphnia</i>	NA	NA	-25.08	NA	5.52	NA	0.00	NA
<i>Gastropoda</i>	NA	NA	-24.79	NA	6.04	NA	4.14	NA
<i>Amphipoda</i>	NA	NA	-21.09	NA	4.57	NA	57.00	NA

Table 8. **Dusty Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -28.28 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -21.28 (SD = 5.72). Note that brown trout sample size equaled one ($n = 1$). Linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated no significant ontogenetic shift of energy source utilization or trophic position as rainbow trout grew ($p = 0.55$ and 0.98).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	3+	5	-28.24	0.51	11.56	0.22	0.57	0 – 87
Rainbow Trout	4+	5	-26.90	4.23	11.49	1.07	19.71	0 – 100
Tiger Trout	2+	3	-24.91	1.92	11.55	0.62	48.14	0 – 100
Brown Trout	2+	1	-26.89	0.00	11.42	0.00	19.85	NA
<i>Daphnia</i>	NA	NA	-28.28	NA	10.70	NA	0.00	NA
<i>Ephemeroptera</i>	NA	NA	-28.56	NA	6.15	NA	0.00	NA

Table 9. **Fishtrap Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -36.28 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -29.28 (SD = 5.72). Linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated significant ontogenetic shifts of relying more heavily on littoral carbon and higher-level trophic position prey as rainbow trout grew ($p < 0.001$ and 0.004). No significant ontogenetic shifts of energy source utilization or trophic position as brown bullhead grew were detected using linear regression analysis of brown bullhead length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($p = 0.13$ and 0.71).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	1+	4	-29.36	0.52	8.10	0.16	98.86	0 – 100
Rainbow Trout	2+	5	-26.5	0.47	8.82	0.42	100	0 – 100
Pumpkinseed	1+	5	-25.69	0.78	8.91	0.67	100	0 – 100
Brown Bullhead	1+	5	-26.69	0.40	8.91	0.34	100	0 – 100
Brown Bullhead	2+	5	-26.32	0.87	8.50	0.96	100	0 – 100
Brown Bullhead	3+	5	-26.99	1.11	9.09	0.34	100	0 – 100
<i>Daphnia</i>	NA	NA	-36.28	NA	8.07	NA	0.00	NA
<i>Gastropoda</i>	NA	NA	-28.97	NA	3.39	NA	100	NA

Table 10. **Hog Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -41.25 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -34.25 (SD = 5.72).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	2+	5	-26.41	1.14	8.36	0.16	100	0 – 100
Brown Bullhead	1+	4	-25.36	0.72	9.80	0.16	100	0 – 100
<i>Daphnia</i>	NA	NA	-41.25	NA	6.74	NA	0.00	NA
<i>Ephemeroptera</i>	NA	NA	-30.59	NA	5.67	NA	100	NA
<i>Chironomidae</i>	NA	NA	-34.52	NA	1.73	NA	96.14	NA

Table 11. **Lower Hampton Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -34.62 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -27.62 (SD = 5.72). No significant ontogenetic shifts of energy source utilization or trophic position as rainbow trout grew were detected using linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($p = 0.006$ and 0.23). Note a close to significant ontogenetic shift to relying on higher-level trophic position prey as rainbow trout grew ($p = 0.006$).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	2+	5	-26.77	1.12	9.92	0.89	100	0 – 100
Rainbow Trout	3+	4	-28.59	1.12	13.63	0.16	86.14	0 – 100
Rainbow Trout	4+	4	-28.62	5.8	12.07	0.78	85.71	0 – 100
Pumpkinseed	1+	5	-24.25	0.60	12.25	0.49	100	0 – 100
<i>Daphnia</i>	NA	NA	-34.62	NA	9.24	NA	0.00	NA
<i>Gastropoda</i>	NA	NA	-25.16	NA	7.13	NA	100	NA

Table 12. **Quincy Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -28.22 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -21.22 (SD = 5.72). No significant ontogenetic shifts of energy source utilization or trophic position as rainbow trout grew were detected using linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($p = 0.008$ and 0.08). Note a close to significant ontogenetic shift of relying more heavily on littoral carbon as rainbow trout grew ($p = 0.008$).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	1+	5	-24.01	0.78	9.04	0.29	60.14	0 – 100
Rainbow Trout	2+	5	-23.96	0.53	8.79	0.22	60.85	0 – 100
Rainbow Trout	3+	5	-24.17	0.26	8.26	0.20	57.86	0 – 100
Rainbow Trout	4+	3	-21.79	0.59	8.76	0.35	91.86	0 – 100
<i>Daphnia</i>	NA	NA	-28.22	NA	3.73	NA	0.00	NA
<i>Ephemeroptera</i>	NA	NA	-29.90	NA	3.89	NA	0.00	NA

Table 13. **Rat Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -35.71 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -28.71 (SD = 5.72). Linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated no significant ontogenetic shift of energy source utilization or trophic position as rainbow trout grew ($p = 0.63$ and 0.07). A significant ontogenetic shift to higher trophic level prey as brown trout grew was detected using linear regression analysis of brown trout length versus $\delta^{15}\text{N}$ ($p = 0.01$). Linear regression analysis of brown trout length versus $\delta^{13}\text{C}$ indicated no significant ontogenetic shift of energy source utilization as brown trout grew ($p = 0.08$).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	2+	5	-31.54	0.69	8.61	0.38	59.57	0 – 100
Rainbow Trout	3+	5	-31.00	1.32	8.94	0.47	67.29	0 – 100
Brown Trout	2+	5	-26.55	1.59	7.85	0.38	100	0 – 100
Brown Trout	3+	5	-28.69	0.83	9.82	0.34	100	0 – 100
<i>Daphnia</i>	NA	NA	-35.71	NA	8.07	NA	0.00	NA
<i>Gastropoda</i>	NA	NA	-30.36	NA	3.36	NA	76.43	NA

Table 14. **Spectacle Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -40.60 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -33.60 (SD = 5.72). Linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ indicated a significant ontogenetic shift of relying more heavily on littoral carbon as rainbow trout grew ($p = 0.003$). No significant ontogenetic shift of trophic position as rainbow trout grew was detected using linear regression analysis of rainbow trout length versus $\delta^{15}\text{N}$ ($p = 0.50$).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	2+	5	-30.37	0.69	10.17	0.38	100	0 – 100
Rainbow Trout	3+	5	-24.10	1.32	10.27	0.47	100	0 – 100
Largemouth Bass	1+	3	-18.45	1.59	7.95	0.38	100	0 – 100
<i>Daphnia</i>	NA	NA	-40.60	NA	7.77	NA	0.00	NA
<i>Ephemeroptera</i>	NA	NA	-31.29	NA	3.89	NA	100	NA

Table 15. **West Medical Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -25.96 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -18.96 (SD = 5.72). Linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated significant ontogenetic shifts of relying more heavily on littoral base carbon and higher trophic position prey as rainbow trout grew ($p = 0.002$ and 0.0001). No significant ontogenetic shifts of energy source utilization or trophic position as pumpkinseed grew were detected using linear regression analysis of pumpkinseed length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($p = 0.43$ and 0.55).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	2+	5	-22.52	1.74	13.04	1.16	49.14	0 – 100
Rainbow Trout	3+	5	-20.50	0.51	16.05	0.80	78.00	0 – 100
Rainbow Trout	4+	5	-19.44	0.85	16.37	1.18	93.14	0 – 100
Brown Trout	4+	5	-19.14	0.67	16.72	0.58	97.43	0 – 100
Pumpkinseed	1+	5	-19.71	0.44	14.64	0.40	89.29	0 – 100
Pumpkinseed	2+	5	-19.60	0.33	14.71	0.60	90.86	0 – 100
<i>Daphnia</i>	NA	NA	-25.96	NA	17.23	NA	0.00	NA
<i>Ephemeroptera</i>	NA	NA	-23.99	NA	14.58	NA	28.14	NA
<i>Chironomidae</i>	NA	NA	-26.70	NA	11.54	NA	0.00	NA

Table 16. **Williams Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -31.63 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -24.63 (SD = 5.72). A significant ontogenetic shift of relying more heavily on littoral carbon as yellow perch grew was detected using linear regression analysis of yellow perch length versus $\delta^{13}\text{C}$ ($p = 0.003$). Linear regression analysis of yellow perch length versus $\delta^{15}\text{N}$ indicated no significant ontogenetic shift of trophic position as yellow perch grew ($p = 0.50$).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	2+	4	-31.00	0.42	9.05	0.56	9.00	0 – 88
Yellow Perch	1+	5	-28.30	0.98	9.89	1.07	47.57	0 – 100
Yellow Perch	2+	5	-25.90	0.85	9.50	0.80	81.86	0 – 100
<i>Daphnia</i>	NA	NA	-31.63	NA	5.13	NA	0.00	NA
<i>Gastropoda</i>	NA	NA	-23.77	NA	1.99	NA	100	NA

Table 17. **Z Lake** research data, including species, age class (if applicable), sample size, mean $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}$, standard deviation (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, percent (%) littoral carbon utilization, and associated 95% confidence interval. Base pelagic $\delta^{13}\text{C}$ reference = -34.04 (SD = 4.88). Base littoral $\delta^{13}\text{C}$ reference = -27.04 (SD = 5.72). Linear regression analysis of rainbow trout length versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated no significant ontogenetic shift of energy source utilization or trophic position as rainbow trout grew ($p = 0.53$ and 0.76).

Species	Age Class	Sample Size	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	% Littoral C Utilization	95% Confidence Interval
Rainbow Trout	3+	5	-29.44	1.83	10.34	0.31	65.71	0 – 100
Rainbow trout	4+	5	-27.99	2.41	10.55	0.51	86.43	0 – 100
Brown Bullhead	YOY	5	-32.00	0.58	10.12	0.13	29.14	0 – 89
<i>Gastropoda</i>	NA	NA	-29.28	NA	4.76	NA	68.00	NA
<i>Ephemeroptera</i>	NA	NA	-30.02	NA	6.06	NA	57.43	NA
<i>Daphnia</i>	NA	NA	-34.04	NA	6.61	NA	0.00	NA

Table 18A. **ANOVA results** for resident fish community complexity and rainbow trout estimated percent littoral carbon use. According to ANOVA, resident fish community complexity does predict rainbow trout estimated percent littoral carbon use.

Rainbow trout estimated percent littoral carbon use					
Source of Variation	SS	df	MS	F	P
Resident fish community complexity	14,178.919	4	3544.73	6.215	0.0011
Error	15,398,635	27	570.32		

Table 18B. **ANOVA results** for resident fish community complexity and rainbow trout $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. According to ANOVA, resident fish community complexity does predict rainbow trout $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$.

Source of Variation	$\delta^{13}\text{C}$					$\delta^{15}\text{N}$				
	SS	df	MS	F	P	SS	df	MS	F	P
Resident fish community complexity	139.67	4	34.92	5.894	0.0015	0.1029	4	0.0257	8.866	0.0001
Error	159.95	27	5.92			0.078	27	0.0029		

Table 19. **ANOVA results** for rainbow trout age class and estimated littoral carbon use. According to ANOVA, rainbow trout age class does not predict rainbow trout estimated littoral carbon use.

Rainbow trout estimated percent littoral carbon use					
Source of Variation	SS	df	MS	F	P
RBT age class	0.0007	1	0.0007	0.0037	0.952
Error	5.643	30	0.188		

Table 20A. **Linear regression analysis results of fish length versus $\delta^{13}\text{C}$** , including lake, species, length range (mm), length versus $\delta^{13}\text{C}$, P-value, R^2 , and associated regression equation. For rainbow trout, $P \leq 0.004$ are considered significant. For all other fish species, $P \leq 0.05$ are considered significant. Significant P-values are **bolded**.

Lake	Species	Length Range	Length vs. $\delta^{13}\text{C}$ P-Value	Length vs. $\delta^{13}\text{C}$ R^2
Alta Lake	Rainbow Trout	279 – 349	0.08	0.33
Amber Lake	Rainbow Trout	230 – 519	0.07	0.21
Burke Lake	Rainbow Trout	290 – 372	0.20	0.19
Dry Falls Lake	Rainbow Trout	168 – 540	0.52	0.04
Dusty Lake	Rainbow Trout	325 – 509	0.55	0.07
Fishtrap Lake	Rainbow Trout	54 – 204	< 0.001	0.88
	Brown Bullhead	146 – 236	0.13	0.22
Lower Hampton Lake	Rainbow Trout	215 – 512	0.23	0.13
Quincy Lake	Rainbow Trout	101 – 480	0.008	0.37
Rat Lake	Rainbow Trout	240 – 310	0.65	0.03
	Brown Trout	145 – 290	0.08	0.31
Spectacle Lake	Rainbow Trout	236 – 322	0.003	0.77
West Medical Lake	Rainbow Trout	239 – 487	0.002	0.54
	Pumpkinseed	96 – 122	0.43	0.07
Williams Lake	Yellow Perch	108 – 202	0.003	0.66
Z Lake	Rainbow Trout	292 – 480	0.53	0.04

Table 20B. **Linear regression analysis results of fish length versus $\delta^{15}\text{N}$** , including lake, species, length range (mm), length versus $\delta^{15}\text{N}$, P-value, R^2 , and associated regression equation. For rainbow trout, $P \leq 0.004$ are considered significant. For all other fish species, $P \leq 0.05$ are considered significant. Significant P-values are **bolded**.

Lake	Species	Length Range	Length vs. $\delta^{15}\text{N}$ P-Value	Length vs. $\delta^{15}\text{N}$ R^2
Alta Lake	Rainbow Trout	279 – 349	0.68	0.02
Amber Lake	Rainbow Trout	230 – 519	0.05	0.38
Burke Lake	Rainbow Trout	290 – 372	0.06	0.35
Dry Falls Lake	Rainbow Trout	168 – 540	0.03	0.42
Dusty Lake	Rainbow Trout	325 – 509	0.98	< 0.001
Fishtrap Lake	Rainbow Trout	54 – 204	0.004	0.65
	Brown Bullhead	146 – 236	0.71	0.01
Lower Hampton Lake	Rainbow Trout	215 – 512	0.006	0.54
Quincy Lake	Rainbow Trout	101 – 480	0.08	0.18
Rat Lake	Rainbow Trout	240 – 310	0.07	0.43
	Brown Trout	145 – 290	0.01	0.56
Spectacle Lake	Rainbow Trout	236 – 322	0.50	0.07
West Medical Lake	Rainbow Trout	239 – 487	< 0.001	0.72
	Pumpkinseed	96 – 122	0.55	0.04
Williams Lake	Yellow Perch	108 – 202	0.50	0.05
Z Lake	Rainbow Trout	292 – 480	0.76	0.01

FIGURES

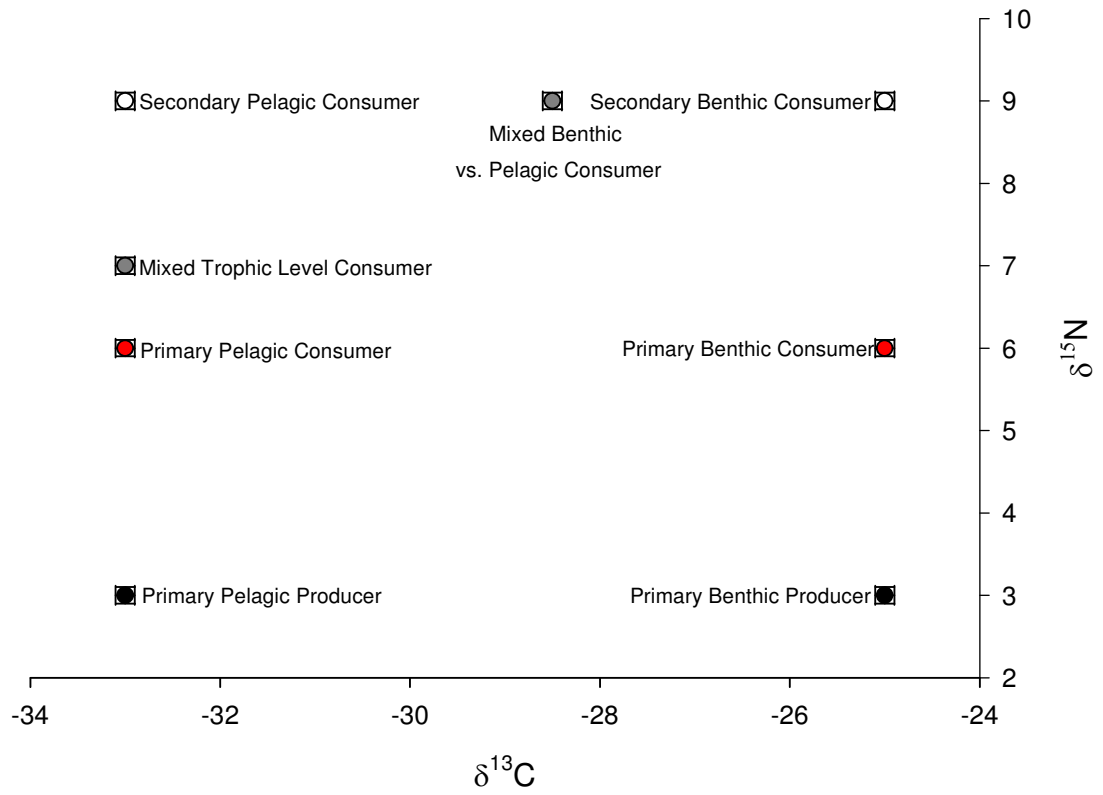


Figure 1. **Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot** for a hypothetical lake food web



Figure 2. **Eastern Washington State study sites** – 15 lakes in Okanogan, Spokane, Grant, Lincoln, and Stevens counties

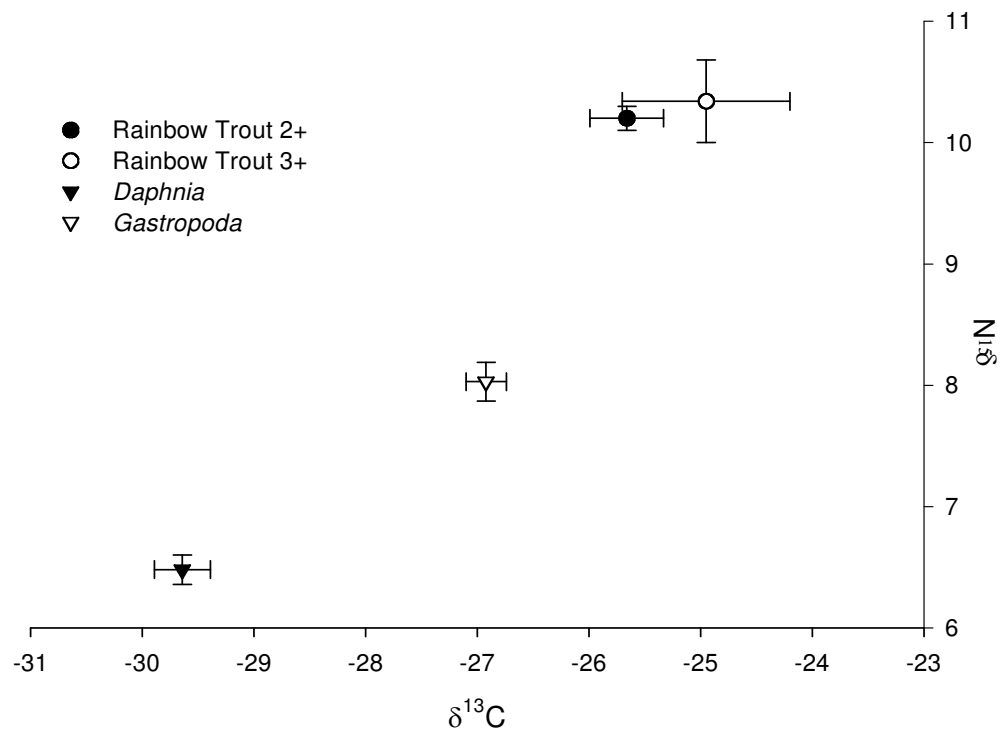


Figure 3. **Alta Lake**, Okanogan County, Washington. 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

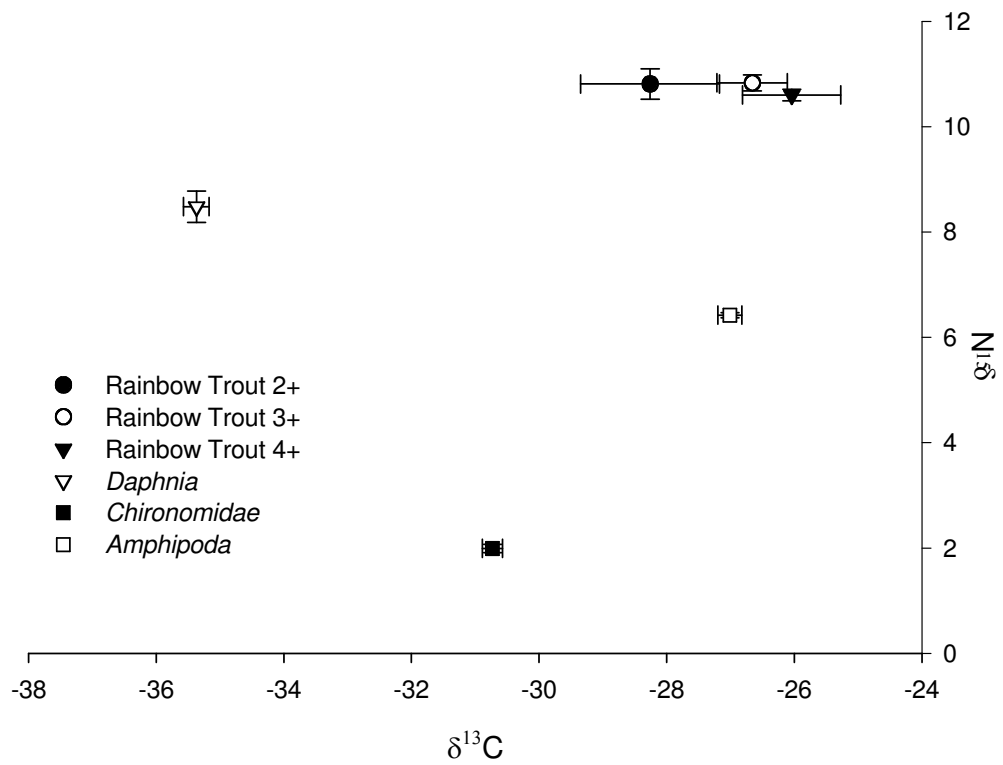


Figure 4. **Amber Lake**, Spokane County, Washington. 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

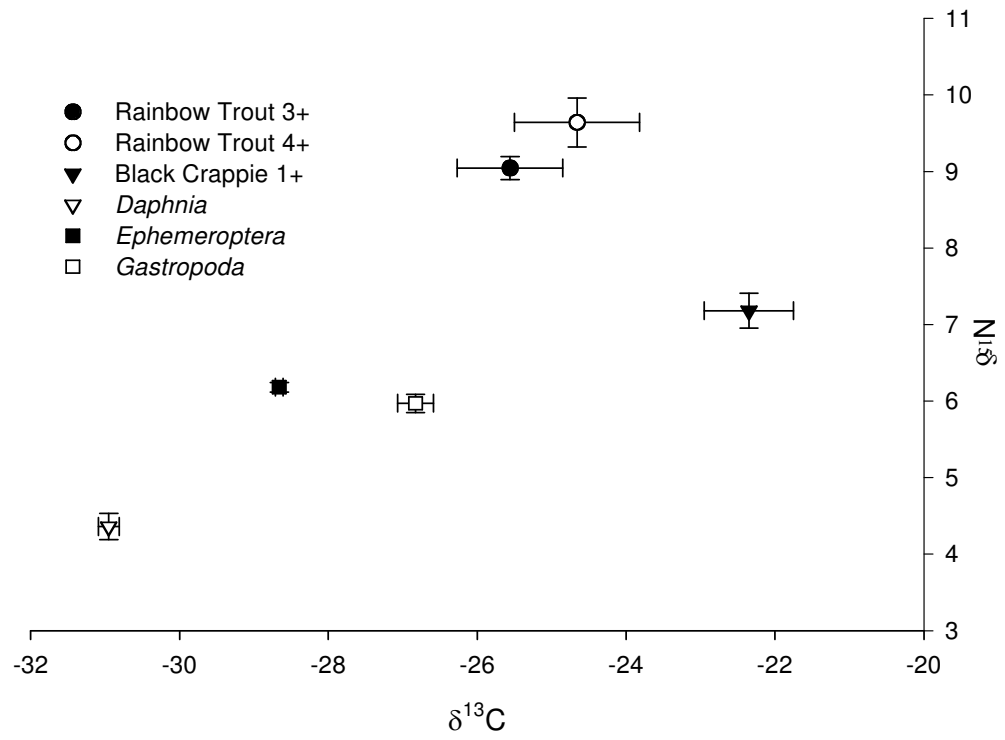


Figure 5. **Burke Lake**, Grant County, Washington. 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

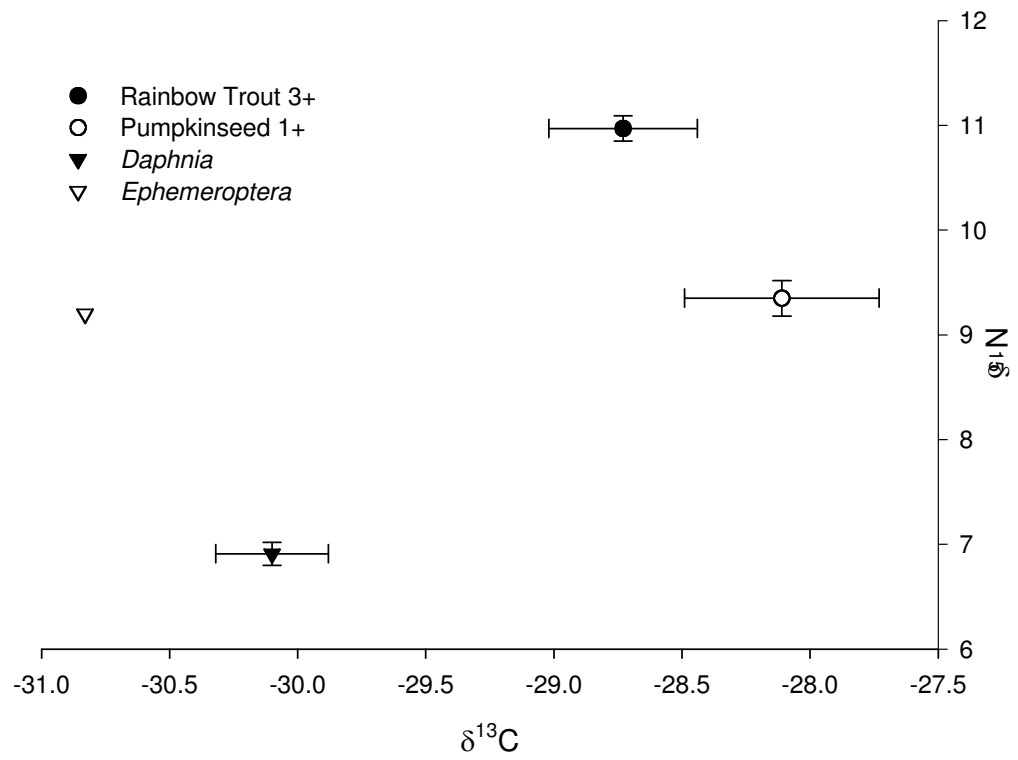


Figure 6. **Corral Lake**, Grant County, Washington. 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

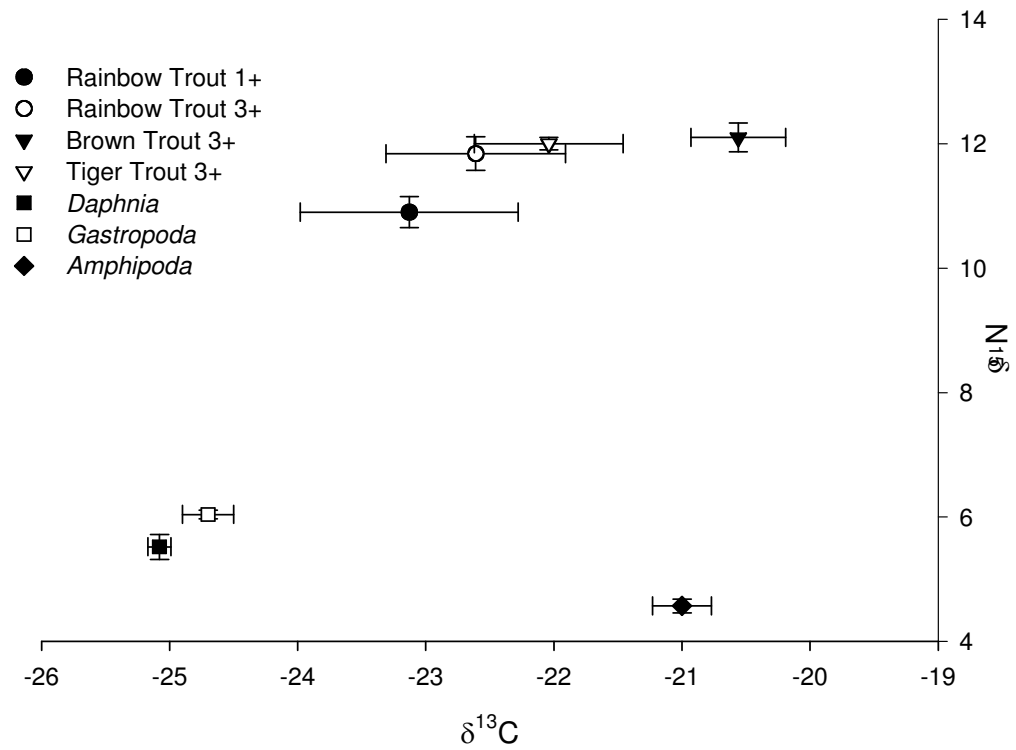


Figure 7. **Dry Falls Lake**, Grant County, Washington. 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

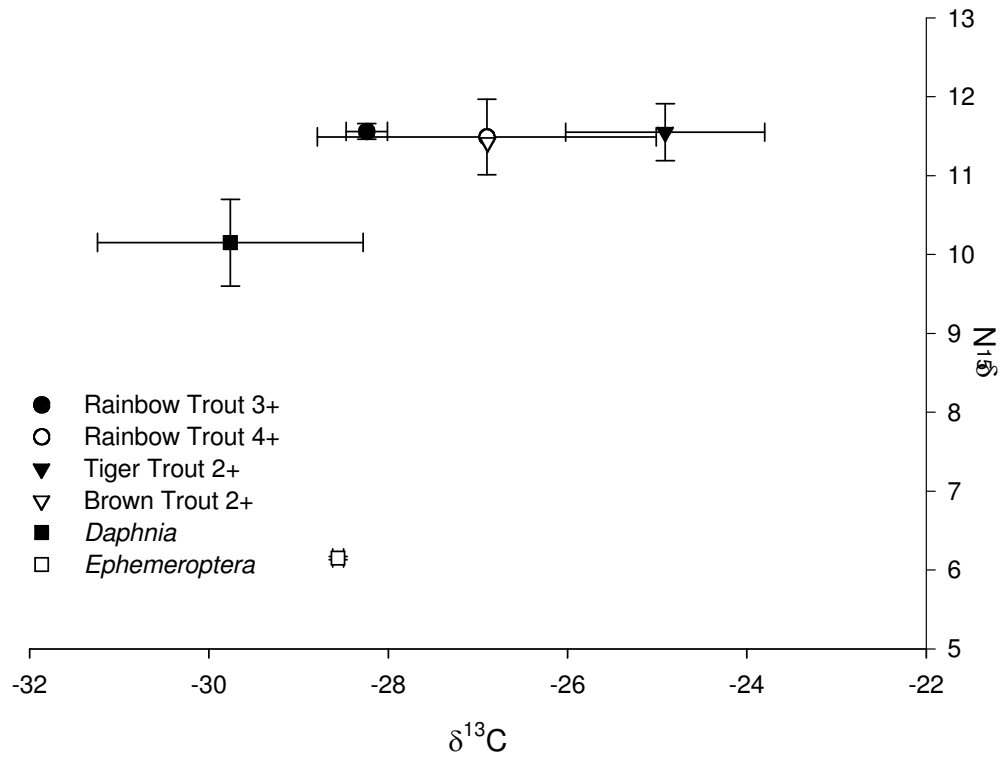


Figure 8. **Dusty Lake**, Grant County, Washington. 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

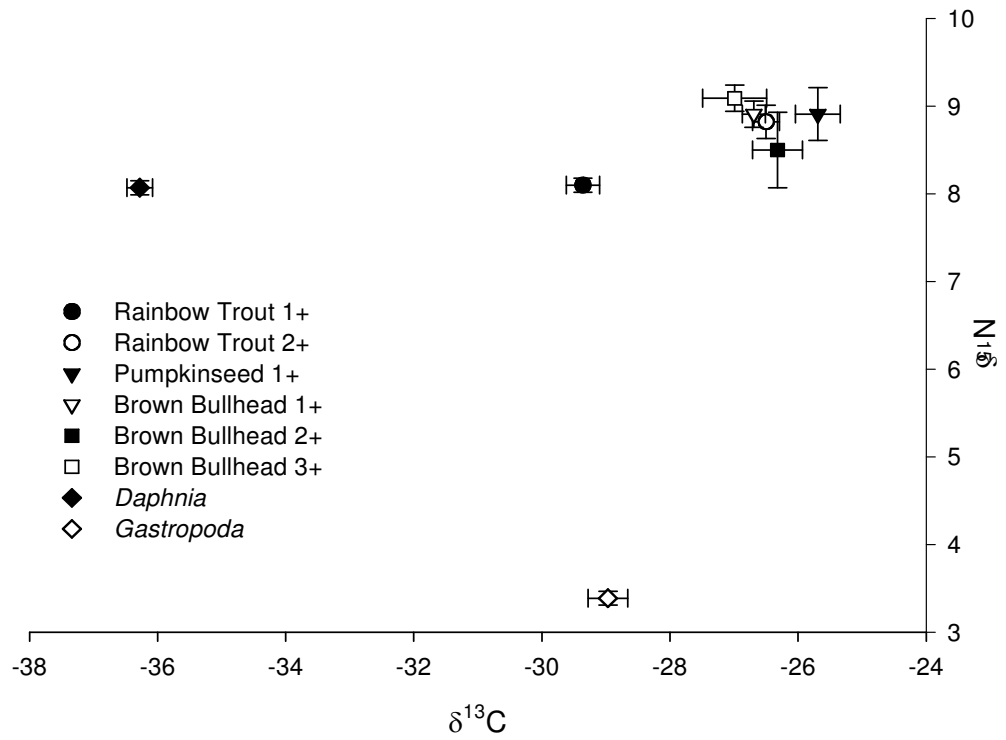


Figure 9. **Fishtrap Lake**, Lincoln and Spokane County, Washington. 2006 and 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

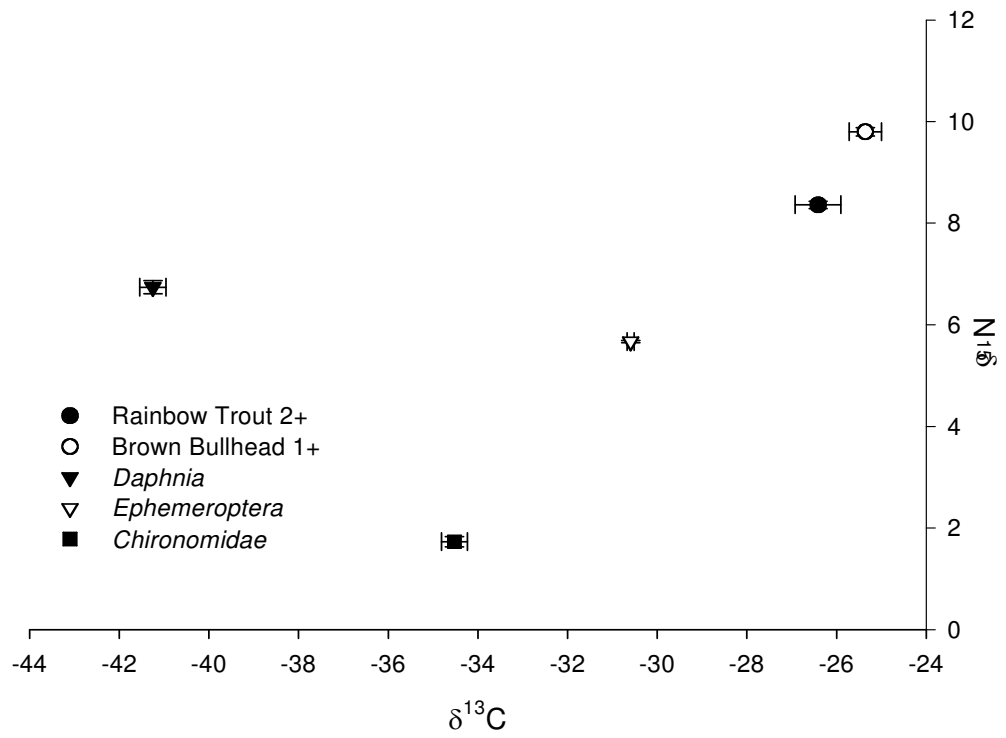


Figure 10. **Hog Lake**, Spokane County, Washington. 2006 and 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

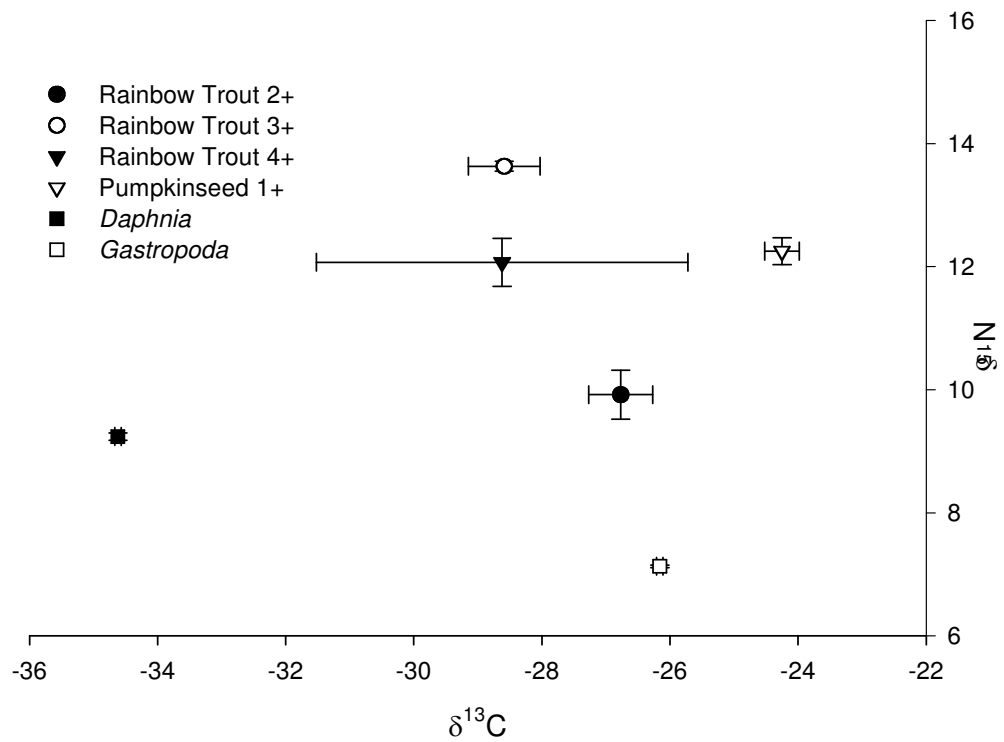


Figure 11. **Lower Hampton Lake**, Grant County, Washington. 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

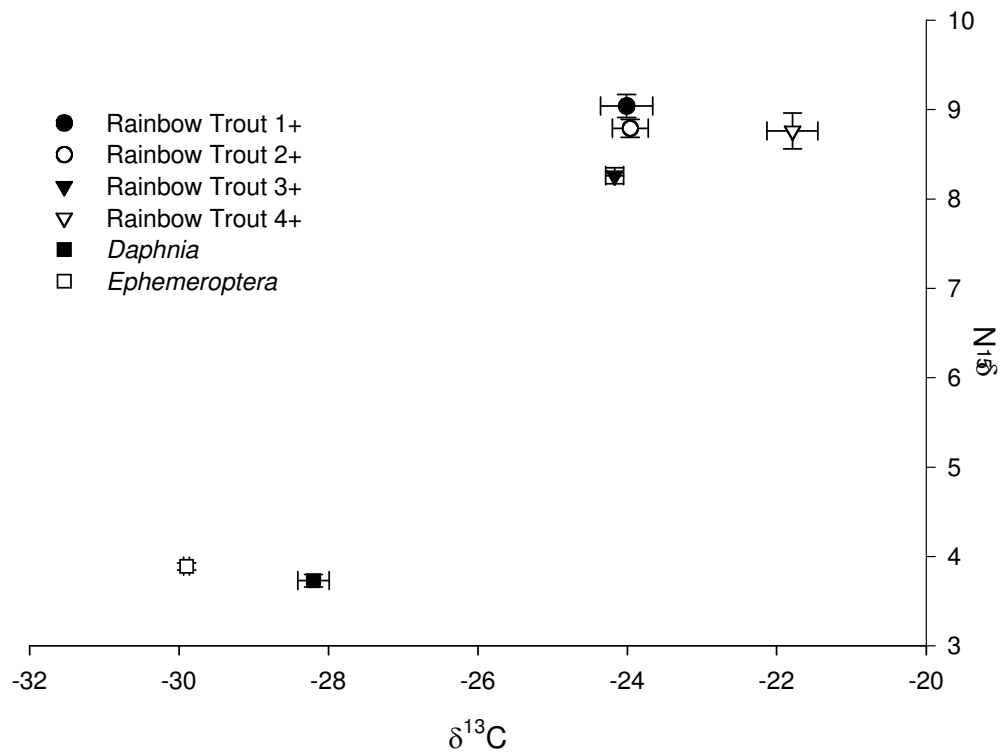


Figure 12. **Quincy Lake**, Grant County, Washington, 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

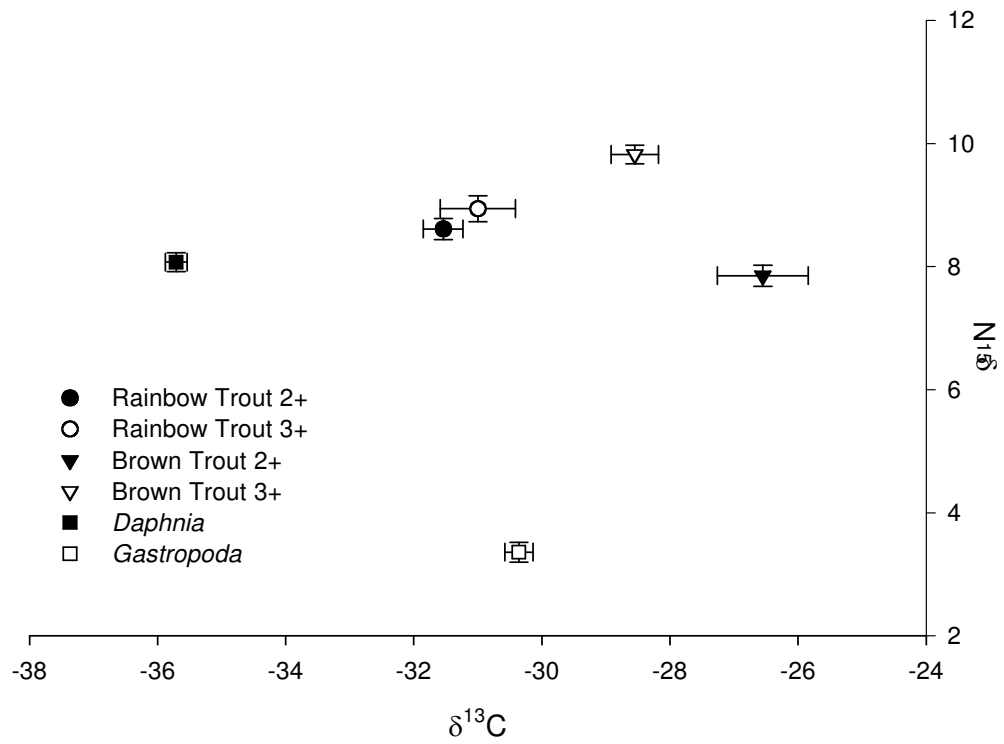


Figure 13. **Rat Lake**, Okanogan County, Washington. 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

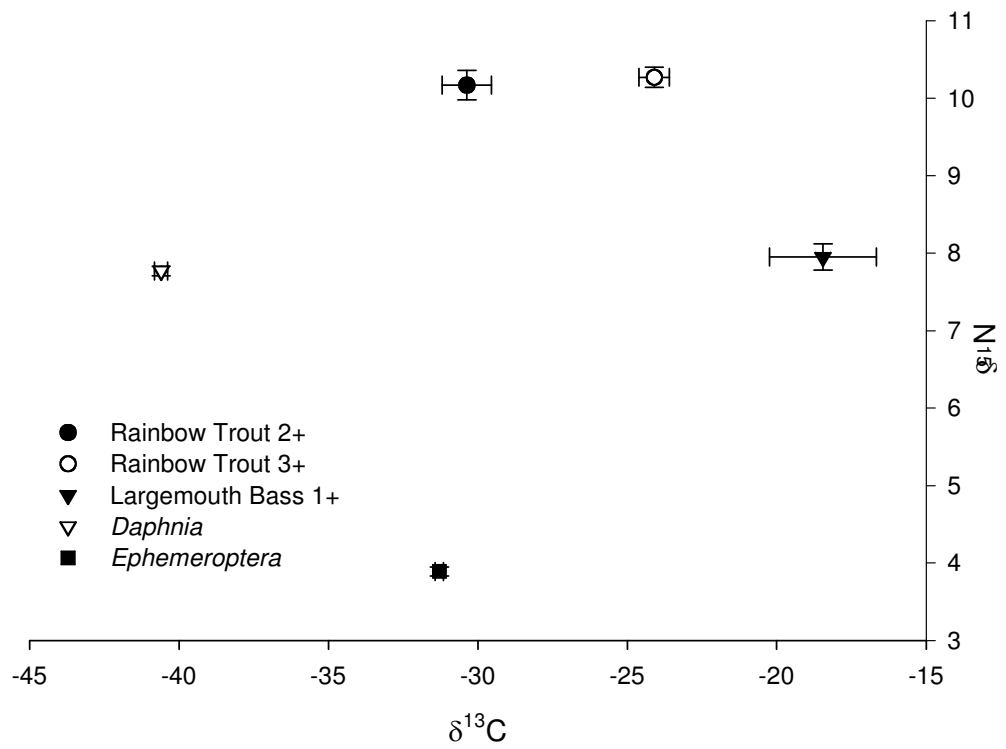


Figure 14. **Spectacle Lake**, Okanogan County, Washington. 2006 and 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

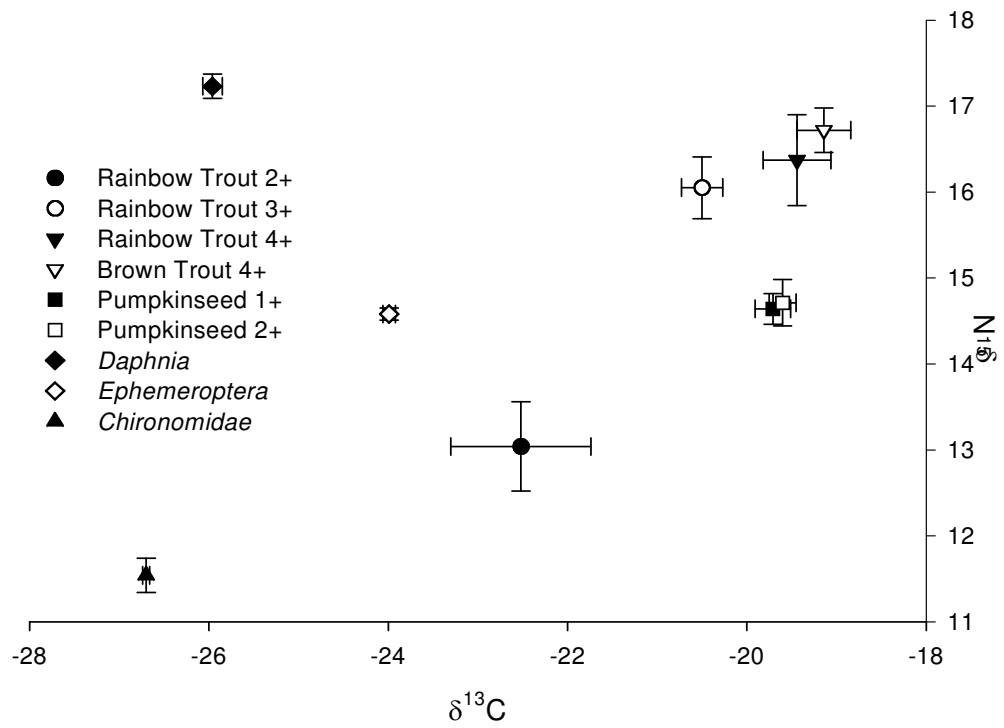


Figure 15. **West Medical Lake**, Spokane County, Washington, 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

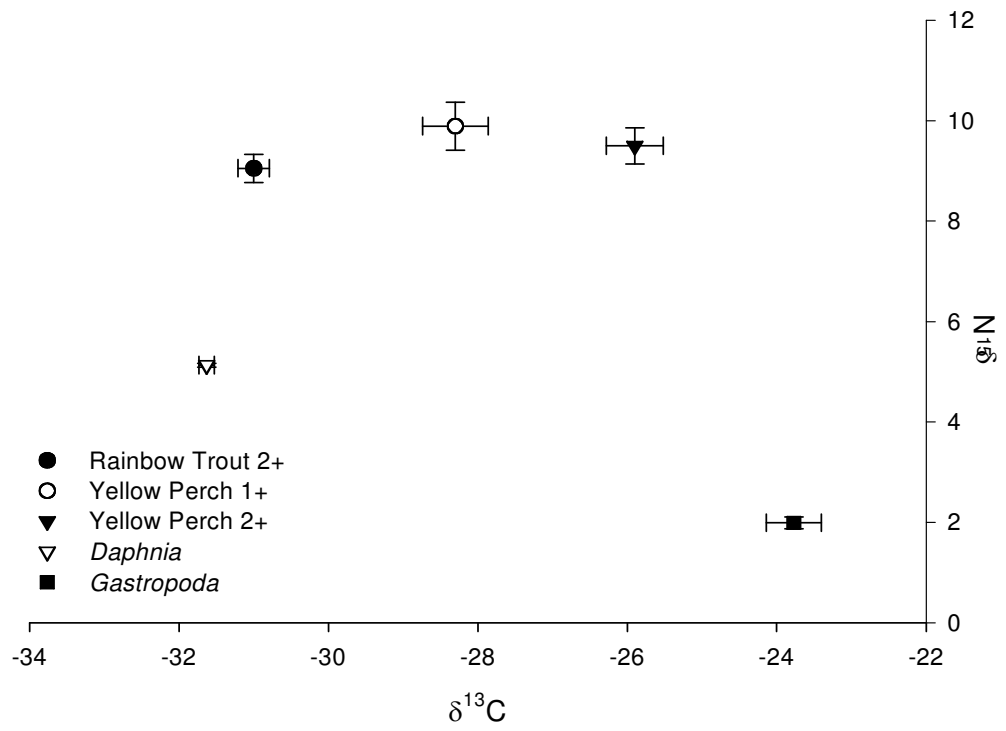


Figure 16. **Williams Lake**, Stevens County, Washington. 2006 and 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

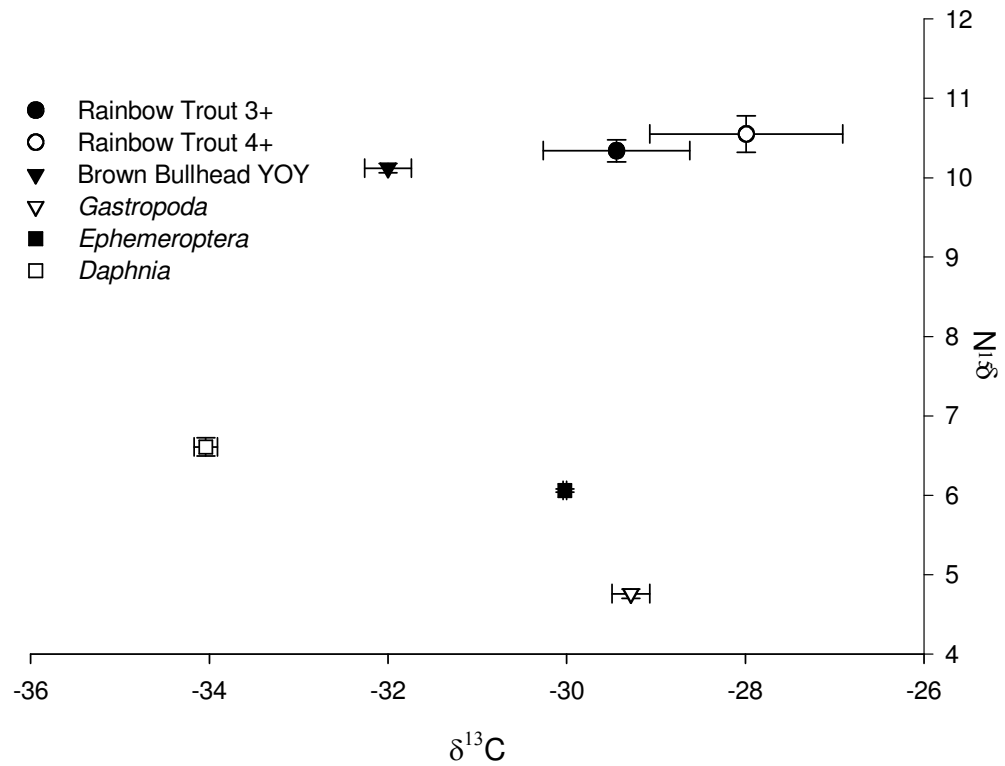


Figure 17. **Z Lake**, Lincoln County, Washington, 2007. Stable isotope ratio ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) biplot. Points represent means with S.E. bars.

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