SEASONAL PROXIMATE COMPOSITION AND FOOD SOURCE COMPARISONS OF DOLLY VARDEN CHAR IN THE KUGURUROK RIVER, ALASKA

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SEASONAL PROXIMATE COMPOSITION AND FOOD SOURCE COMPARISONS OF DOLLY VARDEN CHAR IN THE KUGURUROK RIVER, ALASKA

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Abstract

The Kugururok River on the Noatak River System is an important spawning tributary for Dolly Varden char (*Salvelinus malma*), an important subsistence resource, occur bycatch in commercial fisheries, and are the basis of a sport fishery. The feeding habits and energetic condition of two spawning run patterns in the Noatak River Drainage were studied. Isotope ratio analysis revealed a predominantly marine carbon and nitrogen composition in all adult char. No internal isotopic fractionations were found either between tissues or seasons in any tissue. Proximate analysis revealed patterns of lipid and protein utilization characteristic of periodic starvation in fishes. Significant shifts of energy between key tissues were noted during the production of gonads. Data suggest that energetic minimums must be reached at sea before char can enter freshwater and successfully spawn.

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Introduction

The northern form of Dolly Varden char (*Salvelinus malma* Walbaum) in North America ranges from the Alaska Peninsula to the Mackenzie River in the Yukon Territory (McPhail 1961; Morrow 1980; DeCicco 1990). Meristic data differentiate between the northern and southern forms of Dolly Varden char as well as the Arctic char (*Salvelinus arcticus* Linnaeus) complex in North America (Armstrong and Morrow 1980; Benke 1980; Morrow 1980; McCart 1980; DeCicco 1985). The northern form of Dolly Varden char has between 20 and 25 gill rakers whereas the southern form has between 16 and 19 gill rakers (Morrow 1980). Counts of gill rakers from the fish in this study coincide with counts characteristic of the northern form described in current literature. This study focused on the northern form of Dolly Varden char in the Noatak River drainage, Alaska, and are hereafter referred to as char.

Northern form Dolly Varden char exhibit both stream resident and anadromous life history strategies. One stream resident strategy includes residual fish which are an exclusively male portion of the population that do not migrate to the sea (DeCicco 1990). Parr marks are retained throughout their life (Craig 1977). These fish are younger and smaller than other males when they mature and actively spawn using a sneak strategy (Hino et al. 1990; DeCicco 1990). Another

Month	Summer-spawners	Fall-spawners
October - May	• overwinter in Noatak	• overwinter in springs
breakup	• go to sea and feed	• go to sea and feed
August		• migrate up river
September		• *spawn*
October - May	• overwinter in Noatak	• overwinter in springs
breakup	• migrate up river	• go to sea and feed
August	• *spawn*	• migrate up river
September	• migrate to Noatak	• *spawn*

Figure 1. Life histories of summer and fall-run Dolly Varden char in the Noatak River System. Timeline shows the one year cycle for fall-spawners and two years for summer-spawners.

stream resident strategy exists in the upper Babbage River and Cache Creek in Canada's Yukon territory. In this situation, char have been isolated by impassable water falls. Genetic and meristic data suggest that these populations are Dolly Varden char (Reist et al. 1992).

Anadromous char populations exhibit one or more life history strategies in Northwest Alaska and the Yukon Territory (Glova and McCart 1974; Alt and Furniss 1976; Craig 1977). In the Noatak River drainage, two life history strategies have been described (DeCicco 1989). Migration patterns that relate to overwintering and spawning have been used to identify "summer" and "fall" spawners. Both patterns utilize riverine habitat for rearing, spawning and overwintering. Feeding occurs in the marine environment during the summer months. Overwintering, after feeding at sea, may occur in any large river system. Char do, however, home to natal streams to spawn in tributaries. For instance, a char that spawns in the Noatak River may overwinter in the Wulik or Kivalina River but will only spawn in the Noatak River. Fish that were tagged and known to spawn in the Wulik River, Alaska, were found overwintering 1690 km away in the Anadyr River, Russia (DeCicco 1992).

Fall-spawners represent the normal life history exhibited by the majority of anadromous char. After overwintering in a large river, fall-spawners enter the sea to feed along with the summer-spawners that are in a nonspawning summer and

juvenile nonspawners. Although the summer and nonspawners stay out at sea the entire summer, the fall-spawners reenter the river in August and go directly to the spawning grounds. Fall-spawners spawn between mid September and the middle of October. Spawning takes place directly in spring areas and side channels. After spawning, fall-run char overwinter in spring areas in the upper tributaries, most of which will have some flowing water throughout the winter. Some fall-spawners do, however, migrate to lower parts of the river to overwinter in large, deep pools. This spawning life history strategy allows for annual spawning because fall-spawners return to sea each summer to feed and re-build their energy reserve.

Summer-spawners represent a unique life history strategy for char that has been reported only in northwest Alaska (DeCicco 1989). After overwintering from September to June, a mature summer-spawner migrates upstream during breakup. Char that do not overwinter in their natal river require additional time to migrate to that river thus arriving later than other fish of the same run. This activity can give the false appearance of a separate run in the river. By the middle of July, most summer-spawners are occupying the spawning grounds. Spawning occurs from mid August to early September near spring areas in the upper tributaries. Spent fish fall out of the tributary to the lower river to overwinter. After this 20 month cycle of overwintering and spawning, summer-spawners migrate to sea at breakup in the spring and feed until the next fall when they reenter a large river to

overwinter and possibly repeat the spawning cycle. This spawning strategy only allows for spawning every other year at most. Some summer-spawners have been known to exhibit yet another strategy: fish that have spawned in the earlier part of the spawning period have been known to go to sea for a short time before re-entering the river to overwinter.

Summer and fall-spawners are spatially separated while feeding at sea and when on the spawning grounds. It is possible to observe postspawned summer-run fish leaving the tributary while the fall-spawners are entering. Overwintering areas are, however, shared by both runs of fish from various natal rivers.

A comparison of the life history strategies of char in the Noatak River drainage leads to various hypotheses as to the energetic benefit of each. Figure 1 illustrates the major differences between both runs during a two-year cycle. After feeding in the ocean, fall-spawners enter freshwater to spawn immediately and overwinter. These fish are expected, therefore, to have a larger energetic reserve after spawning for overwintering. Their annual marine feeding behavior allows for the possibility of annual spawning, which would increase their genetic contribution to the stock. Summer-spawners, on the other hand, must use considerable amounts of stored energy to overwinter before, as well as after, spawning. This behavior does not allow for annual spawning and may result in lower fecundity.

It is hypothesized that the total energetic cost of living between spawning events is greater for the summer-spawners than for the fall-spawners. Previous observation suggests that char in the Noatak system do not actively feed in fresh water (DeCicco 1985). Stable isotope analysis of diet source was used to test the validity of this hypothesis. Assuming that these char do not feed in fresh water, the overwintering strategy of the summer-spawners necessitates enough reserves of energy to survive 20 months without feeding. Proximate analysis of the gastrointestinal (gi) tract, muscle, and liver energetics of the summer-spawners throughout the time spent in freshwater was used to determine how low the energetic reserves get during a 20 month starvation period.

Stable Isotopes

Stable isotope ratio analysis has become increasingly important in diet source studies. Multiple stable isotopes of carbon and nitrogen occur naturally in the environment. The natural proportions of ^{12}C and ^{13}C are 98.9 percent and 1.1 percent, respectively; those of ^{14}N and ^{15}N are 99.64 percent and 0.36 percent, respectively. During chemical and metabolic processes, however, the isotopic ratios change in a process called fractionation. It is fractionation that allows the isotopic ratios to be useful in ecological studies. During metabolic processes, the heavier isotope is preferentially retained which slightly increases the isotopic ratio of the tissue (DeNiro and Epstein 1978; Tieszen 1978). Isotopic ratios of carbon

(C) and nitrogen (N) are expressed as $\delta^{13}C$ and $\delta^{15}N$, which is the difference between the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and a standard and are expressed in parts per thousand (‰). The ratios are calculated by the equation:

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

where R is the ratio $\delta^{13}C$ or $\delta^{15}N$, the standard for carbon is an isotopic equivalent to the Chicago Pee Dee belemnite ratios (Craig 1957), and the standard for nitrogen is atmospheric nitrogen (Rau et al. 1992). Samples showing increased concentrations of the ^{13}C or ^{15}N are termed "heavy" or "enriched" whereas those with lower concentrations are termed "light" or "depleted".

Carbon isotopes have been used to study food webs in ecological studies (Fry and Sherr 1984). Carbon isotopic fractionations between trophic levels have been relatively conservative, usually less than 1‰ difference (DeNiro and Epstein 1978). This characteristic has allowed researchers to determine diet sources within a food web having two distinct sources. An aspect which is important to this study is that carbon sources in a marine environment differ markedly from those of terrestrial origin (DeNiro and Epstein 1978; Rau et al. 1983; Peterson and Fry 1987). It has also been useful for multiple isotopes to be analyzed when looking at trophic relationships (Fry and Sherr 1984). Peterson et al. (1985) found that using ratios from more than one element increased the information gained about trophic structure and nutrient origin in aquatic systems. The initial

differences in isotope ratios of primary producers from marine and freshwater sources allow for the determination of whether the diet source had marine or freshwater origin.

Whereas carbon isotopes are conservative and therefore can only describe potential diet sources, nitrogen isotope fractionations become more enriched with increasing trophic levels (Owens 1987). The lighter isotope is preferentially excreted or respired by the consumer (Rau et al. 1983; Minagawa and Wada 1984; Rau et al. 1992). Therefore $\delta^{15}N$ values can be used to differentiate between potential trophic levels in a food web. Differences from 3 to 5 ‰ have been found between consumer and diet trophic levels.

Fractionations greater than 2 ‰ arise during metabolic processes within an organism (Parker 1964; van der Merwe 1982; Fry and Sherr 1984). It is therefore expected that changes in tissue isotope ratios will be apparent through time. Lipid has lighter $\delta^{13}C$ values and therefore complicates the interpretation of diet source data. In order to compensate for lipid differences, lipid is usually removed from the tissue prior to analysis. For this study, only lipid-free tissues were used for comparisons so as to remove any effects of variable lipid concentrations.

Proximate Analysis

Proximate analysis is the determination of the proportions of protein, water, lipid, and ash of a tissue (Love 1970). In my study, carbohydrates were not considered because they are found in negligible amounts in most fish species (Love 1970). Most fishes show seasonal changes in proximate composition, whether in response to environmental (exogenous) changes or behavioral (endogenous) changes such as maturation and metabolism. Upon reaching the adult stage, a fish in good condition attains a composition where the percent protein and lipid remains constant prior to sexual maturation (Moulton 1923 and Shearer 1994). At the time of sexual maturation, the relative weight of organs in the abdominal cavity decreases in proportion to the whole fish. This is due to decreased organ growth while the remainder of the fish continues to grow and store reserve energy. Shearer (1994) discussed the exogenous and endogenous factors that affect proximate composition of a fish. He found that primary determinants of proximate analysis of a growing fish are body size, life history stage, and energy intake. Whole body lipid was dependent on dietary input and metabolic demands of the fish. According to Love (1970), the highest recorded proportion of lipid in a fatty fish is 67 percent. Whole body protein, tissue weights, and ash contents, however, remain within more narrowly defined limits at any given life history stage of a fish species.

When a fish goes through a starvation period, the depletion and redistribution of proximate components are pronounced (Love 1970 and McGurk et al. 1980). Lipids reach a critically low value after which proteins are utilized (Love 1970). Lipids yield 9.45 kcal of metabolizable energy per gram whereas protein only yields 4.8 kcal/g (Brett et al 1979). For this reason, Dutil (1982) found that 65 percent of the metabolic cost of Arctic char is derived from lipid and only 35 percent comes from protein. Ash content in the fish also decreases slightly, but only after a critical maximum of water is reached within the tissue.

Reproductive strategies of the two spawning groups of char in the Noatak system are also expected to differ in order to compensate for the time spent in freshwater. Analysis of the gonadal tissue was used to test the hypothesis that the fecundities of the summer-spawners will be lower in order to conserve energy for overwintering.

Prior to reproduction, somatic growth slows as the gonads increase in size and protein and lipid are utilized from muscle and liver. Energetic costs due to reproduction include the production of gonads as well as secondary sexual characteristics such as coloration and kype formation. Behavior such as stream migration, redd development, and interactions with other fish also demand an energetic cost from the spawning fish. Atlantic salmon *(Salmo salar)* expend up to 50 percent of their total energy reserves for reproduction (Love 1970). Although

females incorporate half of this energy into development of gonadal tissue, males expend the majority of it on territorial defense and on secondary sexual characteristics. Therefore, char in the Noatak river system must acquire a large enough energy reserve to support general metabolism, overwintering, and migration after spawning. A possible adaptation to compensate for a lack of necessary energetic reserves, especially for summer spawning char, is to reduce the energetic allocation to gonads, thus reducing fecundity and increasing energy available to overwintering costs; this results in non-annular spawning.

Study Objectives

The overwintering and reproductive strategies of char in the Kugururok River, a major tributary of the Noatak River, have led me to question the benefit of the summer-spawner's life history strategy. The purpose of my study was to determine energetic and diet source characteristics of the summer-spawners, from which the rationale for this life history strategy can be interpreted. To fulfill this purpose, my objectives were to:

1. Determine the relative importance of the two potential diet sources, marine or freshwater;

2. Determine energetic characteristics of five tissues (liver, gonads, gastrointestinal tract, ventral, and dorsal muscle) of summer-spawners, fall-spawners, and overwintering nonspawning char;

3. Compare energetic composition of summer spawning char before and after spawning;

4. Determine fecundity of summer-spawners.

Study Area

The Kugururok River is an important spawning tributary for anadromous char in the Noatak River drainage. Char are an important subsistence resource for local residents and are becoming an increasingly desirable sport fish. Char are also incidentally taken in the fall chum (*Oncorhynchus keta*) fishery in Kotzebue Sound.

The Kugururok River is located approximately 191.5 km from the mouth of the Noatak River in Northwest Alaska (DeCicco 1985)(Figure 2). The river drains a 2434.6 square km area south of the Delong Mountain Range and runs for 98 km. Major tributaries important to this study include Nunaviksak Creek, Kagvik Creek, and Trail Creek. The upper Kugururok River, as well as its tributaries, is heavily braided and contains numerous spring areas derived from hyporheic flow. The stream bed of the upper river is comprised of medium sized gravel and larger bedrock. Riparian habitat consists primarily of willow and large gravel bars. The lower 32 km of the river are regrouped into a single channel. The stream bed composition varies from fine gravel to large boulders. Riparian habitat of the lower river consists of spruce forest, tundra, and willow. The Kugururok River is

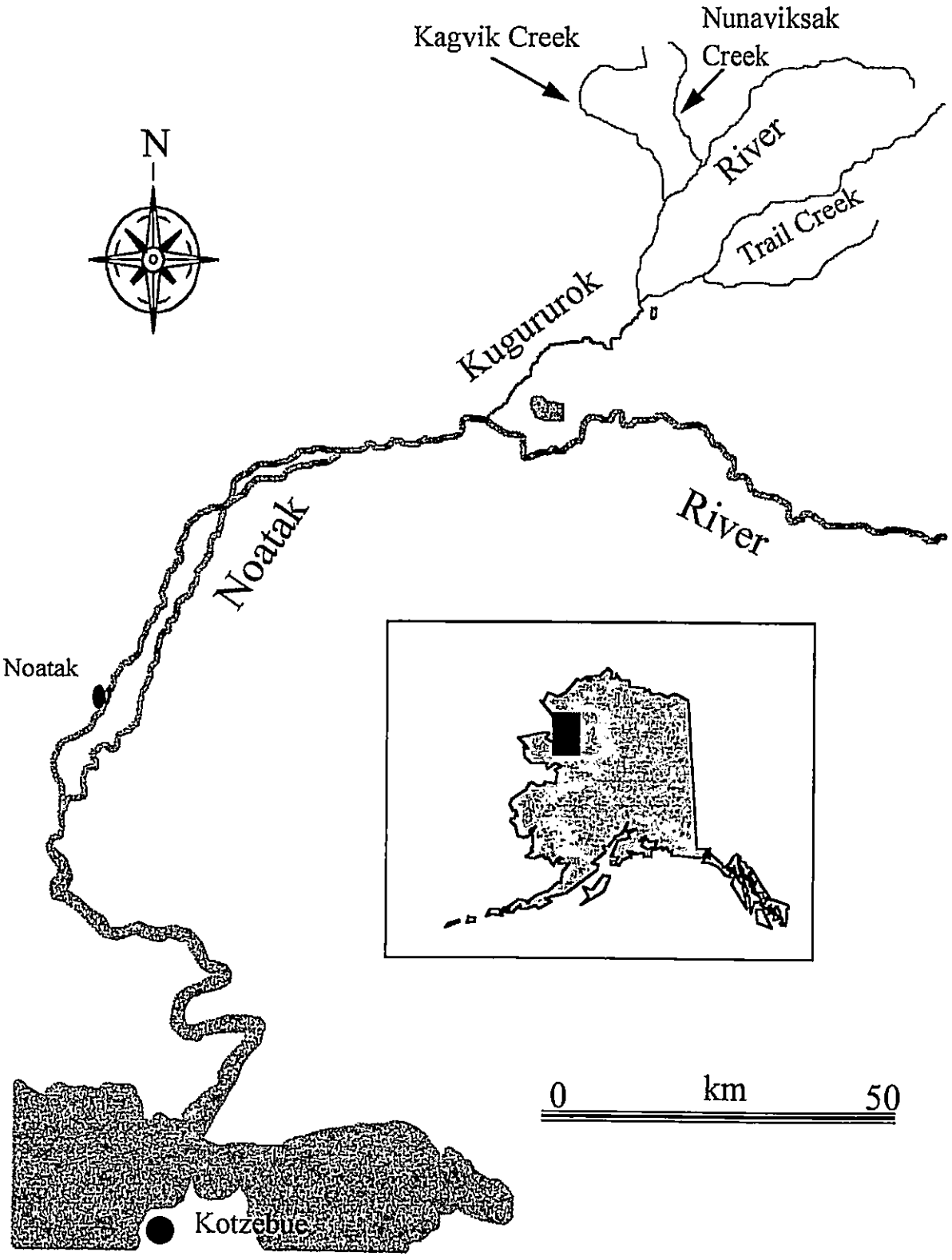

Figure 2. Kugururok River collection area in the Noatak River Drainage.

subject to seasonal flooding resulting in periodic turbid flow and marked gravel displacement.

Fish species encountered on the Kugururok River include Dolly Varden char, chum salmon, pink salmon (*O. gorbuscha*), sockeye salmon (*O. nerka*), chinook salmon (*O. tshawytscha*), slimy sculpin (*Cottus cognatus*), humpback whitefish (*Coregonus pidschian*), round whitefish (*Prosopium cylindraceum*), long-nose sucker (*Catostomus catostomus*), burbot (*Lota lota*), and northern pike (*Esox lucius*).

Methods

Fish Sampling

Char were collected from the Kugururok River during the summers of 1994 and 1995. A field camp was established during the summer of 1994 approximately 8 km upstream from the mouth. Thirteen prespawning summer-run char were collected by angling during two float trips on the spawning grounds near the mouth of Nunaviksak Creek in late July and early August. The collection goal of 100 fish was not attained due to high water levels throughout the field season, which lasted from 10 June to 10 September. A total of 20 individual aquatic invertebrates were also collected using a kick screen during this period. The invertebrates were identified and dried in the field.

The 1995 field season consisted of four periods of collection in order to target particular reproductive stages of the char life history. In May, 10 nonspawning fish were collected from the lower Noatak River, near the village of Noatak, by gill net. Gonadal development was not apparent and there was no sign of secondary sexual characteristics such as increased coloration or kype formation.

Thirty prespawning summer-run char were collected by angling from 20 June to 7 July while they migrated up the river. All fish showed visible signs of maturity (developing gonads) and the ability to spawn at the end of the summer. These char were collected within a 32 km stretch of river in the lower Kugururok River.

During the second collection period, 31 spawning summer-run fish were collected from 5 September to 12 September by hook and line and beach seining. These char were collected between the confluence of Nunaviksak Creek and Trail Creek during a 3-week float trip. Seven of the 31 fish were collected with ripe gonads intact whereas the remaining 24 fish had already spawned. Spawning activity was noted in all fish captured during this time period. Thirty nonspawning fish were collected from 17 September to 19 September, by angling, within 3.2 km of the mouth of the Kugururok River. Condition of these fish suggests that they had recently been feeding at sea and had re-entered the river to overwinter. Also,

reduced yet still noticeable secondary sexual characteristics suggested that all the fish collected during this period had spawned in a previous season.

In October, a known overwintering area on the Kugururok River near the confluence of Trail Creek was sampled by angling. Three postspawned fall-run fish were collected. Shore-fast ice and minimal access to flowing water impeded the further collection of fish. Ten Arctic grayling and numerous aquatic invertebrate species were collected as representative of freshwater residents in the spring and summer of 1995 from the Kugururok River.

Biological Analysis

Upon capture, blood and heart samples were taken and preserved in sodium heparin and ethanol, respectively, for genetic studies. Fork length for each fish was recorded to the nearest 1 mm and total weight was recorded to the nearest 0.1 kg. The remains of the fish were flown to Kotzebue within one day, where they were kept frozen until being transported to Fairbanks for analysis. After thawing, gut contents were removed from each fish and analyzed for species composition and abundance. Gill rakers were counted using magnification up to 10x when necessary magnification to accurately determine the numbers of rakers. Upper gill rakers and total gill rakers were counted from the first arch of both the left and right gills of each fish caught in 1995.

Stable Isotope Analysis

The stable isotope ratios of carbon and nitrogen for the individual char tissues were determined from a sample of the dry, lipid free protein remaining following lipid extraction. The protein was finely ground in a coffee grinder before analysis. A 1 to 2 mg aliquot was analyzed using a Europa Continuous Flow Isotope Ratio Mass Spectrometry System (CF-IRMS) to determine the $\delta^{13}C$ and $\delta^{15}N$ values.

The stable isotope values of pure lipid from each of the tissues were determined from a 0.4 to 0.6 mg subsample of extracted lipid. The consistency of the lipid was such that a sample could be directly put into a weighing tin for analysis in the CF-IRMS.

In order to establish a freshwater diet end member, 10 Arctic grayling were ground whole in a Waring blender after gut contents had been removed. The homogenate was dried to constant weight for 48 h and then finely ground in a coffee grinder. A 1 to 2 mg aliquot was submitted to CF-IRMS to determine the $\delta^{13}C$ and $\delta^{15}N$ values. Stable isotope values were also determined for freshwater invertebrates (Tipulidae, Heptageniidae, and Chloroperlidae) from a dried, ground sample. In order to establish the marine diet end member from which to compare the char tissues, the stable isotope values of 12 herring (Clupeidae) and 12 smelt

(Osmeridae) from Kotzebue Sound (July, 1995) were also determined by the same methods previously described.

Proximate Analysis

The following tissues were extracted from each fish and were analyzed for lipid, water, ash, and protein content: gastrointestinal (gi) tract, liver, gonads, ventral muscle, dorsal muscle, and carcass. The gi tract included the esophagus, stomach, pyloric caecae, and intestine. After extracting the gi tract, the contents were emptied, identified, and saved for isotopic analysis. The ventral muscle included that part of the white muscle in contact with the gut cavity of the fish below the ribs. The dorsal muscle consisted of the remaining hypaxial and epaxial white muscle. Red muscle has been found to contain significantly different amounts of lipid than white muscle in salmonids and was therefore separated (Sheridan 1988 and Sänger 1993). The carcass consisted of the head, vertebrae, red muscle, and skin of the fish.

Subsequent to extraction, each tissue was weighed to the nearest 0.01 g using a Mettler balance. Each tissue was combined with an amount of water equivalent to 49 percent of the tissue weight and then homogenized in a Waring commercial blender for 5 to 10 minutes. The water served to facilitate maceration and aid in lipid extraction.

Lipid

Lipid was extracted from each tissue using a modified Bligh and Dyer method (Bligh and Dyer 1959); 25 or 50 g aliquots of homogenate were analyzed, depending on the total weight of the tissue, with duplicates being analyzed periodically. The 50 g aliquot was blended with 100 ml chloroform, 100 ml methanol and 50 ml water for approximately 3 minutes. This homogenate was filtered through a #4 Whatman filter. The filtrate was poured into a graduated cylinder and allowed to separate. Volumes of the chloroform and methanol layers were measured to the nearest 1 ml. The entire methanol layer and a small amount of the chloroform layer were suctioned off and discarded. The remaining filtrate was poured into a tared porcelain dish and allowed to evaporate for 48 h such that only lipid remained in the dish. At this time, the dish was reweighed to determine the amount of pure lipid present. The following formula was used to determine total lipid, reported as a percentage of wet weight, while compensating for the amount of chloroform layer extracted:

$$\text{total lipid} = \frac{(\text{weight of lipid in aliquot}) * (\text{volume of chloroform layer})}{\text{volume of aliquot}}$$

Total lipid content of the sample was then used to extrapolate, by direct proportion, the total lipid content of both the tissue and the fish. The lipid, as well

as the lipid free precipitate on the Whatman filter, was dried and saved for future isotope analysis.

Water

Water content was determined by isolating two 15 to 30 mg duplicate aliquots of homogenate in separate ceramic crucibles. The crucibles were placed in a 65°C oven, dried until the contents attained constant weight (approximately 24 h), and reweighed. Dry weight was subtracted from wet weight to determine the water content, which was then reported as a percentage of wet weight. The dried sample was saved for future isotope analysis.

Protein

Protein content was determined by finely grinding a subsample of dried homogenate from the water content analysis. Nitrogen content was determined on an aliquot of 1 to 2 mg during isotope ratio analysis from the relative ion currents of the sample and standard ofknown N content. Protein was then estimated by multiplying percent nitrogen by a factor of 6.25 (Dowgiallo 1975).

Ash

Ash content was determined by combusting duplicate 3 g aliquots of each tissue homogenate in a muffle furnace at 600°C until constant weight was attained. Samples were reweighed and ash content was reported as a percentage of wet weight.

Fecundity

Subsequent to extracting the female gonads (ovaries), a small sample was taken from the middle of each ovary, weighed for gravimetric fecundity measurements, and immediately frozen. The ovary subsamples were fixed in formalin for later enumeration. The fixed eggs were counted and fecundity was estimated by extrapolating egg counts as a ratio of the sample weight to the total ovary weight.

Data Analysis

Duplicate water, ash, and protein content values as well as $\delta^{13}C$ and $\delta^{15}N$ values, were subtracted and the differences compared. Criteria were set before analysis that a case with a difference more than 10 percent of the mean would be deleted. This never occurred, however, suggesting successful reproducibility. The mean and standard deviation of the differences were reported at each life history stage. All values were reported as proportions of the fish wet weight. Shearer (1994) discusses that more accurate comparisons of proximate compositions are made with respect to wet weight, especially when utilizing analysis of variance tests.

Indices were developed for each tissue in each of the periods of the char life stages studied. The index of each tissue represents the relationship of the tissue weight to that of the whole fish:

index = tissue wet weight (g) / total fish wet weight (g)

Each of the analyses done (gill raker counts, indices, isotope, and proximate analysis) underwent statistical analysis before any comparisons were made with regard to the life history stage of the char. Males and females were tested for significant differences in analyses using an analysis of covariance test with length of the fish as the covariate (Systat version 5.02)(α=0.05). Length was used because it accounted for a significant amount of error in most analyses. It has been pointed out that failing to account for fish size as a covariate has often led to misleading conclusions (Shearer 1994). When length did not to account for a significant amount of error, an independent-samples t-test was utilized. For further comparisons of analysis values, the sexes were either separated or combined, depending on the results of the previous test. Analyses of covariance were applied to the analyses values to detect differences in means among the collection time periods. If a significant difference was found, a Tukey pairwise comparison test was utilized to test individual differences within the test periods.

Length-weight regressions of the natural logarithms of original length and weight data were developed based on second order polynomial or linear regression depending on a maximized r^2 value. Analysis of covariance tests were considered more accurate for comparing length-weight relationships than condition factors (Wooton and Mills 1979). Male and female length-weight regressions were

compared for differences in slope and intercept through and analysis of covariance (SYSTAT version 5.02). Differences in slope and intercept were also tested among and between collection periods by an analysis of covariance test, followed by the same post hoc Tukey pairwise comparison test used previously.

Results

Biological Data

Differences between replicates of each analysis proved to be consistent and well within the set boundaries in the study. Mean and standard deviations of the differences for stable isotope and proximate analyses were reported in Appendices 1 through 9.

Samples collected from the 1994 and 1995 seasons were divided into seven periods: May nonspawners, June prespawners, July prespawners, spawners, summer-run postspawners, September nonspawners, and fall-run postspawners. These periods represented a timeline for char collected from the first week of freshwater starvation through approximately 20 months of freshwater residence. This allowed for comparisons of meristic data, indices, isotopic ,and energetic composition throughout their reproductive life cycle.

Gill rakers were counted from both the left and right sides of all fish runs except July prespawners. Upper gill raker counts and total counts were compared between males and females and between each of the runs. There were no

significant differences between males and females from any collection period. (Appendix 10). There were also no significant differences of gill raker counts among or between periods. Mean (standard deviation) upper gill raker counts for left and right sides were 11 (0.68) and 11 (0.64) respectively. Mean (standard deviation) total gill raker counts for left and right sides were 22 (1.31) and 22 (1.27) respectively.

In 1995, during the first collection period in May, 10 nonspawning fish were caught in the lower Noatak River. It was believed and later confirmed that these char had not previously spawned due to the lack of gonadal development and secondary sexual characteristics. These were juvenile char that were in the 3 to 5 year period of feeding before commencing their first spawning run. Mean lengths (standard deviations) of the 4 females and 4 males were 539 (26) mm and 530 (70) mm respectively. Mean weights (standard deviations) of the same males and females were 1131 (215) g and 1266 (407) g, respectively. A second order polynomial regression of the natural logarithms of length and weight was developed and had an r^2 of 0.96 (Figure 3). Regressions of May nonspawning males and females were not significantly different ($\alpha = 0.05$, $p = 0.841$). Analysis of covariance tests, however, indicated significant differences among collection period length-weight regressions ($\alpha = 0.05$, $p = 0.000$). May nonspawners were significantly different from June prespawners, post spawners, spawners, and

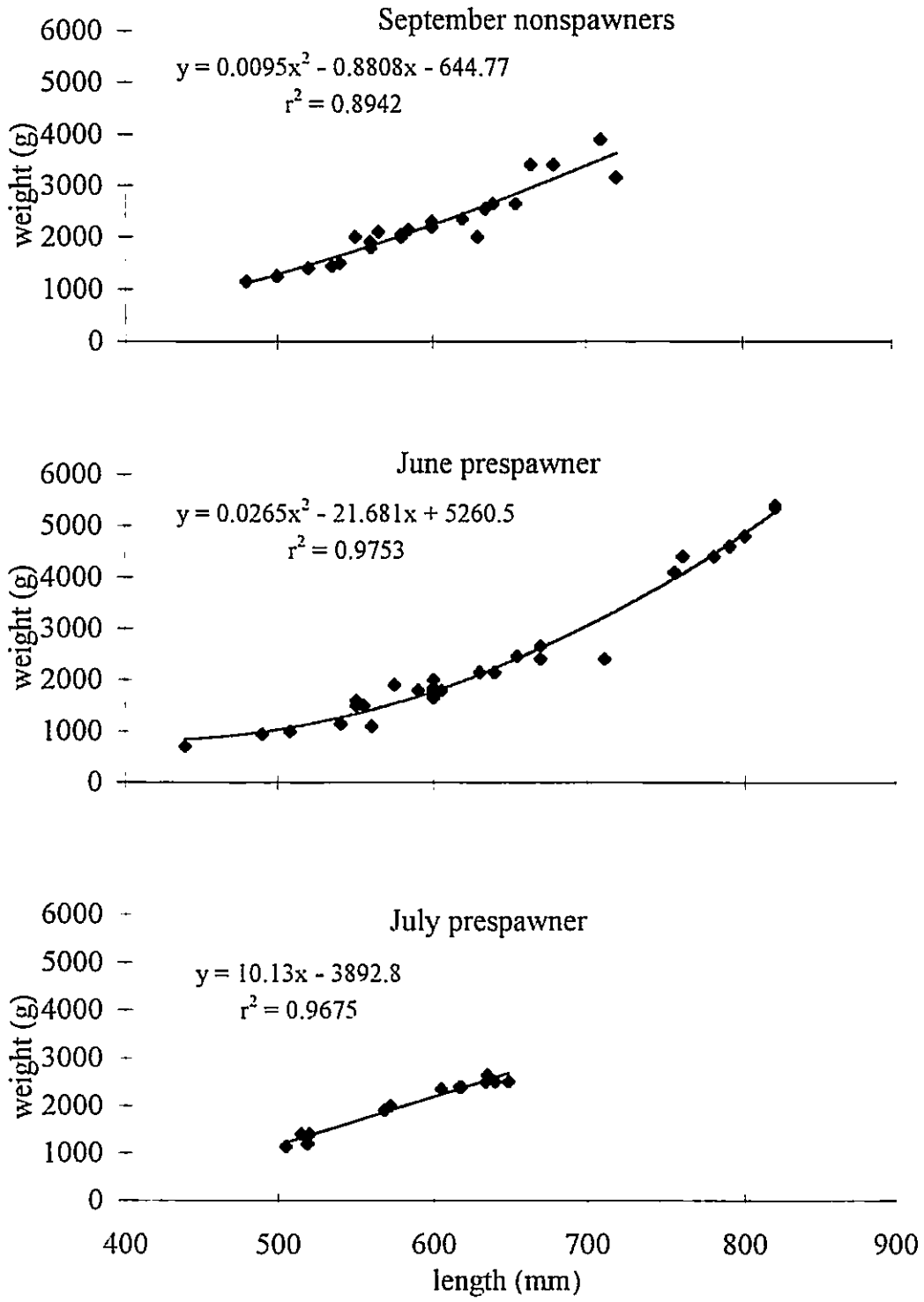

Figure 3. Length-weight regressions for each of the collection periods. Either polynomial or linear regression equations are reported with r - squared values.

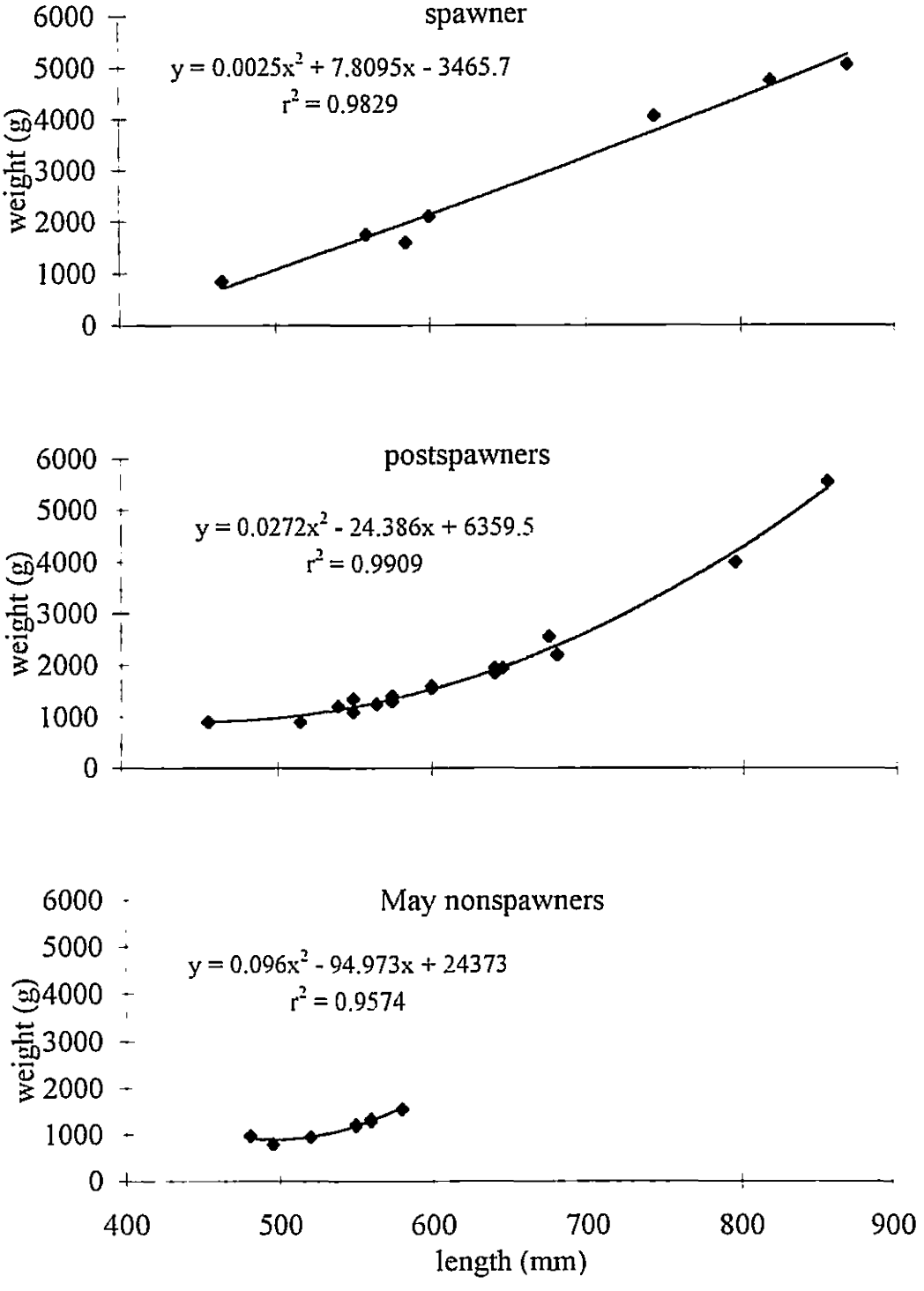

Figure 3. Continued.

September nonspawners ($\alpha = 0.05$, $p = 0.000$, 0.000, 0.009, and 0.000, respectively).

In June of 1995, 30 char were collected. These fish were summer-run prespawning fish preparing to spawn in August. Gonadal formation was minimal. At the time of collection, these fish had overwintered once and migrated up the Noatak River into the Kugururok River. Mean lengths (standard deviations) of the 16 females and 14 males were 603 (52) mm and 673 (132) mm, respectively. Mean weights (standard deviations) of the same females and males were 1847 (463) g and 3114 (747) g, respectively. In order to test the overall reproducibility of the proximate analysis, each component of proximate analysis was summed for each fish. The total sample size was 230 fish. The summation of all components had a mean of 1.03 and a standard deviation of 0.06, suggesting excellent reproducibility in the data. A second order polynomial regression of the natural logarithms of length and weight was developed and had an r^2 of 0.98 (Figure 3). Regressions of June prespawning males and females were significantly different ($\alpha = 0.05$, $p = 0.002$). Analysis of covariance tests indicated significant differences among collection period length-weight regressions ($\alpha = 0.05$, $p = 0.000$) where June prespawners were significantly different from May

nonspawners, July prespawners, postspawners, and September nonspawners (α = 0.05, p = 0.000, 0.000, 0.001, and 0.042 respectively).

Char collections from 1994 were made in July and represented prespawning summer-run fish. Like the prespawners from June, these 13 female fish had overwintered once and migrated to the Kugururok River. Mean length (standard deviation) of the 13 females was 584 (54) mm. Mean weight (standard deviation) of the same females was 2027 (555) g. A linear regression of the natural logarithms of length and weight had an r^2 of 0.97 (Figure 3). Analysis of covariance tests indicated significant differences among collection period length-weight regressions (α = 0.05, p = 0.000) where July prespawners were significantly different from June prespawners, postspawners, spawners and September nonspawners (α = 0.05, p = 0.001, 0.000, 0.010, and 0.000 respectively).

In September of 1995, 31 summer-run char were collected. Seven of these char were within one or two days of spawning and therefore had fully mature gonads; these char were designated 'spawners'. The remaining 24 char were designated 'postspawners' due to their empty gonads. Each postspawner had just spawned and completely evacuated all gonadal products except residual tissue. The mean lengths (standard deviations) of the 4 female and 3 male spawners were 553 (61) mm and 812 (63) mm, respectively. Mean weights (standard deviations)

of the same males and females were 1575 (527) g and 4617 (513) g, respectively. A second order polynomial regression of the natural logarithms of length and weight had an r^2 of 0.98 (Figure 3). Regressions of spawning males and females were significantly different ($\alpha = 0.05$, $p = 0.043$). Analysis of covariance tests indicated significant differences among collection period length-weight regressions ($\alpha = 0.05$, $p = 0.000$) where spawners were significantly different from May nonspawners and postspawners ($\alpha = 0.05$, $p = 0.009$ and 0.010, respectively).

Mean lengths (standard deviations) of the 12 female and 12 male postspawners were 597 (48) mm and 636 (137) mm, respectively. Mean weights (standard deviations) of the same males and females were 1533 (382) g and 2350 (1644) g, respectively. A second order polynomial regression of the natural logarithms of length and weight had an r^2 of 0.99 (Figure 3). Regressions of postspawned males and females were significantly different ($\alpha = 0.05$, $p = 0.035$). Analysis of covariance tests indicated significant differences among collection period length-weight regressions ($\alpha = 0.05$, $p = 0.000$) where postspawners were significantly different from May nonspawners, July prespawners, June prespawners, and spawners ($\alpha = 0.05$, $p = 0.000$, 0.000, 0.001, and 0.010, respectively).

Also in September, 30 nonspawning char were collected in the lower Kugururok River. These char had been at sea feeding the entire summer. They had entered freshwater to stage for overwintering. Based on the condition of these char it is hypothesized that they would have spawned the subsequent summer. Slight secondary sexual characteristics such as coloration of the lips and small kype formation in the males suggests that these fish had previously spawned. Mean lengths (standard deviations) of the 13 females and 12 males were 583 (53) mm and 614 (68) mm, respectively. Mean weights (standard deviations) of the same males and females were 2096 (611) g and 2408 (759) g, respectively A second order polynomial regression of the natural logarithms of length and weight had an r^2 of 0.89 (Figure 3). Regressions of postspawned males and females were significantly different ($\alpha = 0.05$, $p = 0.007$). Analysis of covariance tests indicated significant differences among collection period length-weight regressions ($\alpha = 0.05$, $p = 0.000$) where September nonspawners were significantly different from May nonspawners, June prespawners, and July prespawners ($\alpha = 0.05$, $p = 0.000$, 0.042. and 0.000 respectively).

Three fall-spawners were collected in October. These char were postspawned fish. Although this sample size was too small for most comparisons, the mean values are reported. Mean length (standard deviation) of the 3 males was 725 (60) mm. Mean weight (standard deviation) of the same males was 4150

(1003) g. A length-weight relationship was not generated due to inadequate sample size.

Indices Data

Indices were developed to determine trends in tissue size through each of the life stages collected. Indices results were reported as decimal proportions.

Table 1 shows the mean indices for the tissues of males and females from each run. Ranges of the means from pooled time period were: gastrointestinal (gi) tract (0.01 - 0.05), liver (0.01 - 0.03), gonads (0.01 - 0.21), ventral muscle (0.03 - 0.07), dorsal muscle (0.28 - 0.53), and carcass (0.29 - 0.53). Ranges of standard deviations also reported for each time period were: gi tract (0.00 - 0.01), liver (0.00 - 0.01), gonads (0.00 - 0.03), ventral muscle (0.00 - 0.010), dorsal muscle (0.03 - 0.10), and carcass (0.01 - 0.07).

Figure 4 represents the change in gi tract indices of males and females through time. Both sexes have an index around 3.2 percent. Females, however, lose more gi tract weight relative to whole fish weight prior to spawning in September. Both male and female gi tract indices rise back up to approximately 4.5 percent after spawning probably indicating reduction of whole body weight during starvation. Similar trends can be seen in ventral muscle and dorsal muscle proportion index changes through time (Figure 7 and Figure 8, respectively). In both cases female indices drop more than male indices due either to an increase in

Table 1. Mean proportion indices of males and females in each period sampled. Sample sizes are also reported where male sample sizes are in parentheses.

			gi tract mean		liver mean		gonads mean		belly mean		muscle mean		carcass mean	
run	month	n (males)	f	m	f	m	f	m	f	m	f	m	f	m
summer														
(non-)	Sept	12(13)	0.031	0.033	0.018	0.021	0.009	0.001	0.065	0.056	0.510	0.525	0.291	0.299
(pre-)	June	16(14)	0.025	0.023	0.024	0.014	0.059	0.030	0.034	0.033	0.456	0.418	0.404	0.462
(pre-)	July	13(0)	0.013		0.025		0.138		0.032		0.282		0.532	
(spawn)	Sept	4(4)	0.016	0.022	0.017	0.013	0.210	0.030	0.036	0.048	0.337	0.422	0.292	0.455
(post-)	Sept	9(9)	0.027	0.020	0.013	0.013	0.022	0.023	0.043	0.049	0.443	0.425	0.378	0.394
(non-)	May	6(3)	0.050	0.045	0.019	0.021	0.017	0.006	0.045	0.047	0.444	0.485	0.425	0.383
fall														
(post-)	Sept	0(3)		0.024		0.010		0.012		0.051		0.419		0.483

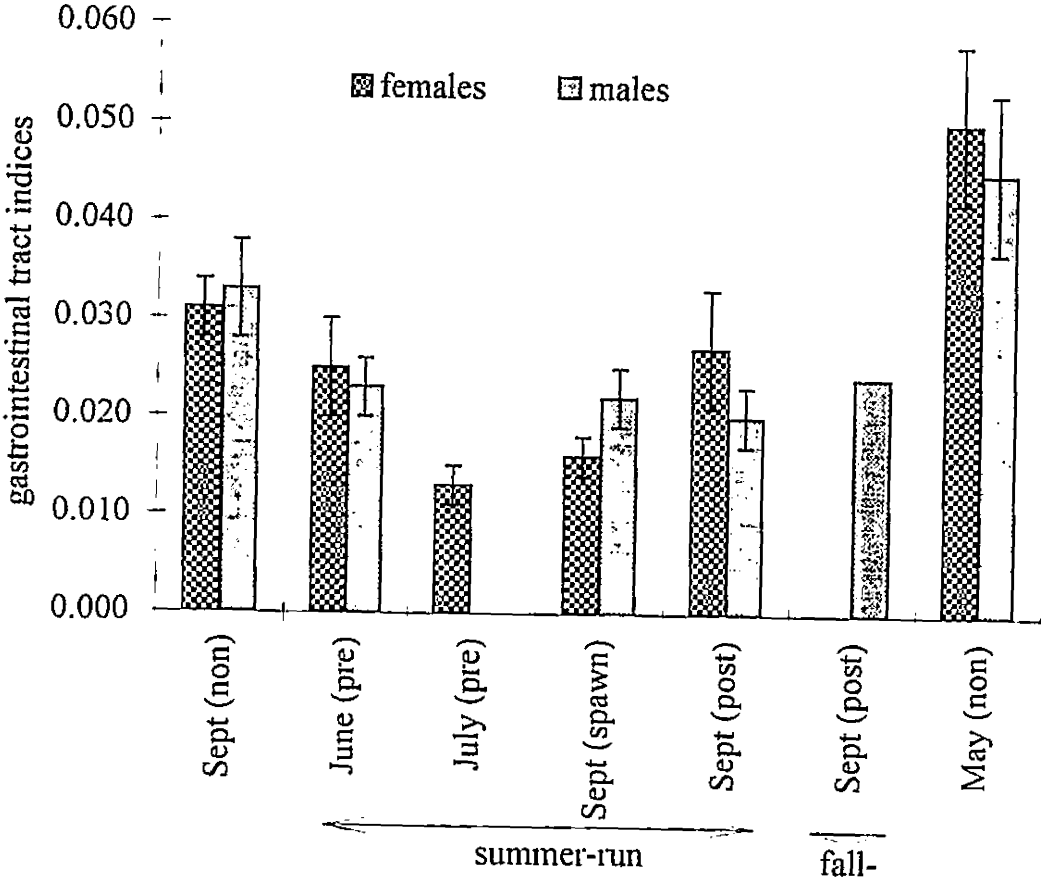

Figure 4. Timeline of mean gastrointestinal tract indices of male and female char. Error bars represent one standard deviation.

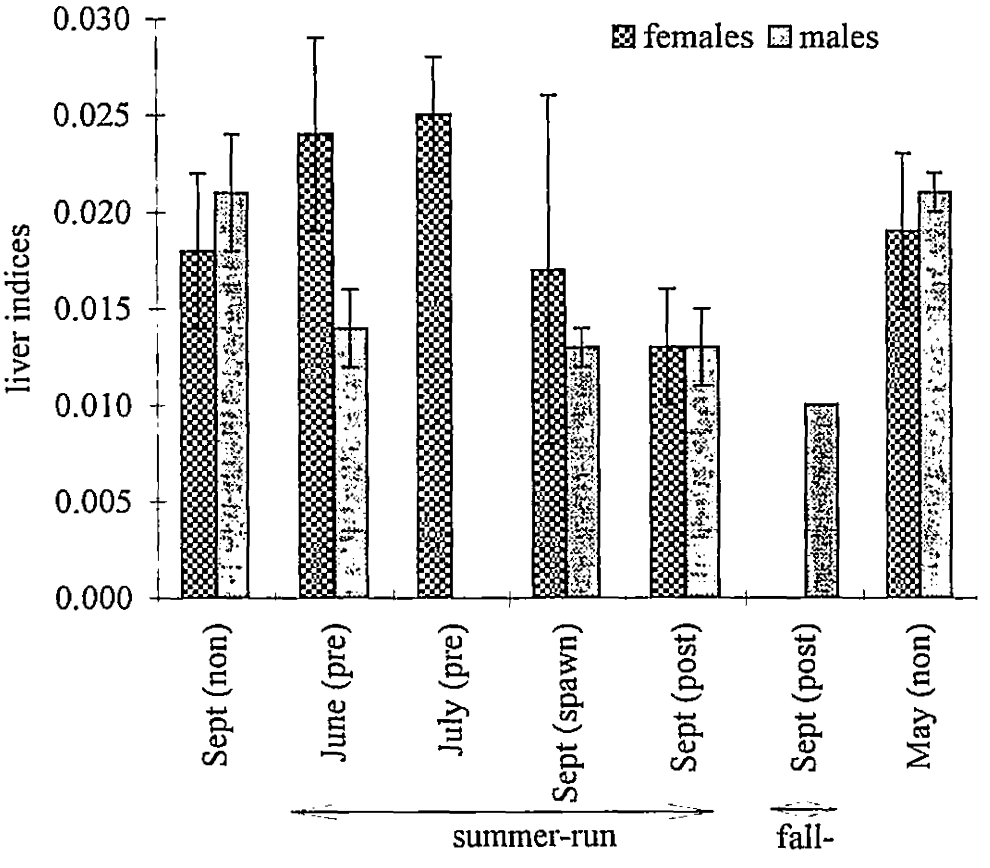

Figure 5. Timeline of mean liver indices of male and female char. Error bars represent one standard deviation.

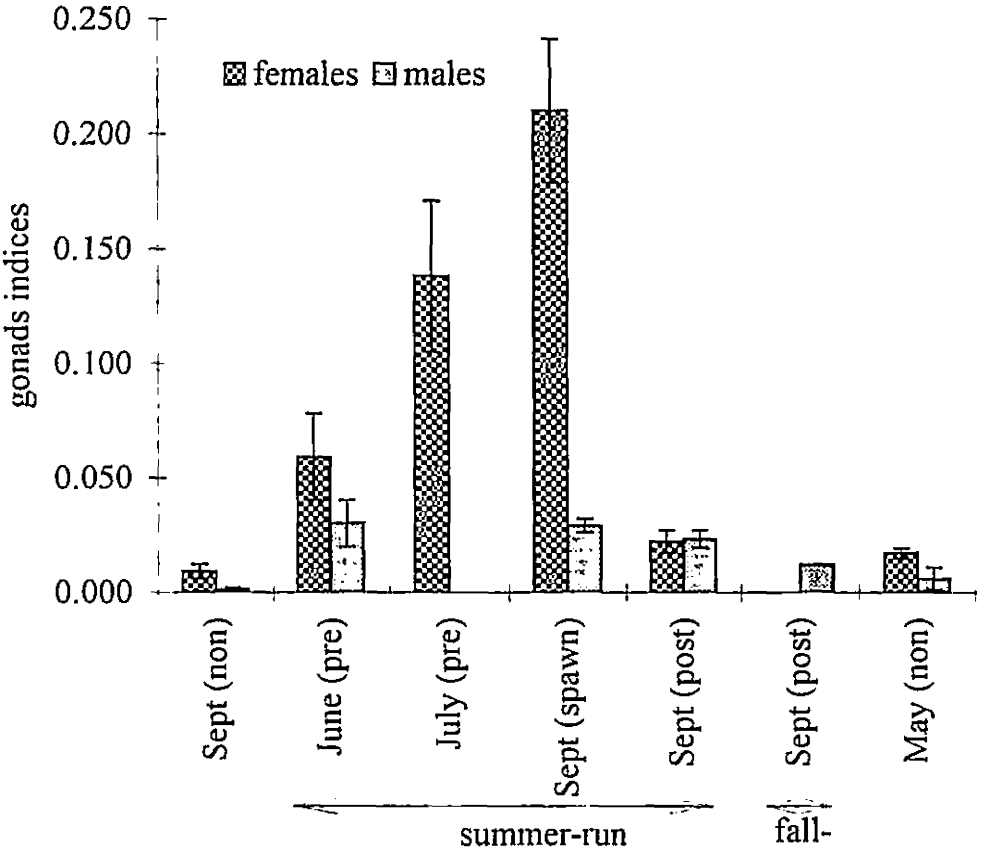

Figure 6. Timeline of mean gonad indices of male and female char. Error bars represent one standard deviation.

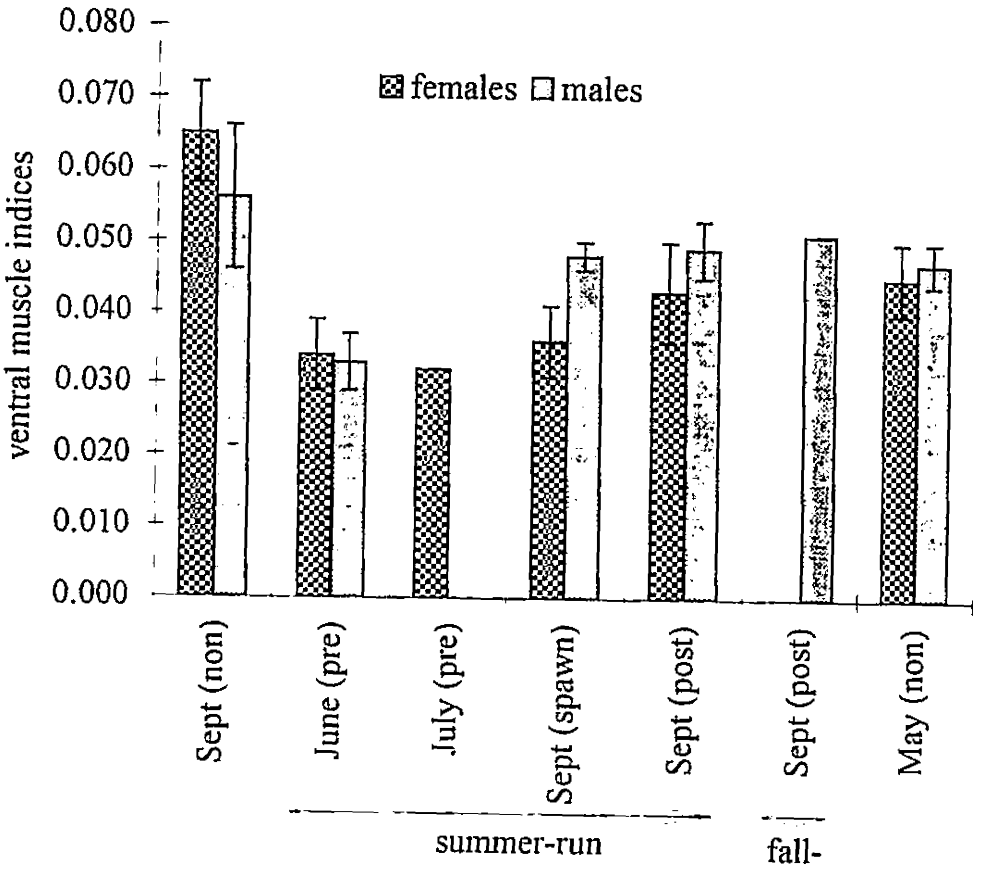

Figure 7. Timeline of mean ventral muscle indices of male and female char. Error bars represent one standard deviation.

whole body weight (from gonads) or to the energy taken from the muscle for gonad production. Indices of female liver and carcass increase as spawning is approached, significantly decrease near spawning and again increase before going to sea to feed (Figure 5 and Figure 9, respectively). Indices of male and female gonads appear to be significantly different (Figure 6). Female indices increase significantly prior to spawning due to gonadal formation; male indices less so. The remainder of gonadal weight is due to residual tissue left behind to be reabsorbed during the winter.

In each of the tissues examined, except the dorsal muscle, at least one time period showed a significant difference between male and female indices (Table 2). Data for those tissues (except dorsal muscle) were therefore separated by sex for further analysis. Length was used as a covariate in all tests except liver indices from nonspawning char caught in September and ventral muscle from spawning char, where length was found not to be a significant determinant of proportion index. July prespawners and fall-run char were not included in the test because only one sex of fish was collected.

Analysis of covariance tests using length as a covariate were applied to test for differences between time periods. Significant differences were found in all cases ($\alpha = 0.05$, $p = 0.000$ in all tests). Tukey pairwise comparison tests were then applied to test individual differences between each of the reproductive stages of

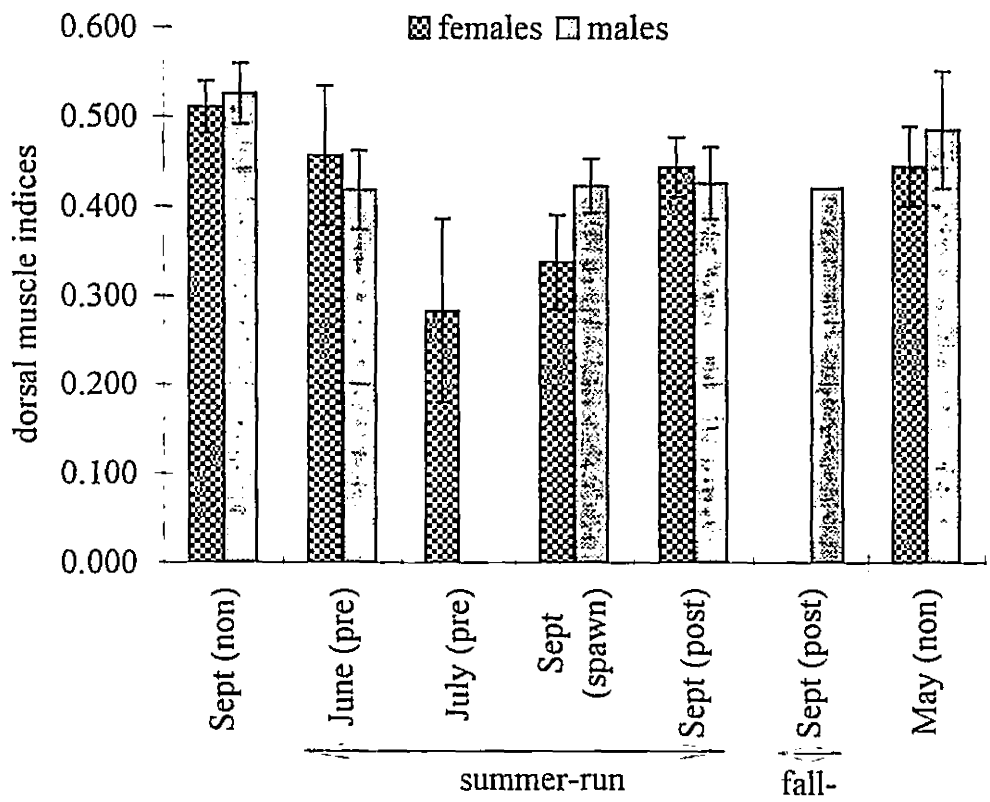

Figure 8. Timeline of mean dorsal muscle indices of male and female char. Error bars represent one standard deviation.

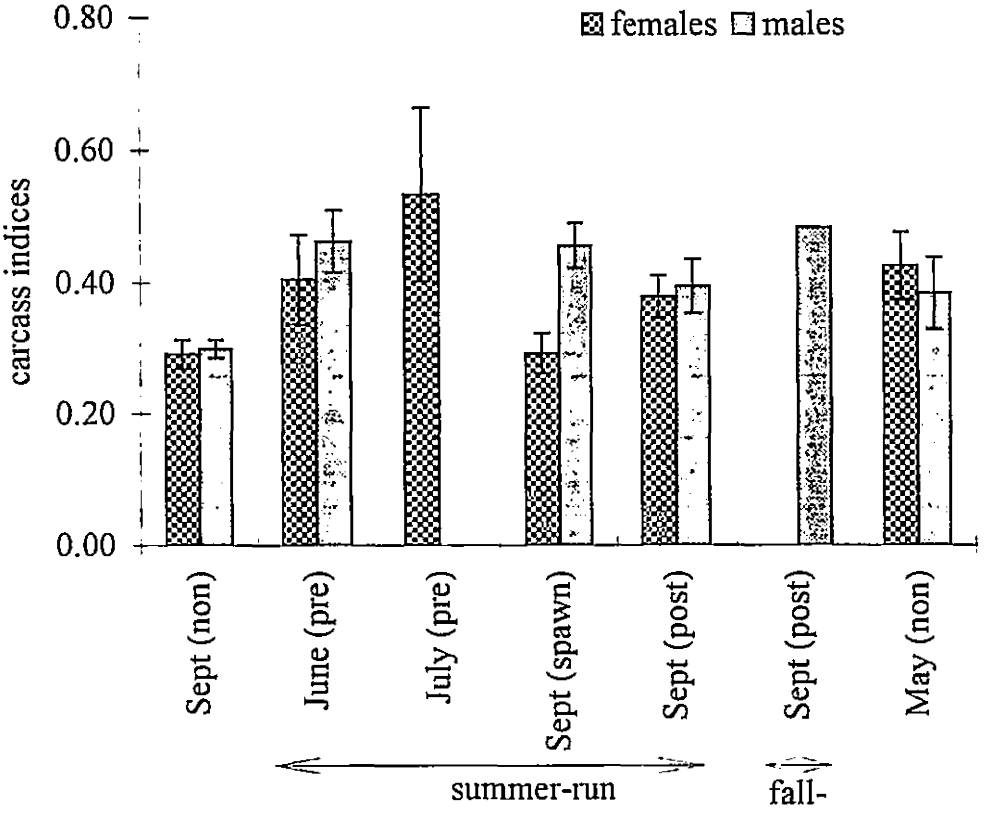

Figure 9. Timeline of mean carcass indices of male and female char. Error bars represent one standard deviation.

Table 2. Independent samples t-test probabilities comparing male versus female proportion indices of each tissue examined in each of the time periods collected. Boxed areas cover probabilities of tests that were significantly different. Bold numbers represent probabilities where length was not used as a covariate.

run	month	n	gi tract P	liver P	gonads P	ventral muscle P	dorsal muscle P	carcass P
summer								
(non-)	Sept	25	0.534	**0.056**	0.000	0.016	0.345	0.490
(pre-)	June	30	0.492	0.000	0.000	0.760	0.149	0.008
(pre-)	July	na	na	na	na	na	na	na
(spawn)	Sept	7	0.018	0.516	0.003	**0.014**	0.438	0.147
(post-)	Sept	17	0.004	0.803	0.500	0.031	0.396	0.514
(non-)	May	8	0.902	0.663	0.000	0.838	0.219	0.370
fall								
(post-)	Oct	na	na	na	na	na	na	na

Table 3. Matrix of tukey pairwise probabilities comparing proportion indices in each collection period of each tissue examined of female char. Boxed areas cover probabilities of tests that were significantly different.

tissue	run	month	(non-) Sept	(pre-) June	(pre-) July	(spawn) Sept	(post-) Sept	(non-) May
GI tract	(non-)	Sept	1					
	(pre-)	June	0.003	1				
	(pre-)	July	0.000	0.000	1			
	(spawn)	Sept	0.000	0.023	0.853	1		
	(post-)	Sept	0.350	0.670	0.000	0.002	1	
	(non-)	May	0.000	0.000	0.000	0.000	0.000	1
liver	(non-)	Sept	1					
	(pre-)	June	0.010	1				
	(pre-)	July	0.003	0.979	1			
	(spawn)	Sept	1.000	0.096	0.037	1		
	(post-)	Sept	0.093	0.000	0.000	0.571	1	
	(non-)	May	0.999	0.179	0.067	0.994	0.127	1
gonads	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(pre-)	July	0.000	0.000	1			
	(spawn)	Sept	0.000	0.000	0.000	1		
	(post-)	Sept	0.675	0.001	0.000	0.000	1	
	(non-)	May	0.960	0.001	0.000	0.000	0.998	1
ventral	(non-)	Sept	1					
muscle	(pre-)	June	0.000	1				
	(pre-)	July	0.000	0.999	1			
	(spawn)	Sept	0.000	0.994	0.992	1		
	(post-)	Sept	0.000	0.009	0.499	0.349	1	
	(non-)	May	0.000	0.005	0.345	0.182	0.988	1
carcass	(non-)	Sept	1					
	(pre-)	June	0.002	1				
	(pre-)	July	0.000	0.001	1			
	(spawn)	Sept	1.000	0.073	0.000	1		
	(post-)	Sept	0.077	0.955	0.000	0.330	1	
	(non-)	May	0.017	1.000	0.041	0.090	0.943	1

Table 4. Matrix of tukey pairwise probabilities comparing proportion indices in each collection period of each tissue examined of male char. Boxed areas cover probabilities of tests that were significantly different.

				summer				fall
			(non-)	(pre-)	(spawn)	(post-)	(non-)	(post-)
tissue	run	month	Sept	June	Sept	Sept	May	Oct
gi tract	summer							
	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(spawn)	Sept	0.005	0.991	1			
	(post-)	Sept	0.000	0.335	0.978	1		
	(non-)	May	0.000	0.000	0.000	0.000	1	
	fall							
	(post-)	Oct	0.310	1.000	0.995	0.898	0.000	1
liver	summer							
	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(spawn)	Sept	0.000	0.906	1			
	(post-)	Sept	0.000	0.974	0.997	1		
	(non-)	May	1.000	0.001	0.001	0.000	1	
	fall							
	(post-)	Oct	0.001	0.572	0.940	0.785	0.003	1
gonads	summer							
	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(spawn)	Sept	0.992	0.992	1			
	(post-)	Sept	0.000	0.164	0.918	1		
	(non-)	May	0.994	0.000	0.012	0.011	1	
	fall							
	(post-)	Oct	0.680	0.085	0.281	0.555	0.941	1

Table 4. Continued

ventral	summer							
muscle	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(spawn)	Sept	0.486	0.008	1			
	(post-)	Sept	0.276	0.000	1.000	1		
	(non-)	May	0.301	0.020	1.000	0.993	1	
	fall							
	(post-)	Oct	0.984	0.096	0.999	1.000	0.992	1
carcass	summer							
	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(spawn)	Sept	0.000	1.000	1			
	(post-)	Sept	0.000	0.005	0.273	1		
	(non-)	May	0.155	0.074	0.333	0.990	1	
	fall							
	(post-)	Oct	0.001	0.995	0.990	0.291	0.262	1

Table 5. Matrix of tukey pairwise probabilities comparing proportion indices in each collection period of each tissue examined of female and male (combined) char. Boxed areas cover probabilities of tests that were significantly different.

				summer					fall
			(non-)	(pre-)	(pre-)	(spawn)	(post-)	(non-)	(post-)
tissue	run	month	Sept	June	July	Sept	Sept	May	Sept
dorsal	summer								
muscle	(non-)	Sept	1						
	(pre-)	June	0.000	1					
	(pre-)	July	0.000	0.000	1				
	(spawn)	Sept	0.000	0.155	0.040	1			
	(post-)	Sept	0.001	1.000	0.000	0.287	1		
	(non-)	May	0.273	0.968	0.000	0.109	0.951	1	
	fall								
	(post-)	Oct	0.677	1.000	0.360	0.993	1.000	0.994	1

the char collected (Table 3 to Table 5). Significant differences in female liver indices were found between September nonspawners and both June and July pre spawners. Postspawner liver indices were also significantly different from both June and July prespawners.

Stable Isotope Analysis

Stable isotope data was generated for each tissue of char from each of the time periods collected in this study. Isotope values are reported as $\delta^{13}C$ and $\delta^{15}N$.

$\delta^{13}C$ values

Table 6 shows the mean $\delta^{13}C$ for the tissues from each run. Ranges of the means from each time period were: gi tract (¯16.14 - ¯17.49 ‰), liver (¯17.32 - ¯17.85 ‰), gonads (¯16.21 - ¯18.44 ‰), ventral muscle (¯16.42 - ¯17.43 ‰), dorsal (¯16.26 - ¯17.08 ‰), and carcass (¯16.25 - ¯17.33 ‰). Ranges of standard deviations also reported for each time period were: gi tract (0.27 - 1.05 ‰), liver (0.25 - 0.90 ‰), gonads (0.35 - 0.93 ‰), ventral muscle (0.17 - 3.25 ‰), dorsal muscle (0.24 - 0.85 ‰), and carcass (0.08 - 1.55 ‰).

In each of the tissues examined there was never a significant difference between males and females (Table 7). The sexes were therefore grouped together for all further analyses. Length was used as a covariate in all tests except dorsal muscle from June pre summer-spawners where length was found not to be a significant determinant of $\delta^{13}C$ values. July prespawners and fall-run char were

Table 6. Mean $\delta^{13}C$ values of males and females (combined) in each period sampled. Sample sizes are also reported where dorsal muscle sample size is in parentheses.

run	month	n (dorsal)	gi tract mean(‰)	liver mean(‰)	gonads mean(‰)	ventral muscle mean(‰)	dorsal muscle mean(‰)	carcass mean(‰)
summer								
(non)	Sept	10(50)	-17.078	-17.561	-17.558	-17.250	-17.075	-16.870
(pre)	June	12(58)	-17.491	-17.845	-17.960	-17.302	-17.034	-16.814
(pre)	July	13(13)	-17.066	-17.745	-18.441	-17.125	-17.010	-17.332
(spawn)	Sept	4(14)	-16.755	-17.388	-17.218	-17.43	-16.931	-16.803
(post)	Sept	6(36)	-17.157	-17.527	-17.068	-16.938	-16.926	-16.885
(non)	May	10(20)	-17.372	-17.518	-17.355	-16.781	-16.617	-16.522
fall								
(post)	Oct	3	-16.135	-17.320	-16.205	-16.415	-16.255	-16.245

Table 7. Independent samples t-test probabilities comparing male versus female $\delta^{13}C$ values of each tissue examined in each of the time periods collected. Bold numbers represent probabilities where length was not used as a covariate.

run	month	n	gi tract P	liver P	gonads P	ventral muscle P	dorsal muscle P	carcass P
summer								
(non-)	Sept	25	0.456	0.649	na	0.179	0.089	0.750
(pre-)	June	29	0.275	0.99	0.473	0.590	**0.628**	0.767
(pre-)	July	na	na	na	na	na	na	na
(spawn)	Sept	7	na	na	na	na	0.805	na
(post-)	Sept	18	na	na	na	na	0.989	na
(non-)	May	5	0.719	0.600	na	0.113	0.727	0.432
fall								
(post-)	Oct	3	na	na	na	na	na	na

not included in the test because only one sex of fish was collected.

Analysis of covariance tests using length as a covariate were applied to test for differences between time periods. In cases where length was found not to be a significant determinant, analyses of variance were used. There were no significant differences among collection periods of gi tract and liver, ventral muscle and carcass $\delta^{13}C$ values. Significant differences were found in gonads and dorsal muscle ($\alpha = 0.05$, $p = 0.000$ in both tests). Tukey pairwise comparison tests were then applied to test individual differences between each of the reproductive stages of the char collected (Table 8).

Summer-run fish in 1995 represent the same group of spawning fish in that they have most likely fed in the same areas and at the same time the previous summer. Figure 10 represents a timeline of $\delta^{13}C$ values for prespawning, spawning, and postspawning summer-run char. Each of the six extracted tissues are reported on both charts. The range of the tissue $\delta^{13}C$ values is between ¯16.5 ‰ and ¯18 ‰. It is noted that there is no significant change in $\delta^{13}C$ values over time spent starving in freshwater.

$\delta^{15}N$ values

Table 9 shows the mean $\delta^{15}N$ for the tissues from each run. Ranges of the means from each time period were: gi tract (14.73 - 16.41 ‰), liver (14.64 - 16.68 ‰), gonads (15.43 - 16.87 ‰), ventral muscle (15.29 - 16.28 ‰), dorsal muscle

Table 8. Matrix of tukey pairwise probabilities comparing δ ^{13}C values in each collection period of the tissues examined of male and female (combined) char. Boxed areas cover probabilities of tests that were significantly different. Bold numbers represent probabilities where length was not used as a covariate.

				summer					fall
			(non-)	(pre-)	(pre-)	(spawn)	(post-)	(non-)	(post-)
tissue	run	month	Sept	June	July	Sept	Sept	May	Sept
gonads	summer								
	(non-)	Sept	1						
	(pre-)	June	0.986	1					
	(pre-)	July	0.461	0.566	1				
	(spawn)	Sept	1.000	0.878	0.259	1			
	(post-)	Sept	0.648	0.075	0.002	0.898	1		
	(non-)	May	0.912	0.273	0.011	0.993	0.997	1	
	fall								
	(post-)	Oct	0.520	0.170	0.031	0.703	0.996	0.953	1
dorsal muscle	summer								
	(non-)	Sept	1						
	(pre-)	June	0.999	1					
	(pre-)	July	0.997	1.000	1				
	(spawn)	Sept	0.917	0.982	0.998	1			
	(post-)	Sept	0.671	0.890	0.990	1.000	1		
	(non-)	May	0.002	0.005	0.050	0.341	0.130	1	
	fall								
	(post-)	Oct	0.111	0.148	0.201	0.350	0.311	0.908	1

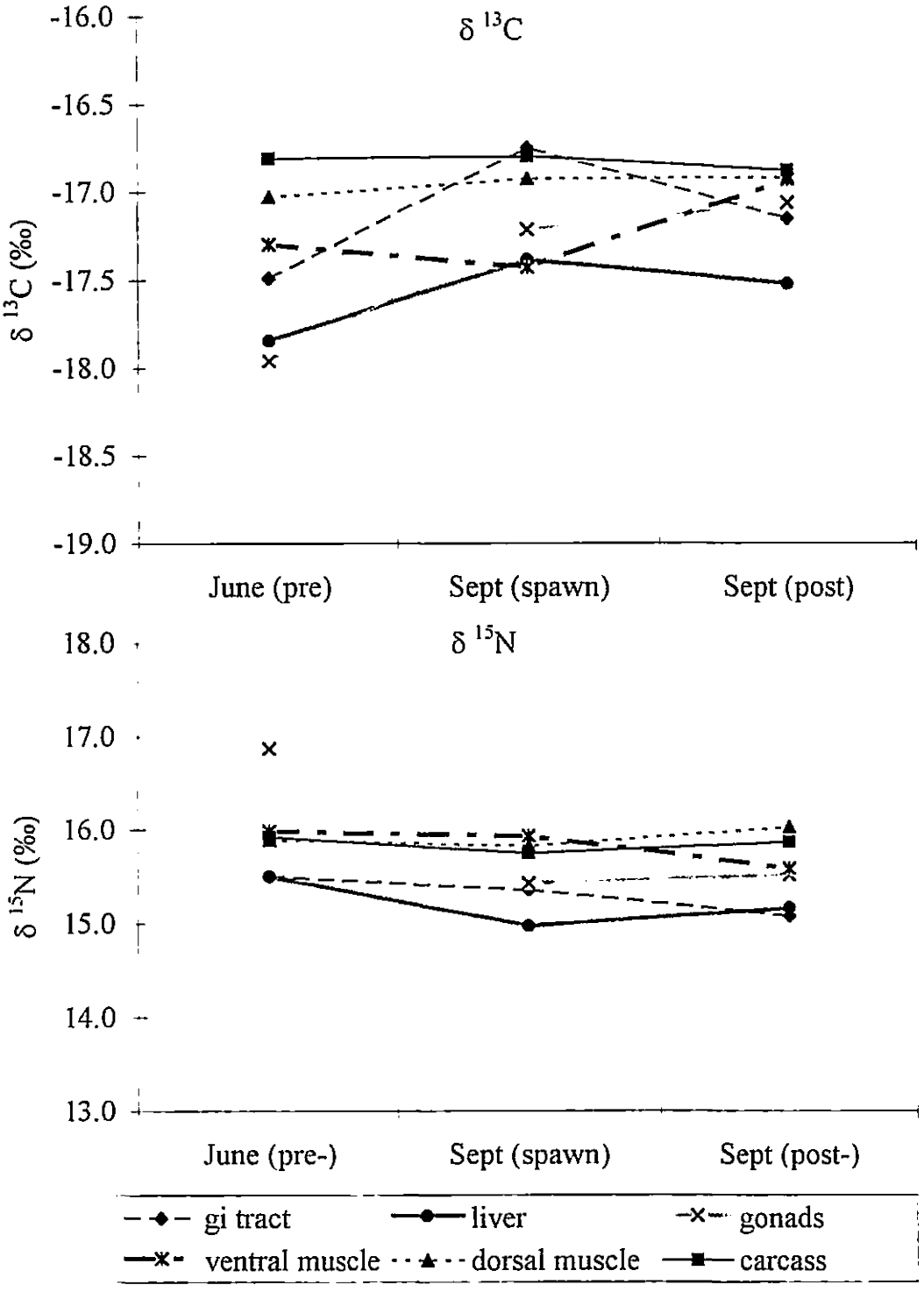

Figure 10. Timeline using three collection periods of δ ^{13}C and δ ^{15}N values for each of the tissues examined.

Table 9. Mean $\delta^{15}N$ values of males and females (combined) in each period sampled. Sample sizes are also reported where dorsal muscle sample size is in parentheses.

run	month	n (dorsal)	gi tract mean(‰)	liver mean(‰)	gonads mean(‰)	ventral muscle mean(‰)	dorsal muscle mean(‰)	carcass mean(‰)
summer								
(non)	Sept	10(50)	14.731	14.636	16.398	15.291	15.290	15.209
(pre)	June	12(58)	15.498	15.498	16.870	15.985	15.884	15.919
(pre)	July	13(13)	15.839	15.230	16.845	15.955	15.923	15.661
(spawn)	Sept	4(14)	15.353	14.97	15.428	15.928	15.823	15.74
(post)	Sept	6(36)	15.077	15.163	15.513	15.582	16.025	15.860
(non)	May	10(20)	16.405	16.254	16.813	16.278	16.107	16.191
fall								
(post)	Oct	3	15.920	16.675	15.530	16.260	16.260	16.490

(15.29 - 16.26 ‰), and carcass (15.21 - 16.49 ‰). Ranges of standard deviations also reported for each time period were: gi tract (0.17 - 0.70 ‰), liver (0.25 - 0.64 ‰), gonads (0.43 - 0.93 ‰), ventral muscle (0.20 - 0.71 ‰), dorsal muscle (0.24 - 0.68 ‰), and carcass (0.09 - 0.55 ‰).

In each of the tissues examined, only dorsal muscle from spawning char showed a significant difference between males and females $\delta^{15}N$ values (Table 10). The sexes for all tissues except the dorsal muscle were, therefore, grouped for subsequent analysis. Length was used as a covariate in all tests except dorsal muscle from June prespawners, postspawners from the summer-run, and nonspawners collected in May from the lower Noatak because length was found not to be a significant determinant of $\delta^{15}N$ values. July prespawners and fall-run char were not included in the test because only one sex of fish was collected.

Analysis of covariance tests using length as a covariate were applied to test for differences between time periods. In cases where length was found not to be a significant determinant, analyses of variance were used. Significant differences were found in gi tract, liver, gonads, ventral muscle and dorsal muscle, and carcass: $p = 0.000, 0.000, 0.003, 0.014, 0.000, 0.032$, respectively ($\alpha = 0.05$ in all tests). Tukey pairwise comparison tests were then applied to test individual differences between each of the reproductive stages of the char collected (Table 11 to Table 13).

Table 10. Independent samples t-test probabilities comparing male versus female $\delta^{15}N$ values of each tissue examined in each of the time periods collected. Boxed areas cover probabilities of tests that were significantly different. Bold numbers represent probabilities where length was not used as a covariate.

run	month	n	gi tract P	liver P	gonads P	ventral muscle P	dorsal muscle P	carcass P
summer								
(non)	Sept	5	0.273	0.462	na	0.435	0.647	0.298
(pre)	June	29	0.787	0.316	0.409	0.489	0.577	0.801
(pre)	July	na	na	na	na	na	na	na
(spawn)	Sept	7	na	na	na	na	**0.032**	na
(post)	Sept	18	na	na	na	na	**0.566**	na
(non)	May	5	0.649	0.701	na	0.486	**0.639**	0.720
fall								
(post)	Oct	3	na	na	na	na	na	na

Table 11. Matrix of tukey pairwise probabilities comparing $\delta^{15}N$ values in each collection period of the dorsal muscle of female char. Boxed areas cover probabilities of tests that were significantly different.

tissue	run	month	(non-) Sept	(pre-) June	(pre-) July	(spawn) Sept	(post-) Sept	(non-) May
dorsal	(non-)	Sept	1					
muscle	(pre-)	June	0.048	1				
	(pre-)	July	0.157	0.951	1			
	(spawn)	Sept	0.876	0.948	0.999	1		
	(post-)	Sept	0.012	0.955	0.542	0.698	1	
	(non-)	May	0.002	0.538	0.157	0.876	0.951	1

Table 12. Matrix of tukey pairwise probabilities comparing δ ^{15}N values in each collection period of the dorsal muscle of male char. Boxed areas cover probabilities of tests that were significantly different.

				summer				fall
			(non)	(pre)	(spawn)	(post)	(non)	(post)
tissue	run	month	Sept	June	Sept	Sept	May	Sept
dorsal	summer							
muscle	(non)	Sept	1					
	(pre)	June	0.000	1				
	(spawn)	Sept	0.007	0.949	1			
	(post)	Sept	0.000	0.967	0.999	1		
	(non)	May	0.033	1.000	0.997	1.000	1	
	fall							
	(post)	Oct	0.114	0.957	1.000	0.996	0.991	1

Table 13. Matrix of tukey pairwise probabilities comparing $\delta^{15}N$ values in each collection period of the tissues examined of male and female (combined) char. Boxed areas cover probabilities of tests that were significantly different. Bold numbers represent probabilities where length was not used as a covariate.

				summer					fall
			(non)	(pre)	(pre)	(spawn)	(post)	(non)	(post)
tissue	run	month	Sept	June	July	Sept	Sept	May	Sept
gi tract	summer								
	(non)	Sept	1						
	(pre)	June	0.069	1					
	(pre)	July	0.002	0.726	1				
	(spawn)	Sept	0.562	0.999	0.747	1			
	(post)	Sept	0.907	0.773	0.136	0.989	1		
	(non)	May	0.000	0.021	0.243	0.073	0.003	1	
	fall								
	(post)	Oct	0.164	0.961	1.000	0.915	0.581	0.930	1
liver	summer								
	(non)	Sept	1						
	(pre)	June	0.120	1					
	(pre)	July	0.358	0.942	1				
	(spawn)	Sept	0.985	0.864	0.994	1			
	(post)	Sept	0.793	0.966	1.000	1.000	1		
	(non)	May	0.001	0.224	0.015	0.077	0.091	1	
	fall								
	(post)	Oct	0.018	0.368	0.139	0.135	0.182	0.988	1
ventral	summer								
muscle	(non)	Sept	1						
	(pre)	June	0.071	1					
	(pre)	July	0.695	1.000	1				
	(spawn)	Sept	0.716	0.986	1.000	1			
	(post)	Sept	0.649	0.967	1.000	1.000	1		
	(non)	May	0.007	0.514	0.849	0.489	0.198	1	
	fall								
	(post)	Oct	0.619	1.000	1.000	0.998	0.999	0.943	1

Table 13. Continued

carcass	summer								
	(non)	Sept	1						
	(pre)	June	0.260	1					
	(pre)	July	0.965	0.682	1				
	(spawn)	Sept	0.763	0.999	0.984	1			
	(post)	Sept	0.432	1.000	0.851	1.000	1		
	(non)	May	0.037	0.955	0.151	0.850	0.926	1	
	fall								
	(post)	Oct	0.150	0.878	0.333	0.764	0.843	0.994	1

A timeline of $\delta^{15}N$ values was made for prespawning, spawning, and postspawning char (Figure 10). The range of $\delta^{15}N$ values was from 15.3 ‰ to 17 ‰ prior to spawning and 15 ‰ to 16 ‰ after spawning. All tissues $\delta^{15}N$ values except gonads remained constant through time. The gonads $\delta^{15}N$ values decreased about 1.3 ‰ prior to spawning. No significant patterns can be recognized regarding the fractionation of isotopes among the tissues.

Freshwater-marine gradient

In order to construct a marine versus freshwater gradient (Figure 11), other aquatic species were also analyzed. For freshwater stable isotopic signals, 6 Heptageniidae, 6 Tipulidae, and 6 Chloroperlidae were analyzed and had mean (standard deviation) $\delta^{13}C$ values of -41.8 (4.2), -34.8 (2.1), and -37.1 (0.8) ‰, respectively. Mean (standard deviation) $\delta^{15}N$ values for the same invertebrates were 5.1(0.3), 1.4 (0.4), and 5.8 (0.7) ‰, respectively. For marine isotopic signals 12 Osmeridae and 12 Clupeidae were analyzed and had mean (standard deviation) $\delta^{13}C$ values of -21.6 (0.4) ‰ and -20.4 (0.9) ‰, respectively. Twelve Arctic grayling were also analyzed having a mean (standard deviation) $\delta^{13}C$ value of -7.2 (0.4) ‰ and a mean (standard deviation) $\delta^{15}N$ value of 8.7 (0.3) ‰. For the purpose of the freshwater versus marine analysis, all adult char were averaged to obtain a mean (standard deviation) $\delta^{13}C$ value of -17.0 (0.5) ‰ and $\delta^{15}N$

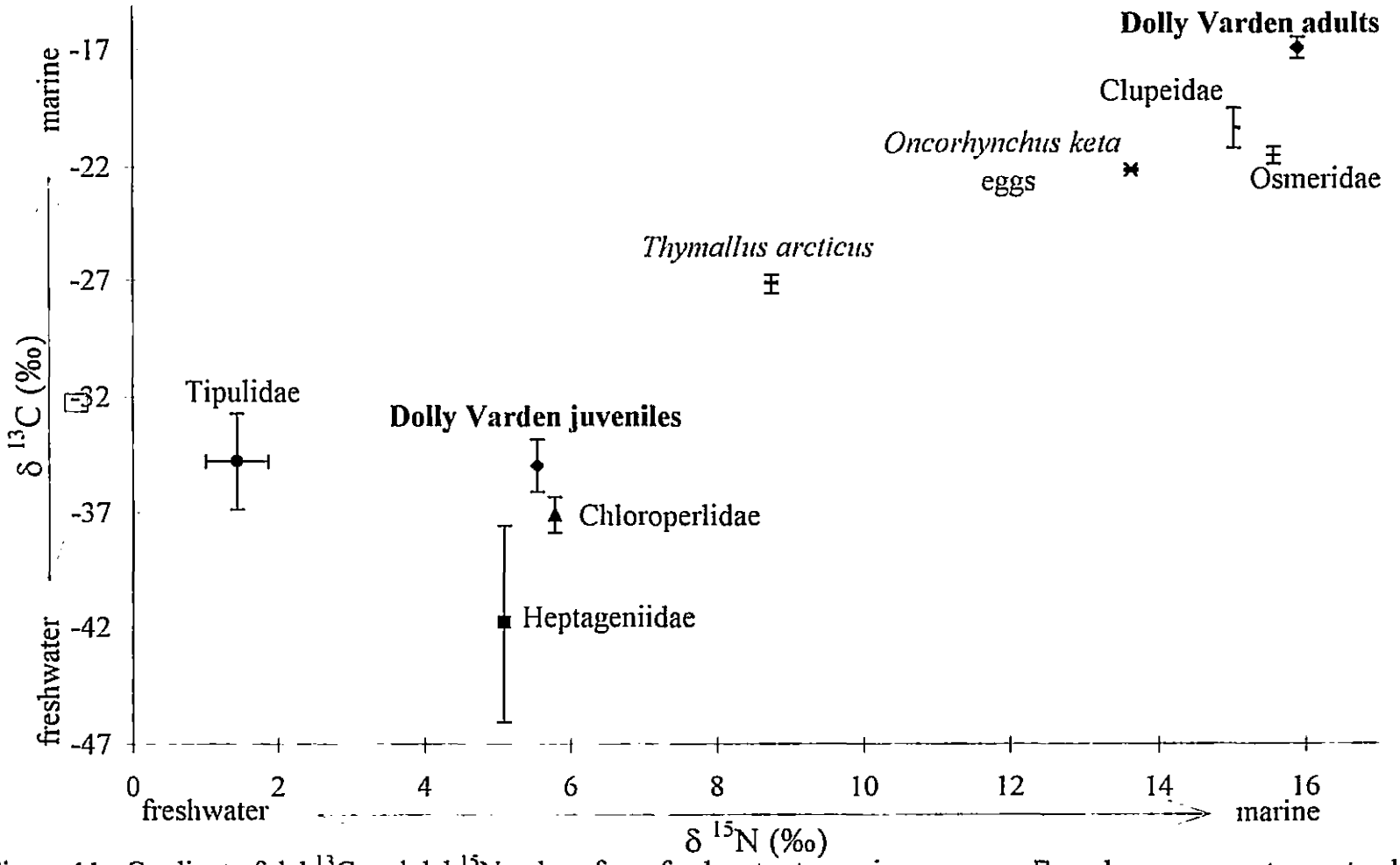

Figure 11. Gradient of del ^{13}C and del ^{15}N values from freshwater to marine sources. Error bars represent one standard deviation.

value of 15.9 (0.5) ‰. Dolly varden parr collected in freshwater had a mean (standard deviation) $\delta^{13}C$ value of -35.0 (1.1) ‰ and mean (standard deviation) $\delta^{15}N$ value of 5.5 (0.4) ‰. Chum eggs found in the gi tract of adult char were also analyzed and had a mean (standard deviation) $\delta^{13}C$ value of -22.2 (0.1) ‰ and mean (standard deviation) $\delta^{15}N$ value of 13.6 (0.1) ‰.

Proximate Analysis

Proximate analyses were determined for each tissue of char from each of the time periods collected in this study. Analyses of percent lipid, protein, water, and ash values are reported as separate sections. Overall repeatability of the proximate analysis was determined by summing the proximate components of each tissue of each fish. A completely accurate analysis should render 100 percent of the proximate composition. For 230 analyses, the mean was 103 percent with a standard deviation of 5 percent. This suggests excellent reproducibility of these results and allows conclusions to be made with confidence that inherent error of the procedures was low.

Lipid

Table 14 reports the mean lipid proportions for tissues examined from each collection period. Ranges of the means from each collection period were: gi tract (0.01 - 0.22), liver (0.02 - 0.21), gonads (0.01 - 0.07), ventral muscle (0.03 - 0.26),

Table 14. Mean lipid proportion of males and females in each period sampled. Sample sizes are also reported where male sample sizes are in parentheses.

			gi tract mean		liver mean		gonads mean		ventral muscle mean		dorsal muscle mean		carcass mean	
run	month	n (males)	f	m	f	m	f	m	f	m	f	m	f	m
summer														
(non)	Sept	12(13)	0.215	0.185	0.193	0.209	0.055	na	0.237	0.255	0.056	0.060	0.186	0.190
(pre)	June	4(4)	0.045	0.012	0.037	0.026	0.060	0.012	0.080	0.043	0.034	0.022	0.108	0.047
(pre)	July	13(0)	0.047		0.045		0.067		0.259		0.046		0.113	
(spawn)	Sept	16(14)	0.040	0.050	0.040	0.126	0.064	0.013	0.091	0.128	0.025	0.047	0.100	0.123
(post)	Sept	9(9)	0.020	0.029	0.019	0.036	0.024	0.019	0.025	0.045	0.031	0.022	0.049	0.058
(non)	May	6(3)	0.024	0.037	0.027	0.080	0.031	0.019	0.029	0.089	0.017	0.029	0.054	0.104
fall														
(post)	Oct	0(3)		0.027		0.039		0.025		0.035		0.020		0.038

dorsal muscle (0.02 - 0.06), and carcass (0.04 - 0.19). Ranges of the standard deviations from each time period were: gi tract (0.02 - 0.04), liver (0.04 - 0.05), gonads (0.01 - 0.04), ventral muscle (0.04 - 0.06), dorsal muscle (0.04 - 0.07), and carcass (0.02 - 0.04).

Among the tissues examined, the liver, gonads, and ventral muscle each had at least one collection period where male and female lipid concentrations were significantly different (Table 15). Males and females were separated for these three tissues in all further analysis. Length was used as a covariate in all tests except dorsal muscle from September nonspawners and June prespawners where length was found not to be a significant determinant of lipid concentrations. July prespawners and fall-run char were not included in the test because only one sex of fish was collected.

Analysis of covariance tests using length as a covariate were applied to test for differences between time periods. In cases where length was found not to be a significant determinant, analyses of variance were used. There were no significant differences among collection periods of male gonad lipid concentrations ($\alpha = 0.05$, $p = 0.130$). Significant differences among collection periods were found in all other tissues ($\alpha = 0.05$ and $p = 0.000$ in all tests). Tukey pairwise comparison tests were then applied to test individual differences between each of the reproductive stages of the char collected (Table 16 to Table 18).

Table 15. Analysis of covariance and independent samples t-test probabilities comparing male versus female lipid proportion of each tissue examined in each of the time periods collected. Boxed areas cover probabilities of tests that were significantly different. Bold numbers represent probabilities where length was not used as a covariate.

run	month	n	gi tract P	liver P	gonads P	ventral muscle P	dorsal muscle P	carcass P
summer								
(non)	Sept	25	0.156	0.452	na	0.482	**0.580**	0.933
(pre)	June	30	0.223	0.000	0.000	**0.010**	0.057	0.145
(pre)	July	na	na	na	na	na	na	na
(spawn)	Sept	7	0.408	0.400	0.005	0.489	0.647	0.524
(post)	Sept	18	0.084	0.004	0.275	0.053	0.459	0.398
(non)	May	8	0.920	0.122	na	0.212	0.617	0.340
fall								
(post)	Oct	3	na	na	na	na	na	na

Table 16. Matrix of Tukey pairwise probabilities comparing lipid content in each collection period of each tissue examined of female char. Boxed areas cover probabilities of tests that were significantly different.

tissue	run	month	(non-) Sept	(pre-) June	(pre-) July	(spawn) Sept	(post-) Sept	(non-) May
liver	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(pre-)	July	0.000	0.992	1			
	(spawn)	Sept	0.000	0.955	0.997	1		
	(post-)	Sept	0.000	0.066	0.147	0.796	1	
	(non-)	May	0.000	0.372	0.624	0.965	0.996	1
gonads	(non-)	Sept	1					
	(pre-)	June	0.161	1				
	(pre-)	July	0.299	0.995	1			
	(spawn)	Sept	0.996	0.780	0.923	1		
	(post-)	Sept	0.000	0.000	0.000	0.000	1	
	(non-)	May	0.000	0.000	0.000	0.000	0.958	1
ventral muscle	(non-)	Sept	1					
	(pre-)	June	0.986	1				
	(pre-)	July	0.000	0.000	1			
	(spawn)	Sept	0.000	0.000	0.988	1		
	(post-)	Sept	0.000	0.000	0.000	0.080	1	
	(non-)	May	0.000	0.000	0.003	0.177	1.000	1

Table 17. Matrix of Tukey pairwise probabilities comparing lipid content in each collection period of each tissue examined of male char. Boxed areas cover probabilities of tests that were significantly different.

				summer				fall
			(non-)	(pre-)	(spawn)	(post-)	(non-)	(post-)
tissue	run	month	Sept	July	Sept	Sept	May	Sept
liver	summer							
	(non-)	Sept	1					
	(pre-)	July	0.008	1				
	(spawn)	Sept	0.001	0.069	1			
	(post-)	Sept	0.000	0.013	0.999	1		
	(non-)	May	0.013	0.665	0.979	0.994	1	
	fall							
	(post-)	Oct	0.047	0.617	1.000	1.000	0.999	1
ventral	summer							
muscle	(non-)	Sept	1					
	(pre-)	July	0.000	1				
	(spawn)	Sept	0.000	0.090	1			
	(post-)	Sept	0.000	0.004	1.000	1		
	(non-)	May	0.000	0.809	0.849	0.737	1	
	fall							
	(post-)	Oct	0.001	0.445	1.000	1.000	0.923	1

Table 18. Matrix of Tukey pairwise probabilities comparing lipid content in each collection period of each tissue examined of male and female (combined) char. Boxed areas cover probabilities of tests that were significantly different.

				summer					fall
			(non-)	(pre-)	(pre-)	(spawn)	(post-)	(non-)	(post-)
tissue	run	month	Sept	June	July	Sept	Sept	May	Sept
gi tract	summer								
	(non-)	Sept	1						
	(pre-)	June	0.000	1					
	(pre-)	July	0.000	1.000	1				
	(spawn)	Sept	0.000	0.948	0.945	1			
	(post-)	Sept	0.000	0.551	0.347	0.999	1		
	(non-)	May	0.000	0.746	0.708	1.000	1.000	1	
	fall								
	(post-)	Oct	0.000	0.996	0.998	1.000	1.000	1.000	1
dorsal muscle	summer								
	(non-)	Sept	1						
	(pre-)	June	0.733	1					
	(pre-)	July	0.002	0.782	1				
	(spawn)	Sept	0.025	0.635	0.991	1			
	(post-)	Sept	0.000	0.215	0.798	1.000	1		
	(non-)	May	0.000	0.130	0.554	0.988	0.995	1	
	fall								
	(post-)	Oct	0.000	0.215	0.992	1.000	1.000	1.000	1
carcass	summer								
	(non-)	Sept	1						
	(pre-)	June	0.000	1					
	(pre-)	July	0.000	1.000	1				
	(spawn)	Sept	0.000	0.304	0.259	1			
	(post-)	Sept	0.000	0.000	0.000	0.491	1		
	(non-)	May	0.000	0.009	0.006	0.929	0.996	1	
	fall								
	(post-)	Oct	0.000	0.196	0.206	0.801	0.996	0.980	1

Protein

Table 19 reports the mean protein proportions for tissues examined from each run. Ranges of the means from each time period were: gi tract (0.14 - 0.36), liver (0.13 - 0.44), gonads (0.14 - 0.33), ventral muscle (0.15 - 0.44), dorsal muscle (0.19 - 0.28), and carcass (0.17 - 0.39). Ranges of the standard deviations from each time period were: gi tract (0.02 - 0.05), liver (0.05 - 0.07), gonads (0.01 - 0.09), ventral muscle (0.04 - 0.05), dorsal muscle (0.02 - 0.03), and carcass (0.01 - 0.02).

Among the tissues examined, the gonads had at least one collection period where male and female protein concentrations were significantly different (Table 20). Male and female gonads, however, were not separated due to such a small sample size of males. Length was used as a covariate in all tests except ventral muscle from prespawners (summer-run) collected in June where length was found not to be a significant determinant of protein concentrations. July prespawners and fall-run char were not included in the test because only one sex of fish was collected.

Analysis of covariance tests using length as a covariate were applied to test for differences between time periods. In cases where length was found not to be a significant determinant, analyses of variance were used. There were significant protein concentration differences among collection periods of all tissues ($\alpha = 0.05$,

Table 19. Mean protein proportion of males and females in each period sampled. Sample sizes are also reported where male sample sizes are in parentheses.

			gi tract mean		liver mean		gonads mean		ventral muscle mean		dorsal muscle mean		carcass mean	
run	month	n (males)	f	m	f	m	f	m	f	m	f	m	f	m
summer														
(non)	Sept	12(13)	0.332	0.363	0.443	0.362	0.212	na	0.436	0.431	0.284	0.264	0.391	0.357
(pre)	June	16(14)	0.215	0.197	0.230	0.298	0.315	0.143	0.279	0.351	0.226	0.240	0.250	0.302
(pre)	July	13(0)	0.170		0.181		0.270		0.149		0.203		0.172	
(spawn)	Sept	4(4)	0.266	0.136	0.227	0.172	0.330	0.151	0.326	0.211	0.207	0.202	0.300	0.195
(post)	Sept	9(9)	0.164	0.167	0.134	0.197	0.153	0.158	0.221	0.181	0.185	0.191	0.245	0.191
(non)	May	6(3)	0.186	0.180	0.201	0.243	0.175	na	0.212	0.236	0.192	0.224	0.248	0.253
fall														
(post)	Oct	0(3)		0.222		0.203		0.301		0.206		0.219		0.197

Table 20. Analysis of covariance and independent samples t-test probabilities comparing male versus female protein proportion of each tissue examined in each of the time periods collected. Boxed areas cover probabilities of tests that were significantly different. Bold numbers represent probabilities where length was not used as a covariate.

run	month	n	gi tract P	liver P	gonads P	ventral muscle P	dorsal muscle P	carcass P
summer								
(non)	Sept	5	0.818	0.133	0.000	0.793	0.296	0.281
(pre)	June	6	0.590	0.055	0.017	**0.198**	0.190	0.435
(pre)	July	na	na	na	na	na	na	na
(spawn)	Sept	7	na	na	na	na	0.778	na
(post)	Sept	18	na	na	na	na	0.477	na
(non)	May	5	0.743	0.179	na	0.505	0.631	0.906
fall								
(post)	Oct	3	na	na	na	na	na	na

p [gonads] = 0.017, p [all other tissues] = 0.000). Tukey pairwise comparison tests were then applied to test individual differences between each of the reproductive stages of the char collected (Table 21).

Water

Table 22 reports the mean water proportions for tissues examined from each run. Ranges of the means from each time period were: gi tract (0.57 - 0.83), liver (0.65 - 0.81), gonads (0.62 - 0.84), ventral muscle (0.53 - 0.80), dorsal muscle (0.70 - 0.80), and carcass (0.58 - 0.77). Ranges of the standard deviations from each time period were: gi tract (0.01 - 0.05), liver (0.04 - 0.05), gonads (0.01 - 0.01), ventral muscle (0.04 - 0.05), dorsal muscle (0.02 - 0.03), and carcass (0.02 - 0.04).

Among the tissues examined, each tissue except the carcass had at least one collection period where male and female lipid concentrations were significantly different (Table 23). Males and females were separated for further analysis of these tissues. Length was used as a covariate in all tests except the gi tract from June summer-run prespawners and the liver from May nonspawning char where length was found not to be a significant determinant of water concentrations. July prespawners and fall-run char were not included in the test because only one sex of fish was collected.

Table 21. Matrix of Tukey pairwise probabilities comparing protein content in each collection period of each tissue examined of female and male (combined) char. Boxed areas cover probabilities of tests that were significantly different.

				summer					fall
			(non-)	(pre-)	(pre-)	(spawn)	(post-)	(non-)	(post-)
tissue	run	month	Sept	June	July	Sept	Sept	May	Sept
gi tract	summer								
	(non-)	Sept	1						
	(pre-)	June	0.000	1					
	(pre-)	July	0.000	0.352	1				
	(spawn)	Sept	0.001	0.740	1.000	1			
	(post-)	Sept	0.000	1.000	0.486	0.732	1		
	(non-)	May	0.000	1.000	0.793	0.933	0.993	1	
	fall								
	(post-)	Oct	0.054	0.578	0.991	0.996	0.566	0.782	1
liver	summer								
	(non-)	Sept	1						
	(pre-)	June	0.000	1					
	(pre-)	July	0.000	0.017	1				
	(spawn)	Sept	0.000	0.990	0.747	1			
	(post-)	Sept	0.000	0.926	0.023	0.840	1		
	(non-)	May	0.000	0.702	0.733	1.000	0.351	1	
	fall								
	(post-)	Oct	0.004	0.995	0.946	1.000	0.912	1.000	1
gonads	summer								
	(non-)	Sept	1						
	(pre-)	June	0.758	1					
	(pre-)	July	0.932	0.999	1				
	(spawn)	Sept	0.998	0.986	1.000	1			
	(post-)	Sept	0.878	0.028	0.116	0.556	1		
	(non-)	May	0.984	0.105	0.312	0.811	0.999	1	
	fall								
	(post-)	Oct	0.800	0.997	0.985	0.959	0.226	0.386	1

Table 21. Continued.

ventral muscle	summer (non-)	Sept	1					
	(pre-)	June	0.002	1				
	(pre-)	July	0.012	0.153	1			
	(spawn)	Sept	0.023	0.525	0.981	1		
	(post-)	Sept	0.001	0.951	0.200	0.857	1	
	(non-)	May	0.000	0.857	0.196	0.925	1.000	1
	fall (post-)	Oct	0.016	0.985	0.613	0.951	1.000	1.000
dorsal muscle	summer (non-)	Sept	1					
	(pre-)	June	0.000	1				
	(pre-)	July	0.002	0.319	1			
	(spawn)	Sept	0.001	1.000	0.589	1		
	(post-)	Sept	0.000	0.931	0.004	0.961	1	
	(non-)	May	0.000	0.999	0.241	0.999	0.999	1
	fall (post-)	Oct	0.782	1.000	1.000	1.000	0.986	0.997
carcass	summer (non-)	Sept	1					
	(pre-)	June	0.000	1				
	(pre-)	July	0.004	0.001	1			
	(spawn)	Sept	0.013	0.341	0.991	1		
	(post-)	Sept	0.002	0.337	0.831	1.000	1	
	(non-)	May	0.005	0.015	0.998	1.000	0.978	1
	fall (post-)	Oct	0.007	1.000	0.609	0.927	0.985	0.847

Table 22. Mean water proportion of males and females in each period sampled. Sample sizes are also reported where male sample sizes are in parentheses.

			gi tract mean		liver mean		gonads mean		ventral muscle mean		dorsal muscle mean		carcass mean	
run	month	n (males)	f	m	f	m	f	m	f	m	f	m	f	m
summer														
(non)	Sept	12(13)	0.565	0.604	0.572	0.547	0.773	0.726	0.551	0.528	0.696	0.720	0.575	0.578
(pre)	June	16(14)	0.757	0.759	0.744	0.649	0.655	0.821	0.694	0.651	0.752	0.727	0.661	0.658
(pre)	July	13(0)	0.748		0.736		0.615		0.561		0.732		0.644	
(spawn)	Sept	4(4)	0.768	0.831	0.780	0.795	0.631	0.846	0.743	0.804	0.771	0.787	0.670	0.760
(post)	Sept	9(9)	0.832	0.820	0.811	0.770	0.836	0.822	0.799	0.779	0.793	0.795	0.713	0.728
(non)	May	6(3)	0.799	0.784	0.781	0.710	0.809	0.793	0.793	0.711	0.803	0.767	0.721	0.654
fall														
(post)	Oct	0(3)		0.777		0.771		0.720		0.794		0.777		0.766

Table 23. Analysis of covariance and independent samples t-test probabilities comparing male versus female water proportion of each tissue examined in each of the time periods collected. Boxed areas cover probabilities of tests that were significantly different. Bold numbers represent probabilities where length was not used as a covariate.

run	month	n	gi tract P	liver P	gonads P	ventral muscle P	dorsal muscle P	carcass P
summer								
(non)	Sept	25	0.016	0.251	0.010	0.211	0.302	0.471
(pre)	June	30	**0.718**	0.000	0.000	0.026	0.011	0.882
(pre)	July	na	na	na	na	na	na	na
(spawn)	Sept	7	0.526	0.565	0.000	0.635	0.987	0.526
(post)	Sept	18	0.095	0.007	0.095	0.136	0.990	0.457
(non)	May	8	0.861	**0.025**	0.104	0.135	0.757	0.161
fall								
(post)	Oct	3	na	na	na	na	na	na

Analysis of covariance tests using length as a covariate were applied to test for differences between collection periods. In cases where length was found not to be a significant determinant, analyses of variance were used. There were significant differences in water concentrations among collection periods in all tissues examined ($\alpha = 0.05$ and $p = 0.000$ in all tests). Tukey pairwise comparison tests were then applied to test individual differences between each of the reproductive stages of the char collected (Table 24 to Table 26).

Ash

Table 27 reports the mean ash proportions for tissues examined from each run. Ranges of the means from each time period were: gi tract (0.006 - 0.012), liver (0.007 - 0.019), gonads (0.008 - 0.031), ventral muscle (0.004 - 0.008), dorsal muscle (0.009 - 0.015), and carcass (0.022 - 0.036). Ranges of the standard deviations from each time period were: gi tract (0.001 - 0.002), liver (0.002 - 0.002), gonads (0.002 - 0.004), ventral muscle (0.001 - 0.002), dorsal muscle (0.003 - 0.003), and carcass (0.004 - 0.005).

Among the tissues examined, liver and gonads each had at least one collection period where male and female ash concentrations were significantly different (Table 28). For further analysis, male and female tissues were separated. Length was used as a covariate in all tests except ventral muscle from June summer-run prespawners, where length was found not to be a significant

Table 24. Matrix of Tukey pairwise probabilities comparing water content in each collection period of each tissue examined of female char. Boxed areas cover probabilities of tests that were significantly different.

tissue	run	month	(non-) Sept	(pre-) June	(pre-) July	(spawn) Sept	(post-) Sept	(non-) May
gi tract	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(pre-)	July	0.000	0.962	1			
	(spawn)	Sept	0.000	0.788	0.971	1		
	(post-)	Sept	0.000	0.000	0.000	0.002	1	
	(non-)	May	0.000	0.003	0.014	0.429	0.174	1
liver	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(pre-)	July	0.000	0.982	1			
	(spawn)	Sept	0.000	0.083	0.188	1		
	(post-)	Sept	0.000	0.000	0.000	0.436	1	
	(non-)	May	0.000	0.026	0.074	1.000	0.307	1
gonads	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(pre-)	July	0.000	0.000	1			
	(spawn)	Sept	0.000	0.563	0.244	1		
	(post-)	Sept	0.000	0.000	0.000	0.000	1	
	(non-)	May	0.001	0.000	0.000	0.000	0.128	1
ventral	(non-)	Sept	1					
muscle	(pre-)	June	0.999	1				
	(pre-)	July	0.000	0.014	1			
	(spawn)	Sept	0.000	0.002	0.287	1		
	(post-)	Sept	0.000	0.000	0.000	0.090	1	
	(non-)	May	0.000	0.000	0.000	0.311	0.991	1
dorsal	(non-)	Sept	1					
muscle	(pre-)	June	0.310	1				
	(pre-)	July	0.017	0.872	1			
	(spawn)	Sept	0.036	0.587	0.947	1		
	(post-)	Sept	0.000	0.036	0.238	0.983	1	
	(non-)	May	0.000	0.021	0.151	0.858	0.991	1

Table 25. Matrix of Tukey pairwise probabilities comparing water content in each collection period of each tissue examined of male char. Boxed areas cover probabilities of tests that were significantly different.

				summer				fall
			(non-)	(pre-)	(spawn)	(post-)	(non-)	(post-)
tissue	run	month	Sept	July	Sept	Sept	May	Sept
gi tract	summer							
	(non-)	Sept	1					
	(pre-)	July	0.000	1				
	(spawn)	Sept	0.000	0.013	1			
	(post-)	Sept	0.000	0.001	0.995	1		
	(non-)	May	0.000	0.000	0.467	0.540	1	
	fall							
	(post-)	Oct	0.000	0.995	0.676	0.786	1.000	1
liver	summer							
	(non-)	Sept	1					
	(pre-)	July	0.000	1				
	(spawn)	Sept	0.000	0.001	1			
	(post-)	Sept	0.000	0.000	0.980	1		
	(non-)	May	0.000	0.434	0.349	0.497	1	
	fall							
	(post-)	Oct	0.002	0.222	0.999	1.000	0.906	1
gonads	summer							
	(non-)	Sept	1					
	(pre-)	July	0.000	1				
	(spawn)	Sept	0.001	0.928	1			
	(post-)	Sept	0.000	1.000	0.976	1		
	(non-)	May	0.069	0.940	0.759	0.900	1	
	fall							
	(post-)	Oct	0.999	0.025	0.016	0.025	0.274	1

Table 25. Continued.

ventral	summer							
muscle	(non-)	Sept	1					
	(pre-)	July	0.000	1				
	(spawn)	Sept	0.000	0.000	1			
	(post-)	Sept	0.000	0.000	0.877	1		
	(non-)	May	0.000	0.060	0.570	0.883	1	
	fall							
	(post-)	Oct	0.000	0.015	1.000	0.998	0.893	1
dorsal	summer							
muscle	(non-)	Sept	1					
	(pre-)	July	0.982	1				
	(spawn)	Sept	0.020	0.034	1			
	(post-)	Sept	0.000	0.000	1.000	1		
	(non-)	May	0.044	0.107	1.000	1.000	1	
	fall							
	(post-)	Oct	0.418	0.564	0.999	0.995	1.000	1

Table 26. Matrix of Tukey pairwise probabilities comparing water content in each collection period of each tissue examined of female and male (combined) char. Boxed areas cover probabilities of tests that were significantly different.

				summer					fall
			(non-)	(pre-)	(pre-)	(spawn)	(post-)	(non-)	(post-)
tissue	run	month	Sept	June	July	Sept	Sept	May	Sept
gi tract	summer								
	(non-)	Sept	1						
	(pre-)	June	0.000	1					
	(pre-)	July	0.000	0.840	1				
	(spawn)	Sept	0.000	0.002	0.008	1			
	(post-)	Sept	0.000	0.000	0.000	0.946	1		
	(non-)	May	0.000	0.000	0.002	1.000	0.994	1	
	fall								
	(post-)	Oct	0.000	0.010	0.026	0.640	0.861	0.749	1

Table 27. Mean ash proportion of males and females in each period sampled. Sample sizes are also reported where male sample sizes are in parentheses.

			gi tract mean		liver mean		gonads mean		ventral muscle mean		dorsal muscle mean		carcass mean	
run	month	n (males)	f	m	f	m	f	m	f	m	f	m	f	m
summer														
(non)	Sept	12(13)	0.006	0.007	0.007	0.008	0.008	na	0.007	0.005	0.010	0.010	0.026	0.027
(pre)	June	4(4)	0.006	0.009	0.015	0.009	0.012	0.016	0.006	0.004	0.009	0.011	0.029	0.029
(pre)	July	13(0)	0.012		0.019		0.029		0.008		0.015		0.024	
(spawn)	Sept	16(14)	0.009	0.008	0.015	0.010	0.012	0.018	0.008	0.008	0.010	0.010	0.025	0.024
(post)	Sept	9(9)	0.008	0.008	0.012	0.008	0.006	0.019	0.007	0.008	0.010	0.010	0.034	0.027
(non)	May	6(3)	0.011	0.011	0.008	0.008	0.008	0.017	0.007	0.007	0.011	0.011	0.036	0.028
fall														
(post)	Oct	0(3)		0.008		0.007		0.031		0.004		0.012		0.022

Table 28. Analysis of covariance and independent samples t-test probabilities comparing male versus female ash proportion of each tissue examined in each of the time periods collected. Boxed areas cover probabilities of tests that were significantly different. Bold numbers represent probabilities where length was not used as a covariate.

run	month	n	gi tract P	liver P	gonads P	ventral muscle P	dorsal muscle P	carcass P
summer								
(non)	Sept	25	0.698	0.569	na	0.310	0.508	0.566
(pre)	June	30	0.862	0.000	0.000	**0.873**	0.878	0.660
(pre)	July	na	na	na	na	na	na	na
(spawn)	Sept	7	0.583	0.413	0.092	0.299	0.322	0.641
(post)	Sept	18	0.921	0.052	0.000	0.501	0.621	0.063
(non)	May	8	0.855	0.503	na	0.473	0.706	0.074
fall								
(post)	Oct	3	na	na	na	na	na	na

determinant of ash concentrations. July prespawners and fall-run char were not included in the test because only one sex of fish was collected.

Analyses of covariance tests using length as a covariate were applied to test for differences between time periods. In cases where length was found not to be a significant determinant, analyses of variance were used. There were no significant differences of ash concentration among collection periods of male livers and male and female (combined) ventral muscle ($\alpha = 0.05$, p [male liver]= 0.225, p [ventral muscle]= 0.068). Significant differences among collection periods were found in all other tissues ($\alpha = 0.05$; p [gi tract, carcass, and female liver] = 0.000, p [gonads] = 0.023, dorsal muscle] = 0.003). Tukey pairwise comparison tests were then applied to test individual differences between each of the reproductive stages of the char collected (Table 29 to Table 31).

Fecundity

Total fecundities ranged from 2862 eggs for a 465 mm female char to 6399 eggs in a 655 mm char. The mean fecundity of 24 females was 5224 eggs. Length was correlated to fecundity (p = 0.312).

Table 29. Matrix of Tukey pairwise probabilities comparing ash content in each collection period of each tissue examined of female char. Boxed areas cover probabilities of tests that were significantly different.

tissue	run	month	(non-) Sept	(pre-) June	(pre-) July	(spawn) Sept	(post-) Sept	(non-) May
liver	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(pre-)	July	0.000	0.001	1			
	(spawn)	Sept	0.001	0.156	1.000	1		
	(post-)	Sept	0.004	0.000	0.019	0.415	1	
	(non-)	May	0.994	0.000	0.000	0.008	0.132	1
gonads	(non-)	Sept	1					
	(pre-)	June	0.000	1				
	(pre-)	July	0.062	0.000	1			
	(spawn)	Sept	0.108	0.000	0.976	1		
	(post-)	Sept	0.904	0.000	0.002	0.012	1	
	(non-)	May	0.998	0.000	0.445	0.295	0.776	1

Table 30. Matrix of Tukey pairwise probabilities comparing ash content in each collection period of each tissue examined of male char. Boxed areas cover probabilities of tests that were significantly different.

				summer				fall
			(non-)	(pre-)	(spawn)	(post-)	(non-)	(post-)
tissue	run	month	Sept	July	Sept	Sept	May	Sept
gonads	summer							
	(non-)	Sept	1					
	(pre-)	July	na	1				
	(spawn)	Sept	na	0.960	1			
	(post-)	Sept	na	0.939	0.867	1		
	(non-)	May	na	na	na	na	1	
	fall							
	(post-)	Oct	na	0.017	0.026	0.034	na	1

Table 31. Matrix of Tukey pairwise probabilities comparing ash content in each collection period of each tissue examined of female and male (combined) char. Boxed areas cover probabilities of tests that were significantly different.

				summer					fall
			(non-)	(pre-)	(pre-)	(spawn)	(post-)	(non-)	(post-)
tissue	run	month	Sept	June	July	Sept	Sept	May	Sept
gi tract	summer								
	(non-)	Sept	1						
	(pre-)	June	0.000	1					
	(pre-)	July	0.022	0.021	1				
	(spawn)	Sept	0.995	0.006	0.747	1			
	(post-)	Sept	0.307	0.008	0.990	0.972	1		
	(non-)	May	0.000	0.999	0.164	0.038	0.067	1	
	fall								
	(post-)	Oct	1.000	0.602	0.998	1.000	1.000	0.753	1
dorsal muscle	summer								
	(non-)	Sept	1						
	(pre-)	June	0.002	1					
	(pre-)	July	1.000	0.002	1				
	(spawn)	Sept	1.000	0.017	1.000	1			
	(post-)	Sept	1.000	0.001	0.999	1.000	1		
	(non-)	May	0.999	0.060	0.999	0.998	0.990	1	
	fall								
	(post-)	Oct	0.999	0.928	0.999	0.998	0.996	1.000	1
carcass	summer								
	(non-)	Sept	1						
	(pre-)	June	0.929	1					
	(pre-)	July	0.830	1.000	1				
	(spawn)	Sept	0.977	0.694	0.558	1			
	(post-)	Sept	0.216	0.069	0.006	0.981	1		
	(non-)	May	0.026	0.008	0.001	0.536	0.795	1	
	fall								
	(post-)	Oct	0.993	1.000	1.000	0.947	0.791	0.474	1

Discussion

Biological Data

Gill raker counts of char in this study indicate that these are northern form Dolly Varden char. No differences in gill raker counts were found between the two runs. This conclusion, however, is suspect due to the low sample size of the fall-spawners.

Length-weight of fish caught in the various collection periods differed primarily due to the development and subsequent loss of gonads. However, the initial condition of individual runs feeding at different times or in different years also contributes to these differences.

Due to the excellent condition that the nonspawners caught in September were in at collection, it is not surprising to note that their length-weight relationship is significantly different from all other groups except July prespawners (Figure 3). July prespawners, however, were less than 630 mm, thus neglecting the larger fish which would be more affected by significant increases in weight from gonadal formation such as that seen in June prespawners.

The length-weight relationship of June prespawners was also significantly different from other collection periods except spawners. The length-weight relationship of these fish is positive due to the weight shifted towards gonad development until the eggs and sperm are expelled. The increased weight found in

the larger fish represents lipid and protein aquired at sea. Because energy has been more or less conserved by shifting to gonadal production, a similar length-weight relationship is seen in the spawners.

Length-weight relationships of all collection periods were significantly different from the July prespawners due to the limited size class data collected. By only representing a smaller portion of the population, the increased weight that occurs in the larger fish is not accounted for. It is believed that data from larger fish collected in July would amend the length-weight relationship and make it conform to the other prespawning relationships.

The length-weight relationship of postspawners was significantly different from all other collections of summer-run fish. This is due to extreme loss of weight when the eggs and sperm were released during spawning, therefore significantly dropping the length-weight regression line.

The length-weight relationship of September nonspawners is similar to that of the postspawners. The lack of gonadal tissue and loss of condition due to starvation lowers the slope of the length-weight regression, thus making it significantly different from char in better condition earlier in the year.

Significant differences were noted between males and females in each time period except May nonspawners. Since nonspawners collected in May have not spawned and could still be a year or two away from spawning, there is no need for

there to be differences between males and females. All other groups, however, are within the reproductive cycle. Male gonadal tissue weighs less and males develop more body size during maturation (including secondary sexual characteristics).

Indices Data

Due to the differential weights of the gonads, males and females were expected to have significantly different indices (Table 2). Dorsal muscle indices of males and females, however, were not significantly different which suggests a similar dependence on dorsal muscle by males and females for reproductive and metabolic demands.

Proportion indices for individual tissues were developed to elucidate trends of weight change within a char. Timelines of indices were also developed for each tissue. As will be seen, trends of weight proportions are not only dependent on the energy consumption within the fish, but also shifts in proximate consumption. Parker and Vanstone (1966) found that water uptake had the effect of maintaining the weight of a fish while the lipid and protein content decreased (Ziemann 1986). Gi tract weight declined from 3.0 to 1.5 percent of the fish prior to spawning as energy apparently shifted toward gonadal production. While most of this loss of weight is due to lipid and protein utilization, Jobling (1980) has reported data from other studies in which the gi tract and liver tissue were catabolized and atrophied during starvation. Visual inspection of the gi tracts and livers after significant

starvation revealed that they were extremely emaciated, suggesting that this phenomenon could possibly take place during char starvation periods.

The gi tract indices of male and female nonspawners collected in May were significantly from June prespawners, July prespawners, and spawners. After spawning, gi tract indices rebound because the energy spent spawning, migrating within the river, and overwintering is derived from the rest of the fish. May nonspawners were significantly different from postspawners and spawners. The extent of rebound after spawning was significantly greater for the char than the males. This suggests that the amount of energy put into reproduction is greater for females than males.

Male liver indices revealed similar results to the gi tract indices. A decreasing trend prior to spawning occurs which represents an average of one percent shift of energy stores to reproduction. However, female liver indices did not decrease prior to spawning, suggesting that females depend less on the liver for reproductive energy than other tissues. The female liver indices then decrease after spawning, suggesting that the liver is utilized for metabolic demands subsequent to spawning. Visual inspection of male and female livers through time revealed a smaller, darker tissue as opposed to a large creamy colored liver after feeding at sea. Similar appearances in the liver were reported by Hayashi and

Takagi (1977) of puffer (*Fugu vermiculare porphyreum*) during extended starvation.

Gonadal indices revealed a significant difference between the average proportional weight of male and female gonads. While female ovaries increased in weight to comprise over 20 percent of the total fish weight prior to spawning, male testes only increased to account for 4 percent of the total body weight. Female ovary indices were significantly different at every stage of development until after spawning (Table 3). Male indices, on the other hand, were not significantly different for two months prior to spawning (Table 4). Partial explanation for these data is that the average weight of the is much larger than for females before entering the reproductive cycle. Indices of 1-2 percent for both males and females after spawning represent residual gonadal tissue that may in fact be reabsorbed to compensate for energy lost due to migration and overwintering.

Proportion indices of ventral muscle decrease approximately three percent presumably in compensation for reproductive development. Male and female September nonspawner indices are therefore significantly larger than prespawners caught in June and females are significantly larger than prespawners caught in July (Table 3 and Table 4). Rebound of weight of the ventral muscle proportion is small, however, because of its role in providing energy for migration and overwintering. Therefore, collection periods after spawning are not significantly

different (Table 4). A slight trend can be seen which suggests that females depend more on ventral muscle for reproductive development than males (Figure 7).

Dorsal muscle indices decrease 20-25 percent during reproductive development. Male and female May nonspawners, June prespawners, and July prespawners are significantly different (Table 5). It is also suggested that a large portion of the depletion in dorsal muscle is needed for general metabolism requirements during migration and spawning. Both males and females rebound slowly as the dorsal muscle is still obligated for energy expenditure for migration and overwintering. Therefore, collection periods subsequent to spawning are not significantly different.

Carcass indices showed a 20-25 percent increase as spawning approached. Male and female May nonspawners are significantly smaller than prespawning char (Table 3, Table 4, and Figure 3). A possible explanation is the addition of structural weight from secondary sexual characteristics. This difference could also be illustrating the energetic expenditure of the fish for spawning and migration, which is not visible in the physical additions of gonad production. If this is the case, it shows a very small dependence on structural components (carcass) of char for reproductive development. The decrease in carcass weight of the spawners should be discussed. This could be caused from significant increases in energy expenditure of the fish immediately prior to spawning. It is more likely, however,

a function of small sample size and the fact that the females sampled at this time were small and therefore provided smaller ovaries.

Indices prior to spawning, except carcass and liver due to the lack of dependence on these tissues, are found not to be significantly different from those after spawning due to the rebound after spawning.

An energetic budget solely based on fish weight can be constructed based on the time series of proportion indices. June prespawners, spawners, and postspawners were used because they belong to the same stock of fish that fed and overwintered together. As the percentage of gonadal tissue weight increases, subsequent decreases take place in participating tissues. After spawning, gonad products are expelled allowing each tissue to become a larger portion of the whole fish. However, there is also loss due to metabolic demands of spawning that is represented by the net loss of weight of the fish. Separate budgets were constructed for males and females because of their previously discussed differences in energetic demands. The three collection periods were separated into the time prior to spawning and the time after spawning in order to examine the total increase in gonadal weight.

Mean loss of total female weight prior to spawning was 24.5 ± 7.0 percent. Mean gain in gonadal weight during the same time period prior to spawning was 15.1 ± 1.2 percent. The difference between weight gained and weight lost was -

9.4 ± 5.8 percent. This represents the energetic loss, with respect to weight, due to metabolic demands other than spawning. Maintenance, migration, and energy for spawning demands other than gonad development are included in this estimate. Therefore, from June until August, twice the amount of energy (in terms of weight loss) was used for gonad development than was used for the rest of the metabolic demands.

The total loss of female fish weight after spawning was 18.8 ± 2.6 percent. Total gain in tissue proportion due to the loss of the gonads was 20.6 ± 3.4 percent. There is no significant difference before and after spawning suggesting that this comparison accurately accounted for the amount of weight lost due to spawning. Because these char were caught within days of each other there should be no detectable energetic loss due to general metabolism.

Mean change of total male weight prior to spawning was 0.0 ± 0.7 percent. Mean gain in gonadal weight during the same time period prior to spawning was 4.3 ± 4.8 percent. Due to the large amount of error associated with this estimate, the difference between weight lost and gained may not be accurate. If the amount of weight loss is accurate, however, it suggests that only a small portion of the testes development occurs immediately prior to spawning. Similar discrepancies were found in comparing male weight differences before and after spawning. This

suggests that it will be necessary to look further into the energetic demands of the male char in this study.

Although these estimates are not quantitative due to sample size and the need to sacrifice fish, they allow for a qualitative description of the spawning requirements these female char possibly endure. By comparing male and female budgets, the significantly greater amount of energy used by the females is apparent. It is important to note that water uptake is a possible source of weight addition during starvation. The incorporation of freshwater isotope ratios was not, however, observed in this study. These estimates also assume that the fish were not feeding and have the same tissue composition and proportion. Further analysis of the components of the char that significantly alter the weight if the fish will add to the information extracted from the weight changes through time.

Stable Isotope Analysis

Stable isotope analysis was utilized to accomplish two goals. The first goal was to determine the sources of carbon and nitrogen, and therefore make assumptions as to the diets of these char. The second goal was to follow the fractionation of carbon and nitrogen isotopes in various tissues through time. Although differences were found between collection periods, all were grouped together for comparison with isotope ratios of other species.

Figure 11 shows very clearly that the adult Dolly Varden have a marine carbon and nitrogen isotope ratio. This suggests that the adult char in this study rely solely on marine sources for food and energetic requirements. Marine $\delta^{13}C$ values are consistent with other arctic marine stable isotope values. Dunton et al. (1989) reported values of Chukchi Sea vertebrate and invertebrate $\delta^{13}C$ and $\delta^{15}N$ values. In both cases, char in this study that most likely fed in the Chukchi Sea, are consistent with values of pelagic fish species as well as possible prey species. Fry and Sherr (1984) reported values of fish and zooplankton in the Bering Sea around -19 ‰ and -22.1 ‰ respectively. $\delta^{15}N$ values are reported for vertebrates and invertebrates in Barrow-Lancaster Sound and also encompass the nitrogen isotope values found in this study (Hobson and Welch 1992).

Only four char caught in this study were collected with gut contents in the stomach. One char had a gut full of Chloroperlidae. Due to the number (greater than 30) of invertebrates, this fish was actually preying on this species or had found a significant concentration. Two char that were caught in the lower Kugururok River were found preying on chum salmon eggs (Figure 11). These would therefore also present a marine isotope signal, thus confusing the issue of freshwater feeding. The fourth char was found with a juvenile Dolly Varden char in it's gut, suggesting cannibalism amongst these char. The fish that had cannibalized was found on the spawning grounds. It therefore could have eaten

the juvenile because of its aggressive behavior on the spawning grounds. If chum eggs and juvenile char were a common diet, there would be a change in $\delta^{13}C$ and $\delta^{15}N$ signals toward the freshwater end of the gradient. Since this is not the case and because the incidence of freshwater feeding seems to be so low, it is hypothesized that char are, like most fish, opportunistic feeders. Since the char are most often found in swift current or are engaged in spawning activities, this opportunity is expected to be insignificant. Excess energy is not spent feeding in freshwater, but if prey presents itself in front of the char, it will most likely feed. McCart et al. (1972) found that arctic char caught in the spring in the Ivishak River had marine isotopic compositions also suggesting that these fish do not actively feed in freshwater.

Juvenile Dolly Varden char collected from the Kugururok River had significantly freshwater carbon and nitrogen isotope ratios. Although the eggs from which these parr hatched had a marine carbon and nitrogen isotope signal, 1-2 months after hatching they had an overwhelming freshwater carbon and nitrogen composition. As can be seen from Figure 11, a combination of the three most common species of invertebrates, found in the same pools that the char were found, could very well make up the diet of juvenile char. This is further evidence that the adults are not feeding upon any freshwater food source. Summer-

spawners spent 20 months in freshwater, which provided plenty of time to feed in freshwater and for the isotope ratios within the fish to show it.

Also shown in Figure 11, Arctic grayling (*Thymallus arcticus*) lie between the marine and freshwater gradient. Their diet, which include both freshwater invertebrates and chum or Dolly Varden eggs, explains the isotopic ratios.

Tests for differences between Dolly Varden males and females revealed no significant differences for $\delta^{15}N$ and found only 1 significant difference for $\delta^{13}C$ comparisons. Further inspection of the significantly different male and female dorsal muscle revealed that this was most likely caused by a small sample size. It was therefore assumed that no significant differences were found.

In order to compare $\delta^{13}C$ and $\delta^{15}N$ ratios between collection periods, it must be assumed that they have encountered the same environment and therefore started with the same isotope ratios. Since the char in this study were collected in different years and locations they are from different feeding cohort, this assumption could not be made for all of the data collected. Only data from June prespawners, spawners, and postspawners are from the same feeding cohort and it can, therefore, be assumed that they fed in the same general area and thus would have similar initial isotope ratios from which to compare. Other collection periods could then be used for comparison and possibly represent changes in diet composition as ratios change.

As can be seen in Figure 10, $\delta^{13}C$ values do not change over time. No significant differences were found between the three periods before and after spawning. This information suggests that although energy is being transferred from tissues, there does not appear to be a respiration or loss of the lighter isotope. This contrasts other studies in which significant differences of $\delta^{13}C$ values were found, as in the case of gerbil *(Meriones unguienlatus)* tissues (Tieszen et al. 1983). It should, however, be noted that char in this study had been in freshwater for 1 to 20 months and therefore had already incorporated any energy gained from feeding at sea throughout its tissues.

Only two tissues had any significant differences between collection periods. The $\delta^{13}C$ values of the gonads of prespawners collected in July (-18.44 ‰) were significantly more depleted than from summer-run postspawners (-17.07 ‰), May nonspawners (-17.36 ‰), and fall-run postspawners (-16.21 ‰)(Table 8); this suggests that the July prespawners probably fed at a slightly different trophic level since they were feeding at sea during the summer of 1993. The rest of the summer-spawners fed at sea during 1994. The dorsal muscle $\delta^{13}C$ values of May nonspawners (-16.62 ‰) were significantly more depleted than from September nonspawners (-17.08 ‰) and June prespawners (-17.03 ‰). Just as before, this suggests that the nonspawners in September and May had a different diet

composition, whether it be due to different prey or different concentrations of particular species.

It was expected that the fractionation of isotopes would be different among the tissues. Significant differences were only found in the June prespawners, however. The carcass and dorsal muscle were significantly different from the gonads and liver. If this were a significant phenomenon it would be detected further in the starvation period. This was not the case for the tissues in this study. Also, because the values for Figure 10 represent lipid free tissue, variable lipid concentrations are not a factor.

As with $\delta^{13}C$ values, similar differences among collection periods were observed for $\delta^{15}N$ values (Table 12 and Table 13). Differences between May nonspawners and September nonspawners led to the same conclusions, which were that the original isotopic ratios of these fish were different. No significant differences were found between June prespawners, spawners, and postspawners. Therefore, just as was observed with the $\delta^{13}C$ timeline, no apparent fractionation through time is present for the tissues from these char even though they go through considerable energy expenditure during a long starvation period.

Significantly different $\delta^{15}N$ values were found among June prespawners and September postspawners (Table 13). Gonads from June prespawners were

significantly different from all other tissues. This suggests that the initial gonadal development is preferentially enriching the heavier nitrogen isotope in residual tissue. Postspawner dorsal muscle (16.03 ‰) was significantly different from the gi tract (15.08 ‰) and liver (15.16 ‰) δN^{15} values, suggesting a possible fractionation among tissues as the starvation period progresses.

Proximate Analysis

Lipid

Proximate analysis allows for refinement of what is known about the changes in weight due to reproductive development as well as starvation. During starvation periods, it has been found that lipid is the first major body component to be utilized (Love 1970; Jobling 1980; and Shearer 1994). Length was used in most cases as a predictor of lipid content in the char. It has been found that larger fish, such as Arctic char have a higher percentage of lipid than smaller fish from the same period (Ziemann 1986). Size of the fish, therefore, accounted for a significant amount of the differences between collection periods.

Differences between overall male and female lipid concentrations were expected due to the high lipid content of the ovaries. Significant differences between males and females were found between July prespawners, spawners, and postspawners (Table 15). In salmonids, females lose more somatic lipid and protein than males during sexual maturation (Love 1980). In this study, the lipid

content of the liver and ventral muscle significantly contributed to the gonadal development. Hardy et al. (1985) found that the protein and lipid content of farmed coho salmon decreased during starvation. Less than 10 percent of the lipid used went toward ovary development (Shearer 1994). Lipid content of the ovaries are significantly different from the testes, except however, in the residual gonadal tissue subsequent to spawning.

Male and female lipid content were not significantly different for the gi tract. Significant differences were found between collection periods for each tissue, thus illustrating the dependence char have on lipid for survival. Craig and Haldorson (1981) weighed lipid around the gi tract of Arctic cisco and found that this lipid was a good indicator of fish condition. Further analysis of gi tract lipid content with respect to whole fish lipid content, in this study, revealed a gradient of condition due to lipid content through time. Lipid content of the gi tract was high (20 percent) soon after feeding at sea (Figure 12). The lipid content of September nonspawners was significantly larger than any other time period (Table 18). In no other time period was gi tract lipid content significantly different from that of any other. Therefore, the contribution of the gi tract to gonadal formation is most significant during the initial stages of reproductive development. Metabolic demands are also very high during the first overwintering period when the fish begin starvation, migrate in the river, and perhaps continue a small amount

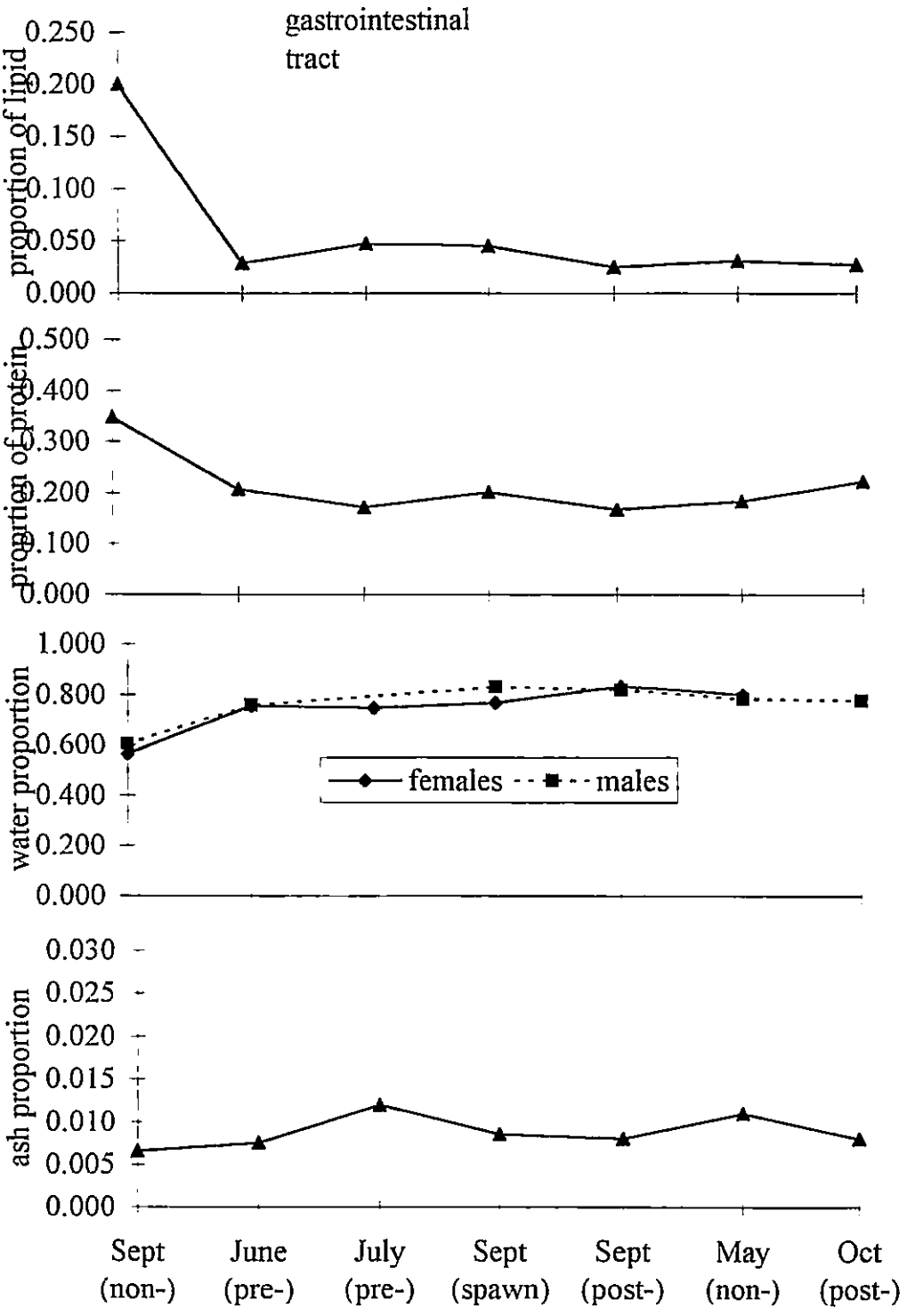

Figure 12. Timeline of proximate component proportions of the gi tract. Where both sexes are not reported, the total means are reported.

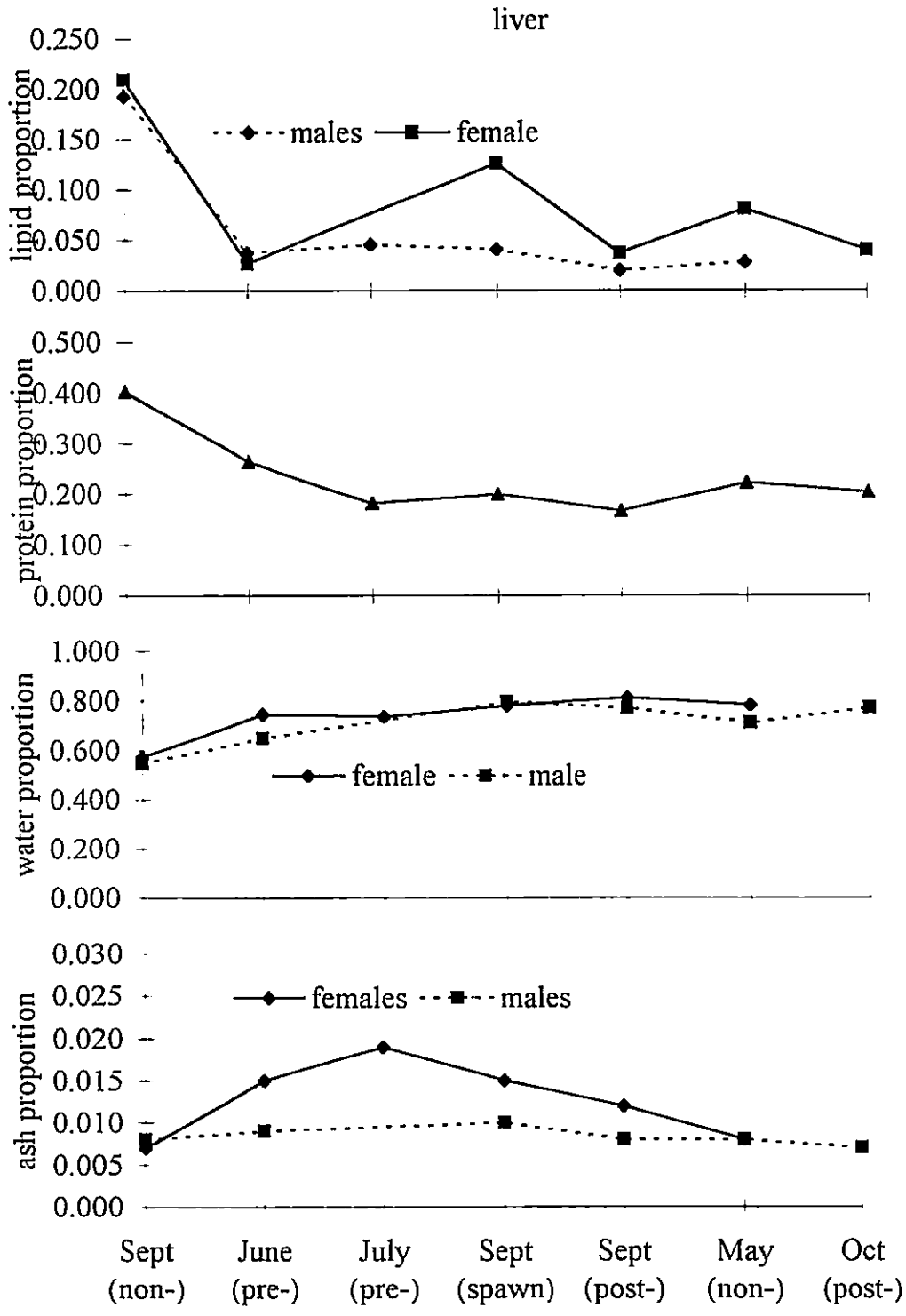

Figure 13. Timeline of proximate component proportions of the liver. Where both sexes are not reported, the total means are reported.

of growth.

Male and female liver lipid content were significantly different. As can be seen in Figure 13, female livers had significantly more lipid before and after spawning. It is possible that males use more lipid from the liver at the time of spawning, whereas the females are not as dependent on the liver as a source of lipid. For females, only the September nonspawners were significantly different from all other collection periods (Table 16). Male nonspawners in September were significantly different from all other periods (Table 17). In addition, July prespawners were also significantly different from postspawners. For both males and females, this demonstrates the initial importance of the liver for reproductive development. After spawning, lipid levels slightly decrease due to metabolic demands, explaining the significant difference of postspawned male livers.

Male and female gonad lipid contents were significantly different in July prespawners and spawners (Table 15). Lipid content in the ovaries is extremely high at the beginning of maturation (Figure 14). Both male and female lipid content in the gonads increase due to development until spawning. Although lipids appear to increase in gonadal tissue subsequent to spawning, this is not significant.

Ventral muscle lipid content decreases in the same manner as other tissues, quickly at first then leveling off (Figure 15). July prespawners were significantly

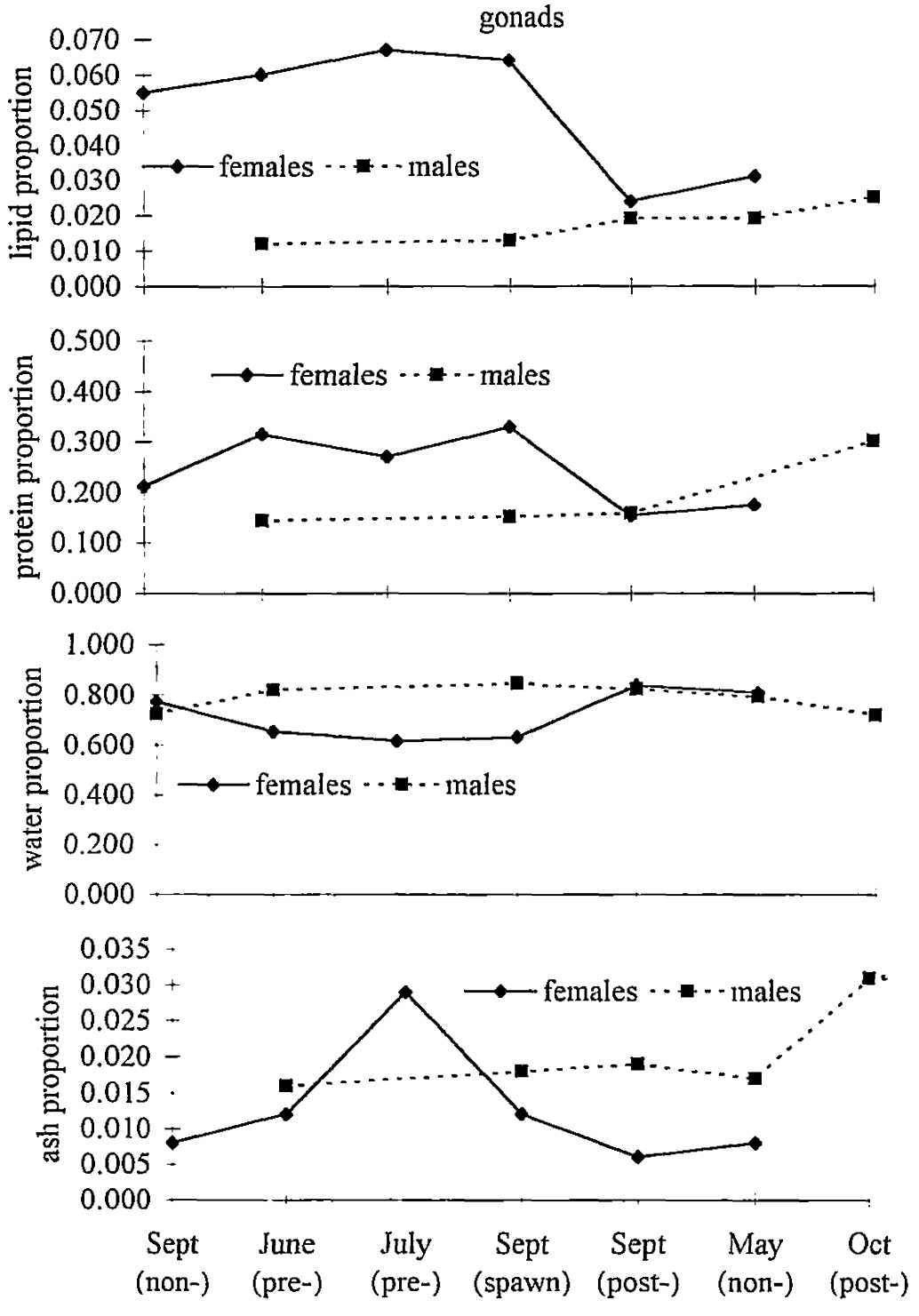

Figure 14. Timeline of proximate component proportions of the gonads.

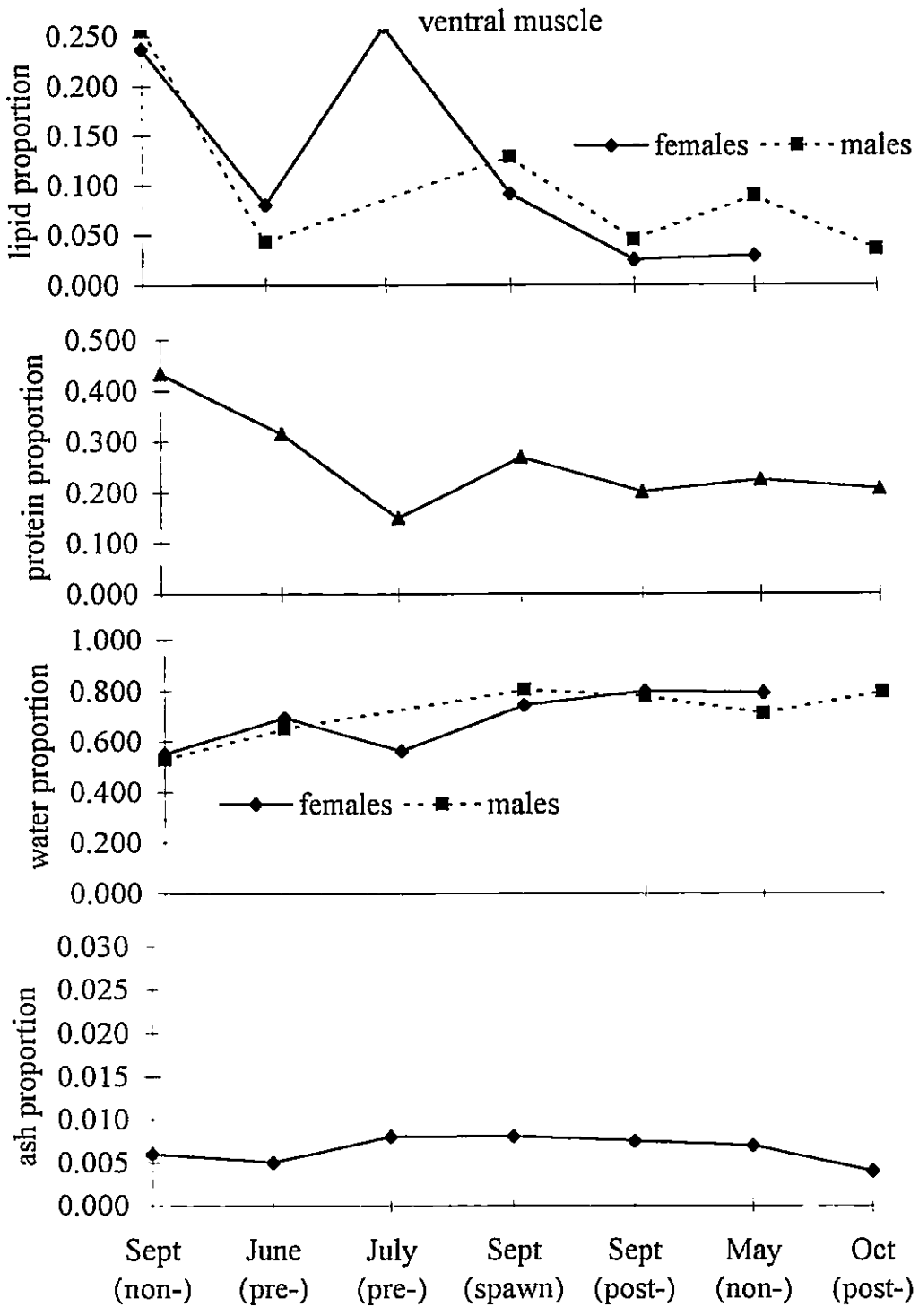

Figure 15. Timeline of proximate component proportions of the ventral muscle. Where both sexes are not reported, the total means are reported

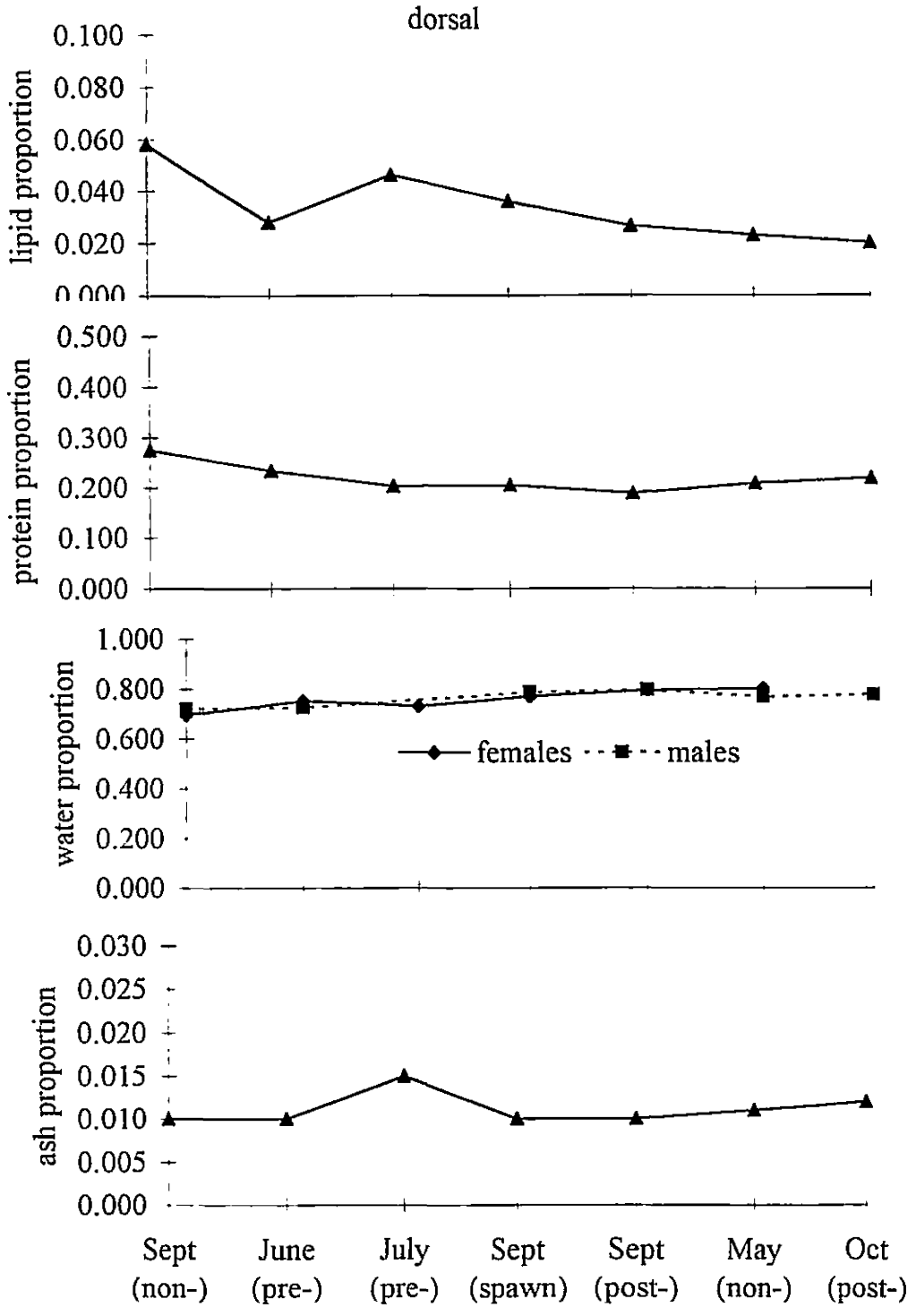

Figure 16. Timeline of proximate component proportions of the dorsal muscle. Where both sexes are not reported, the total means are reported.

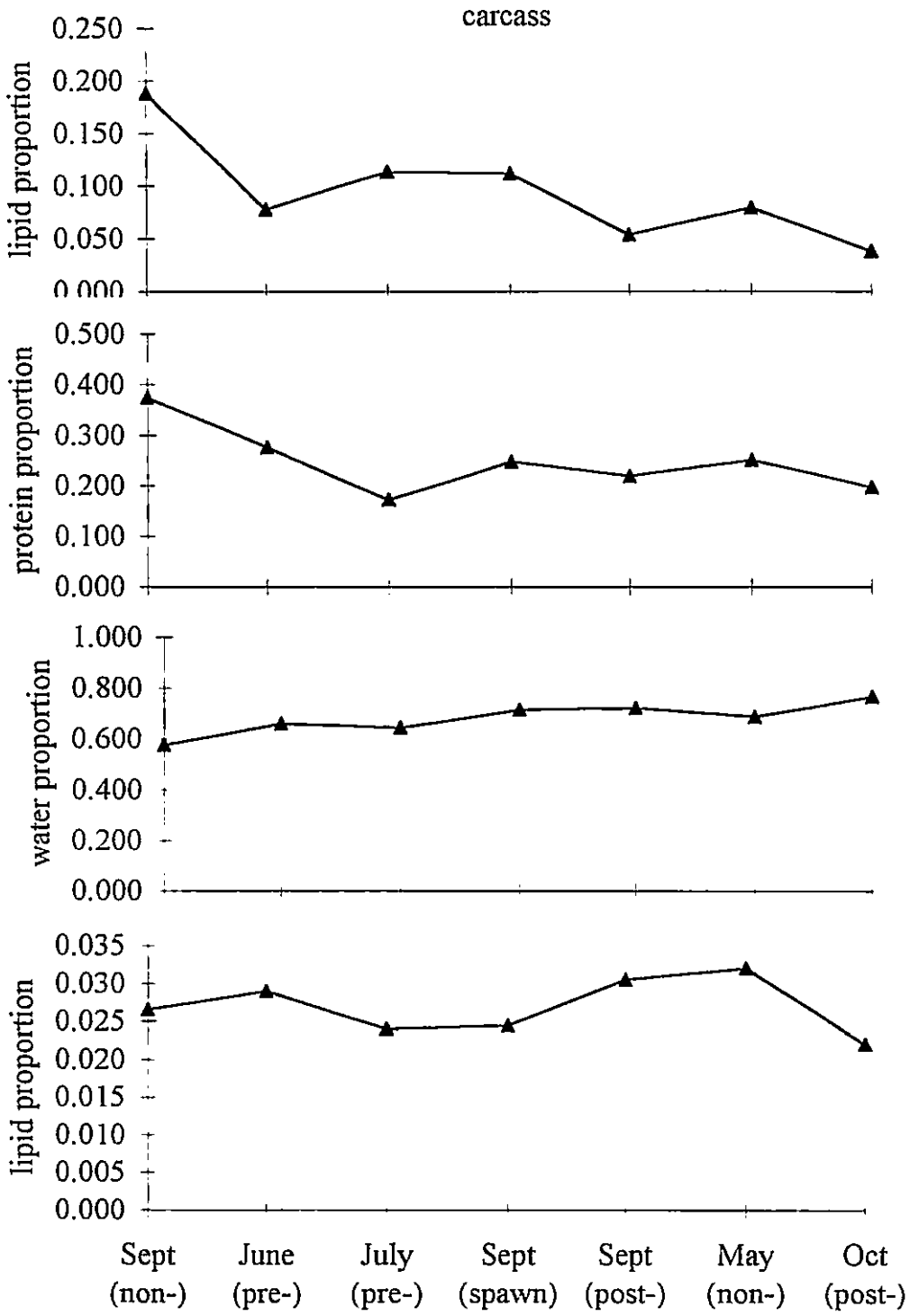

Figure 17. Timeline of proximate component proportions of the carcass. Where both sexes are not reported, the total means are reported.

higher than other periods. September nonspawners were also significantly higher due to the large amount of lipid gained during feeding at sea.

Dorsal muscle and carcass follow the same patterns as other tissues (Figure 16 and Figure 17). September nonspawners were significantly higher than in any other time period (Table 18). For the carcass, post and May nonspawner lipid content was significantly lower than any previous period. Therefore, the dorsal muscle and carcass are also important to the initial reproductive development.

Protein

Patterns of protein content were similar for all tissues except the gonads (Figures 12 to Figure 17). September nonspawners were significantly higher than all other collection periods for each tissue except gonads. This suggests a high utilization of protein from each tissue early in gonadal development. Although lipid is utilized first during starvation, protein often act as a significant source of energy during extended starvation. Jobling (1980) reported 18 to 35 percent protein oxidation in fasting sockeye salmon (*O. nerka*) and 18 to 35 percent protein oxidation in plaice (*Pleuronectes platessa*). Chan and Woo (1978) reported protein oxidation as high as 35 percent in Japanese eels (*Anguilla japonica*) during long term starvation. Each of the tissues in my study, except dorsal muscle, contributed approximately 20 to 25 percent of their protein to gonadal production and metabolic expenditures during the first winter in fresh

water. The dorsal muscle only contributed a small amount (less than 5 percent) during the same time period. It is hypothesized that this represents energy that will be used later for overwintering and migration energetic demands. Love (1970) also suggests that during starvation, protein can be moved into the muscle for future use. It is possible that some of the initial reduction of protein in other tissues is moved to the muscle. If this is the case, it could explain the availability of energy stores later in the starvation period and this excess of muscle protein could allow the fish to survive its second winter.

Protein content of male and female gonads were significantly different (Table 20). The protein content is much higher in the female ovaries than in the male testes. Because the gonads only increase by approximately 15 percent, it suggests protein is being used from other tissues for metabolic requirements as well as gonadal development. It should be noted that up to 3 percent of the protein remains in the gonadal tissue subsequent to spawning. This protein will be utilized for overwintering energy as the residual tissue is reabsorbed..

Water

Water content of all tissues increased significantly through time. This is a common phenomenon in that as lipid decreases in tissues, water replaces it. Water content is also increasing in the gonads as they develop. Statistical differences between water content in male and female char can be explained by observing the

low standard deviations of the data. The mean differences between male and female water content is small. No significant patterns develop through time to otherwise explain these differences. Accuracy of water determination procedures is very high and had a low overall standard deviation. The water content of each tissue is significantly larger before spawning than after (Tables 24 to Table 26). Total change in water content is between 15 and 20 percent in all tissues. Water content in gonadal tissue, however, only increases slightly through time. This is due to the increase of other proximate components which leaves the proportion of water constant. It should be noted that after spawning, water content remains the same in the gonads. This is indicative of the residual tissue remaining approximately 80 percent water.

Ash

Ash content in the gi tract, female liver, and dorsal muscle significantly increases prior to spawning. Due to the inactivity of bone and inorganic salts for energetic demands, this increase is due to the decrease in proportion of other proximate components in the tissue. The significant increase in ash content of the gonads is due to the amount of structural material being accumulated in the developing gonads. Ventral muscle shows no significant change in ash content, suggesting complimentary changes of the proximate components in the tissue through time.

By combining the information in Figure 12 through Figure 17, it can be seen that most tissues contribute some of their proximate components to general metabolism, overwintering, and reproduction. However, 20-25 percent decreases in lipid content of most tissues only result in a 5 percent increase in lipid of the gonads. The energy used for overwintering, secondary sexual characteristics, and to reproduction interactions is greater than that used for the actual development of the gonads.

Values of lipid and protein of the September nonspawners fresh from the marine environment represent the best condition of these fish prior to spawning. After spawning, it can be seen that protein and lipid concentrations drop to less than 4 percent of each tissue. It would be expected that these values would continue to drop during an overwintering period. However, no significant differences were found in either protein or lipid content between postspawners and May nonspawners. This suggests that the overwintering metabolic demands of these char are very low. Because of the extreme cold temperatures these fish endure, it must be hypothesized that these char enter a low metabolic period where nearly all activity is ceased until migration to sea the next spring. Evidence of the lack of fish movement is provided by the Native fishing patterns. Gill nets catch little during the winter compared to the annual fishing season during breakup when the fish move to leave the river and many are caught. Because of the large amount

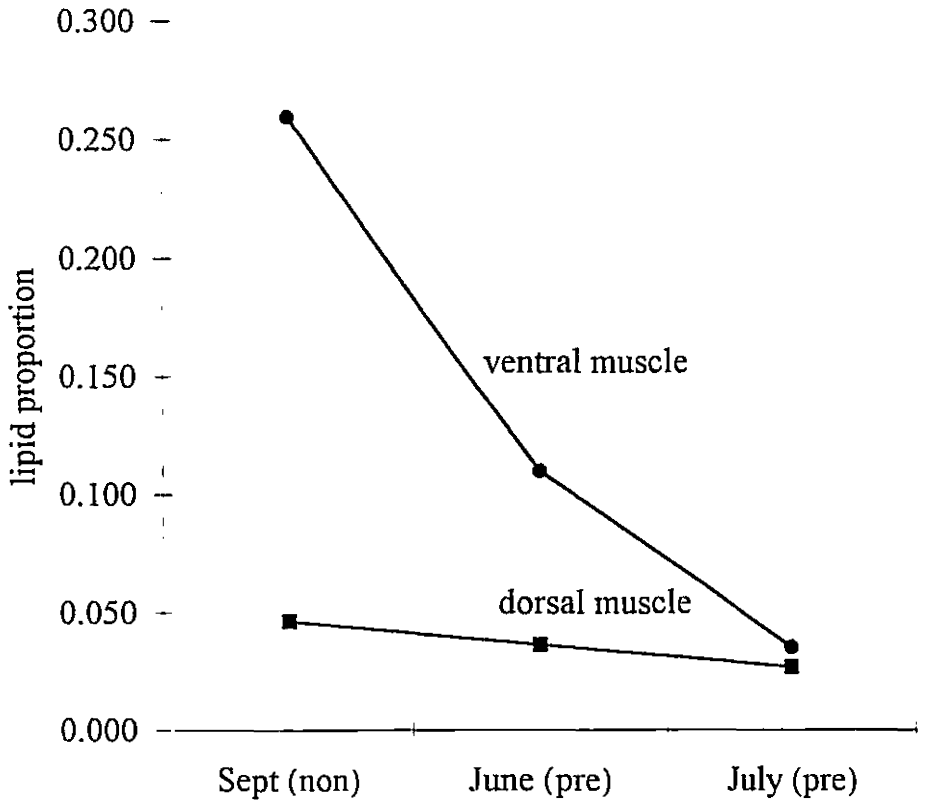

Figure 18. Comparison of lipid proportion of the ventral and dorsal muscles.

of energy lost the previous winter after first entering the river, it is hypothesized that most of this is used for sexual maturation. The good condition of gonads of prespawning fish corroborates this hypothesis.

An important pattern in the utilization of lipid from char muscle is apparent by studying the differences between ventral and dorsal muscle (Figure 18). The ventral muscle accounts for a significantly larger portion of lipid expenditure prior to spawning. This suggests that lipid storage in the ventral muscle tissue is a key factor in a char's life history, allowing it to successfully reproduce. Without this storage of lipid, reproductive efforts would be smaller if the char were to overwinter and survive to spawn the next year. Sheridan (1988) and Sänger (1993) discuss the importance of lipid in red muscle. It is apparent from these results that the lipid content of ventral muscle is significantly greater than the dorsal muscle as well as red muscle from epaxial tissue.

Figures 12 through Figure 17 also reveal that the fall-run postspawning char are not significantly different from summer-run postspawning char. Although the sample of fall-spawners is small, the indices and proximate analysis data are consistent. Conclusions based on these comparisons suggest that the fall-spawners are at the same energetic condition as the summer-spawners after spawning. If this is true, then the fall-spawners do not have to attain the same level of condition while at sea before they are able to enter freshwater to spawn.

Fecundity

Average fecundities found in this study were similar to fecundities reported by DeCicco (1985) for Kugururok River char from the same size classes. He found average fecundities of 5,260 eggs for 478 to 760 mm char and 6,218 eggs for 478 to 760 mm char. It was hypothesized that fecundities of fall spawning char are higher than these fecundity estimates. After observing the similar energetic condition of fall-run fish after spawning it is possible that the fecundities would be similar. Future research regarding the distinctions between these spawning runs should incorporate fecundity estimates so as to determine if there is any reproductive advantage with regard to egg size and number in either run.

Life History

Dolly Varden char have an anadromous life history. In order to evolve this life history strategy, fish must realize a benefit greater than the cost of migration and energy expenditure going to and from the marine and freshwater environment. Char do, in fact, receive considerable benefits by being anadromous. The availability of prey is much greater in the marine environment than in freshwater. This is especially true of the arctic river systems in which this species of char spawns. Because of this, char can attain greater size before spawning. This has the effect of decreasing the threat of predation and increasing reproductive fitness (McCart 1980).

There are two types of anadromous life histories that are exhibited in the Arctic. Pacific salmon species (*Oncorhynchus*) are semelparous meaning that they die shortly after their only spawning event in freshwater. This life history is characterized as having low egg and juvenile mortality whereas adult mortality is total. This requires that only a very limited amount of energy remain after reproduction. Pacific salmon can lose 99 percent of their lipid and 72 percent of their protein (Love 1970 and Shearer 1994). Chum salmon used lipid for maturation of the gonads while protein was used for migration in the river--the only time they were not eating (Ando et al. 1985). Therefore, the breakdown of lipid, and then protein, is too severe for the chum salmon to recover. Love (1970) states that 8 percent of chum lipid depletion went to gonad development in females and 0.5 percent in males. Comparing these numbers to the decrease in lipid of char in this study suggests that char have more lipid to utilize.

Char have an iteroparous life history where two or more spawnings are possible. Therefore, the threshold condition required before a fish will spawn must take into account survival through the second winter. Iteroparous life histories are characterized by high egg and juvenile mortality. The extreme conditions where char spawn exhibit such an environment.

Analysis of data in the literature suggests that protein content with respect to total fish weight is species specific (Shearer 1994). Char have a high protein

reserve which can be mobilized. Data from North Sea herring (*Clupea harengus harengus*) suggest that lipids are metabolized for processes other than reproductive development, whereas storage proteins were used for gonadal development (Iles 1984). This contrasts what was previously discussed regarding the energy utilization of chum salmon. Bradford (1993) found that Northwest Atlantic herring, having long periods of gonadal production, utilize storage proteins sooner than herring with shorter gonad maturation periods. If this is also true of char, fall-spawners would not initially use as much of protein as the summer-spawners do. Future research should try to quantify the utilization of proximate components year round in order to fully comprehend the energetic requirements of each run.

Conclusions

The results of this project revealed that Dolly Varden char from the Kugururok River do not actively feed in freshwater. Energetic requirements are so high during their stay in freshwater that any energy spent looking for food would probably compromise the survival of the fish. Isotope analysis through time also revealed a lack of fractionation during the period of starvation even though there was significant transfer and utilization of proximate components.

Proximate analysis showed the effects of the utilization of the marine carbon and nitrogen sources. Patterns of depletion of lipid and protein within all tissues revealed that the first winter in freshwater as mature adults was the most

important for gonadal production. Other studies support the hypothesis that the largest loss of energy during a starvation period occurs early in the period. Boivin and Power (1990) reported that Arctic char consume the largest amount of energy in the form of lipids early in the overwintering/starvation period. Atlantic salmon have also been reported to have the most significant energy utilization early in winter (Gardiner and Geddes 1980). Large energetic utilization early in the winter was also found in brook trout and brown trout (*Salmo trutta*) (Cunjak et al. 1987). Therefore, acclimation to freshwater, winter, reproductive development, and starvation results in a significant loss of energy perhaps affecting the reproductive success as well as survival of the char. Residual gonadal tissue as well as variable dependence on char muscle, reveal alternative mechanisms whereby char can finish surviving 20 months in freshwater without feeding. Proximate analysis also revealed the key difference between fall and summer-spawners: that being that fall-spawners may not need to attain the same condition (energy reserve) at sea as needed by the summer-spawners.

Data to this point have shown how the summer-spawners on the Kugururok River survive. This still does not answer the question of why they evolved this life history strategy. A lack of data from fall-spawners inhibits a true comparison of both runs. Hypotheses based on knowledge of the least likely life history strategy (summer-spawners) can be made.

Because summer-spawners spend an entire summer feeding there is ample time to reach the energetic level required to spawn whereas the fall-run may be constrained to reach a desired condition in so short of a time spent feeding at sea. There is also danger of not being able to spawn due to the onset of winter in the arctic. It would therefore be advantageous to spawn early if possible. It is probably not possible, however, to gain the required energy after overwintering and be able to spawn early. Therefore, the fall-spawners which do feed at sea after overwintering spawn later. The summer-spawners, in order to spawn earlier, must feed at sea for an entire summer before spawning in order to gain the greater amount of energy required. It is also possible that the two runs are not unique and switch between the two life history strategies. If this is the case, it is probably linked to the success with which the fish find prey while at sea. Another possible explanation for the summer life history strategy is competition and predation. Time spent in freshwater reduces the threat of predation at sea. Also by choosing to spawn earlier than the fall-spawners, they reduce the risk of competition on the spawning grounds. Coincidentally, spawning earlier reduces the chances that reproduction will be compromised due to an early winter and freezing.

Therefore, the summer-run has developed significant energetic storage capacities in order to survive 20 months in freshwater without feeding and remain reproductively successful. However, they must attain a particular energetic

threshold while at sea in order to reproduce successfully. Rowe et al. (1991) found a similar threshold of energy storage levels were required before Atlantic Salmon could enter freshwater to spawn or overwinter. As discussed before, the fall-spawners may have a lower threshold of condition to attain at sea before migrating to the spawning grounds. It is also possible that if this behavior is not a genetic response, once a char becomes a summer-spawner it must remain at sea the entire next summer in order to recover from the 20 month reproduction cycle, thus perpetuating the summer-run. Further research should address this question by comparing the age and size structure of both runs. Anadromous Arctic char have also been found to have a threshold of energy which must be attained before a fish can begin reproduction (Dutil 1986). Char that had previously spawned needed two summers of feeding before enough reserves were attained to spawn. Fish that had only overwintered expended an amount of energy that could be resupplied at the beginning of the next feeding period.

Future management of these stocks of fish will necessarily have to take into account the unique life history of the summer-spawners. Time spent on spawning grounds and poor condition after spawning will increase the risk that any perturbations will decrease the success of this stock. Fall-run char are also at risk as a unique stock of fish. Constant runs between the sea and freshwater increase the risk of being intercepted, either in the commercial or subsistence fisheries.

The small size of this run should also indicate the fragility of these char stocks. The similar size of large char and chum mean that both fish are targeted by commercial gill nets. This would have the effect of thinning out the spawning population of char and possibly change the composition of summer and fall-spawners, since summer-spawners are generally larger.

Future studies will help to elucidate the importance of these two runs of char to the Noatak River system and to each other. Successful estimates of abundance need to be made in order to allow managers to better understand the strength of these stocks. Continued efforts to elucidate the feeding habits and migration controls will allow researchers to better understand the importance of timing in migration and spawning.

Literature Cited

Alt, K. T., and R. A. Furniss. 1976. Inventory and cataloging of North Slope waters. Alaska Department oif Fish and Game, Federal Aid in Fish Restoration, Annual Performance Report, Project F-9-8, 17:129-150.

Ando, S., M. Hatano, and K. Zama. 1985. Deterioration of chum salmon (*Oncorhynchus keta*) muscle during spawning migraton-I. Changes in proximate composition of chum salmon muscle during spawning migration. Comparative Biochemistry and Physiology 80B(2):303-307.

Armstrong, R. H., and J. E. Morrow. 1980. The dolly varden char, *Salvelinus malma*. Pages 99-140 in E. K. Balon, editor. Chars: salmonid fishes of the genus Salvelinus. Dr. W. Junk, The Hague, The Netherlands.

Benke, R. J. 1980. A systematic review of the genus Salvelinus. Pages 441-480 in E. K. Balon, editor. Chars: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk, The Hague, The Netherlands.

Bligh, E. G., and W. J. Dyer. 1959. A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology 37:911-917.

Boivin, T. G. and G. Power. 1990. Winter condition and proximate composition of anadromous arctic charr (*Salvelinus alpinus*) in eastern Ungava Bay, Quebec. Canadian Journal of Zoology 68:2284-2289.

Bradford, R. G. 1993. Differential utilization of storage lipids and storage proteins by Northwest Atlantic herring (*Clupea harengus harengus*). Journal of Fish Biology 43:811-824.

Brett, J. R. 1979. Environmental Factors and Growth. Pages 231-254 in Hoar, W. S., D. J. Randall, and J. R. Brett editors. Fish Physiology, Volume III. Academic Press, New York.

Chan, D. K. O. and N. Y. S. Woo. 1978. Effect of hypophysectomy on the chemical composition and intermediary metabolism of the Japanese eel, *Anguilla japonica*. General and Comparitive Endocrinology 35:169-178.

Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. Geochimica et Cosmochimica Acta 12:133-149.

Craig, P. C. 1977. Ecological studies of anadromous and resident populations of arctic char in the Canning River drainage and adjacent coastal waters of the Beaufort Sea, Alaska. Chapter 1 in McCart, editor. Fisheries investigations along the north slope and Beafort Sea coast in Alaska with emphasis on arctic char. Canadian Arctic Gas Study, Biological Report Series 41:1-116.

Craig, P. C. and L. Haldorson. 1981. Beaufort Sea barrier island-lagoon ecological process studies: final report, Simpson Lagoon. Final Reports of Principal Investigators, BLM/NOAA, OCSEAP. Part 4. Environmental Assessment of the Alaskan Continental Shelf. 7:384-678. Boulder, Colorado.

Cunjak, R. A., R. A. Curry, and G. Power. 1987. Seasonal energy budget of brook trout in streams: implications of a possible deficit in early winter. Transactions of the American Fisheries Society 116:817-828.

DeCicco, A. L. 1985. Inventory and cataloging of sport fish and sport fish waters of western Alaska. Alaska Department of Fish and Game. Federal Aid in Fish Restoration, Annual Performance Report 1984-85, Project F-9-17, 26:41-134.

DeCicco, A. L. 1989. Movements and spawning of adult Dolly Varden char (*S. malma*) in the Chukchi Sea drainages of northwestern Alaska: evidence for summer and fall spawning populations. Physiology and Ecology of Japan, Special Volume 1:229-238..

DeCicco, A. L. 1990. Northwest Dolly Varden Study 1989. Alaska Deopertment of Fish and Game, Fishery Data Series Report 90-8.

DeCicco, A. L. 1992. Long distance movements of anadromous Dolly Varden between Alaska and the U.S.S.R. Arctic 45(2):120-123.

DeNiro, M. J and S. Epstein. 1978. Influence of the diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochima Acta 42:495-506.

Dowgiallo, A. 1975. Chemical composition of an animal's body and of its food. Pages 169-199 in W. Grodzinski, R. Z. Klekowski, and A. Duncan editors. Methods for Ecological Bioenergetics. IBP Handbook, No. 24. Blackwell Sci.

Dunton, K. H., S. M. Saupe, A. N. Golikov, D. M. Schell, and S. V. Schonberg. 1989. Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. Marine Ecology Progress Series 56:89-97.

Dutil, J. D. 1982. Periodic changes in the condition of the arctic charr (*Salvelinus alpinus*) of the Nauyuk Lake system, Kent Peninsula, Northwest Territories. Unpublished PhD. dissertation. University of Manitoba. Winnepeg, Manitoba, Canada.

Dutil, J. D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). Copeia 4:945-955.

Fry, B., and E. B. Sherr. 1984. $\delta^{13}C$ measuremnets as indicators of carbon flow in marine and freshwater ecosystems. Contributions in Marine Science 27:13-47.

Gardiner, W. R. and P. Geddes. 1980. The influence of body composition on the survival of juvenile salmon. Hydrobiologia 69:67-72.

Glova, G., and P. McCart. 1974. Life History of arctic char (*Salvelinus alpinus*) in the Firth Rivber, Yuikon Territory. Chapter 3 in P. J. McCart, editor. Life histories of anadromous and freshwater fish in the western Aerctic. Canadian Arctic Gas Stuidy, Biological Report Series 20.

Hardy, R. W., K. D. Shearer, and I. D. King. 1985. Proximate and elemental composition of the developing eggs and maternal soma of pen-reared coho salmon (*Oncorhynchus kisutch*) fed production and trace element fortified diets. Aquaculture 43:147-165.

Hayashi, K. and T. Takagi. 1977. Lipid metabolism in fish. II. Changes of lipids and fatty acids in the liver of puffer, *Fugu vermiculare porphyreum*, during starvation. Bulletin of the Faculty of Fisheries at Hokkaido University 28(4):193-201.

Hino, T., K. Maekawa, and J. B. Reynolds. 1990. Alternative male mating behaviors in landlocked Dolly Varden (*Salvelinus malma*) in South-central Alaska. Journal of Ethol. 8(1):13-20.

Hobson, K. A. and H. E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series 84:9-18.

Iles, T. D. 1984. Allocation of resources to gonad and soma in Atlantic herring, *Clupea harengus* L. G. W. Potts and R. J. Wootton, editors. Fish Reproduction: strategies and tactics. Academic Press, London.

Jobling, M. 1980. Effects of starvation on proximate chemical composition and energy utilization of plaice, *Pleuronectes platessa*. Journal of Fish Biology 17:325-334.

Love, R. M. 1970. The chemical biology of fishes, volume 1. Academic Press, London and New York.

Love, R. M. 1980. The chemical biology of fishes, volume 2. Academic Press, London and New York.

McCart, P. J. 1980. A review of the systematics and ecology of arctic char, Salvelinus alpinus, in the western Arctic. Canadian Technical Report of Fisheries and Aquatic Sciences 935.

McCart, P., P. Craig, and H. Bain. 1972. Report on fisheries investigations in the Sagavanirktok River and neighboring drainages. Alyeska Pipleline Service Company. Bellevue, Washington.

McGurk, M. D., J. M. Green, W. D. McKone, and K. Spencer. 1980. Condition indices, energy density and water and lipid content of Atlantic herring (*Clupea harengus*) of southeastern Newfoundland. Canadian Technical Report of Fisheries and Aquatic Sciences 958.

McPhail, J. D. 1961. A systematic study of the Salvelinus alpinus complex in North America. Journal of the Fisheries Research Board of Canada 18(5):793-816.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta 48:1135-1140.

Morrow, J. E. 1980. Analysis of Dolly Varden charr, *Salvelinus malma*, of northwestern North America and northeastern Siberia. Pages 323-338 in E. K. Balon, editor. Chars: salmonid fishes of the genus Salvelinus. Dr. W. Junk, The Hague, The Netherlands.

Moulton, C. R. 1923. Age and chemical development in mammals. Journal of Biological Chemistry 57:79-97.

Owens, N. J. P. 1987. Natural variations in ^{15}N in the marine environment. Advances in Marine Biology 24:389-449.

Parker, P. L. 1964. The biogeochemistry of the stable isotopes of carbon in marine bay. Geochimica et Cosmochimica Acta 28:1155-1164.

Parker, R. P. and W. E. Vanstone. 1966. Changes in the chemical composition of central British Columbia pink salmon during early sea life. Journal of the Fisheries Research Board of Canada 23:1353-1384.

Peterson, B. J., R. W. Howarth, and R. H. Garrit. 1985. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. Science 227:1361-1363.

Peterson, B. J. and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293-320.

Rau. G. H., A. J. Mearns, D. R. Young, R. J. Olson, H. A. Schafer, and I. R. Kaplan. 1983. Animal $^{13}C/^{12}C$ correlates with trophic level in pelagic food webs. Ecology 64:1314-1318.

Rau, G. H., D. G. Ainley, J. L. Bengtson, J. J. Tores, T. L. Hopkins. 1992. $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. Marine Ecology and Progress Series 84:1-8.

Reist, J. D., J. D. Johnson, and T. J. Carmichael. 1992. Variation and specific identity of char from northwestern Arctic Canada. in J. B. Reynolds, editor. Proceedings of the symposium on fish ecology in Arctic North America, May 19-21, 1992, University of Alaska Fairbanks. American Fisheries Society Special Publication.

Rowe, D. K., J. E. Thorpe, and A. M. Shanks. 1991. Role of fat inthe maturation of male Atlantic salmon (*Salmo salar*) parr. Canadian Journal of Fisheries and Aquatic Sciences 48:405-413.

Sänger, A. M. 1993. Limits to the acclimation of fish muscle. Reviews in Fish Biology and Fisheries 3:1-15.

Schell, D. 1983. Carbon-13 and carbon-14 abundances in Alaskan aquatic organisms: Delayed production from peat in arctic food webs. Science 219:1068-1071.

Shearer, K. D. 1994. Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. Aquaculture 119:63-88.

Sheridan, M. A. 1988. Lipid dynamics in fish: aspects of absorption, transportation, deposition and mobilization. Comparative Biochemistry and Physiology 90B(4):679-690.

Teiszen, L. L. 1978. Carbon isotope fractionation in biological material. Nature 276:97-98.

Tieszen, L. L., T. W. Boutton, K. G. Tesdahl, and N. A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}C$ analysis of diet. Oecologia (Berlin) 57:32-37.

van der Merwe, N. J. 1982. Carbon isotopes, photosynthesis, and archeology. American Scientist 70:596-606.

Wootton, R. J. and L. A. Mills. 1979. Annual cycle in female minnows *Phoxinus phoxinus* (L.) from an upland Welsh Lake. Journal of Fish Biology 14:607-618.

Ziemann, P. J. 1986. Energetics of arctic Alaskan fishes: carbon isotope evidence. A M.S. thesis, University of Alaska Fairbanks.

Appendices

Appendix 1. Replicate differences for tissue $\delta^{13}C$ values from each collection period.

run	month	n (dorsal)	gi tract mean	liver mean	gonads mean	ventral muscle mean	dorsal muscle mean	carcass mean
summer								
(non-)	Sept	mean	0.336	0.254	0.135	0.136	0.132	0.100
		SD	0.454	0.161	0.049	0.155	0.131	0.075
(pre-)	June	mean	0.095	0.120	0.070	0.090	0.166	0.133
		SD	0.072	0.058	0.054	0.064	0.170	0.074
(pre-)	July	mean	0.211	0.099	0.100	0.140	0.060	0.170
		SD	0.248	0.117	0.071	0.042	0.049	0.180
(spawn)	Sept	mean	0.220	0.165	0.035	0.030	0.070	0.125
		SD	0.269	0.078	0.007	0.028	0.057	0.064
(post-)	Sept	mean	0.547	0.120	0.297	0.050	0.118	0.270
		SD	0.153	0.061	0.382	0.070	0.092	0.233
(non-)	May	mean	0.212	0.076	0.150	0.126	0.132	0.200
		SD	0.235	0.062	0.046	0.076	0.187	0.134
fall								
(post-)	Oct	mean	0.230	0.320	0.050	0.050	0.130	0.010
		SD	na	na	na	na	na	na

Appendix 2. Replicate differences for tissue δ^{15}N values from each collection period.

month		gi tract	liver	gonads	ventral muscle	dorsal muscle	carcass
summer							
Sept (non-)	mean	0.098	0.100	0.035	0.098	0.085	0.028
	SD	0.083	0.058	0.035	0.115	0.079	0.015
June (pre-)	mean	0.087	0.078	0.147	0.147	0.094	0.132
	SD	0.055	0.109	0.070	0.090	0.075	0.108
July (pre-)	mean	0.117	0.128	0.126	0.095	0.113	0.115
	SD	0.086	0.192	0.173	0.092	0.077	0.110
Sept (spawn)	mean	0.055	0.070	0.015	0.005	0.083	0.130
	SD	0.064	0.000	0.007	0.007	0.054	0.141
Sept (post)	mean	0.080	0.160	0.107	0.243	0.101	0.213
	SD	0.095	0.161	0.168	0.268	0.066	0.188
May (non-)	mean	0.138	0.072	0.120	0.056	0.138	0.134
	SD	0.149	0.037	0.100	0.075	0.095	0.046
fall							
Oct (post)	mean	0.020	0.310	0.080	0.020	0.020	0.060
	SD	na	na	na	na	na	na

Appendix 3. Replicate proximate component differences for each tissue from September nonspawners.

	lipid		protein		water		ash	
tissue	mean	SD	mean	SD	mean	SD	mean	SD
GI tract	na	na	0.014	0.021	0.003	0.003	0.002	0.001
liver	na	na	0.007	0.003	0.002	0.001	0.002	0.001
gonads	na	na	0.002	0.002	0.001	na	0.003	0.002
ventral muscle	na	na	0.013	0.011	0.004	0.006	0.002	0.001
dorsal muscle	na	na	0.007	0.009	0.009	0.017	0.002	0.002
carcass	na	na	0.047	0.044	0.004	0.004	0.008	0.007

Appendix 4. Replicate proximate component differences for each tissue from June prespawners.

	lipid		protein		water		ash	
tissue	mean	SD	mean	SD	mean	SD	mean	SD
GI tract	na	na	0.004	0.007	0.009	0.019	0.002	0.001
liver	na	na	0.003	0.002	0.002	0.001	0.002	0.002
gonads	na	na	0.001	0.001	0.002	0.002	0.003	0.001
ventral muscle	na	na	0.003	0.005	0.004	0.006	0.003	0.005
dorsal muscle	0.004	0.000	0.008	0.010	0.004	0.003	0.002	0.002
carcass	0.030	0.010	0.006	0.009	0.007	0.011	0.007	0.006

Appendix 5. Replicate proximate component differences for each tissue from July prespawners.

	lipid		protien		water		ash	
	mean	SD	mean	SD	mean	SD	mean	SD
GI tract	na	na	0.004	0.005	0.020	na	0.001	0.003
liver	na	na	0.003	0.003	0.001	0.003	0.001	0.003
gonads	0.002	na	0.005	0.004	0.001	0.002	0.003	0.004
ventral muscle	na	na	0.003	na	0.003	na	0.001	na
dorsal muscle	0.031	na	0.003	0.003	0.002	0.005	0.001	0.003
carcass	0.001	na	0.006	0.005	0.002	0.006	0.003	0.006

Appendix 6. Replicate proximate component differences for each tissue from the spawner group.

	lipid		protein		water		ash	
tissue	mean	SD	mean	SD	mean	SD	mean	SD
GI tract	na	na	0.011	0.001	0.007	0.006	0.002	0.002
liver	na	na	0.003	0.003	0.002	0.001	0.001	0.001
gonads	na	na	0.003	0.002	0.001	0.001	0.002	0.001
ventral muscle	na	na	0.001	0.001	0.005	0.005	0.002	0.001
dorsal muscle	na	na	0.007	0.007	0.002	0.002	0.002	0.001
carcass	na	na	0.002	0.001	0.006	0.008	0.011	0.007

Appendix 7. Replicate proximate component differences for each tissue from summer-run postspawners.

	lipid		protein		water		ash	
tissue	mean	SD	mean	SD	mean	SD	mean	SD
GI tract	na	na	0.008	0.006	0.003	0.002	0.003	0.002
liver	na	na	0.001	0.000	0.001	0.001	0.002	0.002
gonads	na	na	0.003	0.005	0.001	0.001	0.002	0.002
ventral muscle	na	na	0.004	0.003	0.004	0.005	0.002	0.002
dorsal muscle	na	na	0.006	0.007	0.004	0.003	0.003	0.002
carcass	na	na	0.031	0.020	0.005	0.005	0.007	0.009

Appendix 10. Replicate proximate component differences for each tissue from May nonspawners.

	lipid		protein		water		ash	
tissue	mean	SD	mean	SD	mean	SD	mean	SD
GI tract	na	na	0.005	0.006	0.004	0.005	0.003	0.002
liver	na	na	0.001	0.000	0.000	na	0.001	0.000
gonads	na	na	0.003	0.001	na	na	0.001	0.001
ventral muscle	na	na	0.005	0.009	0.002	0.001	0.002	0.002
dorsal muscle	na	na	0.004	0.005	0.003	0.004	0.002	0.001
carcass	na	na	0.012	0.008	0.010	0.021	0.004	0.004

Appendix 9. Replicate proximate component differences for each tissue from fall-run postspawners.

	lipid		protein		water		ash	
tissue	mean	SD	mean	SD	mean	SD	mean	SD
GI tract	na	na	0.001	na	0.008	na	0.002	na
liver	na	na	0.002	na	0.001	na	0.002	na
gonads	na	na	0.003	na	0.003	na	0.001	na
ventral muscle	na	na	0.000	na	0.001	na	0.001	na
dorsal muscle	na	na	0.001	na	0.002	na	0.004	na
carcass	na	na	0.010	na	0.000	na	0.005	na

Appendix 10. Independent samples t-test probabilities comparing male versus female gill raker counts examined in each of the time periods collected.

		left		right	
		upper arch	total	upper arch	total
month	n	P	P	P	P
Sept (non)	25	0.714	0.427	0.904	0.749
June (pre)	27	0.132	0.110	0.711	0.644
Sept (post)	25	0.614	0.318	0.887	0.210
May (non)	9	0.366	0.845	0.722	0.859