Final report of research

Evaluation of energy expenditure in adult spring Chinook salmon migrating upstream in the Columbia River basin: an assessment based on sequential proximate analysis

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Abstract

The upstream migration of adult anadromous salmonids in the Columbia River Basin (CRB) has been dramatically altered and fish may be experiencing energetically costly delays at dams. We estimated the energetic costs of migration and reproduction of Yakima River-bound spring Chinook salmon *Oncorhynchus tshawytscha* using a sequential analysis of their proximate composition (i.e., percent water, fat, protein, and ash). Tissues (muscle, viscera, and gonad) were sampled from fish near the start of their migration (Bonneville Dam), at a mid point (Roza Dam, 510 km upstream from Bonneville Dam), and from fresh carcasses on the spawning grounds (about 100 km above Roza Dam). At Bonneville Dam, the energy reserves of these fish were remarkably high, primarily due to the high percentage of fat in the muscle (18-20%). The median travel time for fish from Bonneville to Roza Dam was 27 d and ranged from 18 to 42 d. Fish lost from 6 to 17% of their energy density in muscle, depending on travel time. On average, fish taking a relatively long time for migration between dams used from 5 to 8% more energy from the muscle than faster fish. From the time they passed Bonneville Dam to death, these fish, depending on gender, used 97-99% of their muscle and 76-81% of their visceral lipid stores. Also, both sexes used about 32% of their muscular and very little of their visceral protein stores. However, we were unable to relate energy use and reproductive success to migration history. We also attempted to assess the efficacy of muscle biopsies and the use of stable isotope analysis as a non-lethal way to obtain lipid and protein information. Although levels of δN^{15} in a small biopsy and a large muscle sample were similar, δN^{15} was a poor indicator of protein concentration in muscle. Levels of δC^{13} in the biopsy were consistently higher than those in a large muscle sample and δC^{13} did not accurately predict lipid concentration in muscle. Our

results suggest a possible influence of the CRB hydroelectric system on adult salmonid energetics and, perhaps, reproductive success.

Introduction

Pacific salmonids *Oncorhynchus* spp. in the Columbia River Basin (CRB) have declined dramatically in recent years to a fraction of their historical numbers. The ecological, economic, and cultural significance of these fish is substantial and actions are currently being researched and implemented for their recovery. Identifying biological and ecological factors that may limit salmonid production in the CRB is critical for their recovery. One factor that could be detrimental to salmonid production is the amount of energy adults expend during their upstream spawning migrations in the highly modified CRB. Pacific salmonids leave the ocean and enter streams several months before they spawn (Groot and Margolis 1991). Because feeding ceases when they enter freshwater, they have a finite amount of energy reserves for migration, gamete production, and spawning. An excessive use of energy due to various complications associated with dam passage during their upstream migration could result in reduced spawning success (Berman and Quinn 1991), loss of egg production potential, or increased pre-spawning mortality (Beiningen and Ebel 1970; Gray 1990; Snelling et al. 1992).

There are two possible ways that salmon might use an excessive amount of energy during their upstream migration. First, significant numbers of adult salmonids passing dams fall back over that dam, usually over the spillway. Fish may also enter a fishway, travel some distance in it, but eventually fall out. In both instances, extra energy is required to re-ascend the dam. For example, fall back rates of radio-tagged spring and summer Chinook salmon *O. tshawytscha* and steelhead *O. mykiss* at The Dalles Dam during 1996-98 ranged from 6.8% to 18.3% (Bjornn et al. 1999a). Fall back percentages were similar for radio-tagged fish passing Bonneville Dam—13.8%, 15%, and 12.3% in 1996, 1997, and 1998 (Bjornn et al. 1999b). In addition, spill at dams can influence fall back. Liscom et al. (1985) and Bjornn et al. (1999b) reported higher fall back

rates of Chinook salmon at Bonneville Dam when there was spill compared to times of no spill. However, although fall back (and fall out) can be a common behavior shown by adult salmonids, any energetic consequences associated with these events are unquantified.

A second possible contributor to excessive energy use by migrating adult salmonids is delay at dams. The physical characteristics of hydroelectric dams and the ability of fish to find fishway entrances influence the amount of time it takes fish to migrate upstream in the CRB (reviewed in Dauble and Mueller 2000). Changes in flow regimes (e.g., spill) at dams also affects salmonid passage success (Bjornn and Peery 1992). Migration delays at dams in the CRB range from a few hours to several days per dam (Mendel et al. 1992; Dauble and Mueller 2000; Bjornn et al. 1994; Mendel and Milks 1997). The time spent migrating through the dam and reservoir system is of concern because a lengthened migration period could deplete the energy reserves of fish.

To provide some information on the energetics of spring Chinook salmon during their upstream migration through the CRB, we estimated the costs of migration and reproduction using a sequential analysis of the proximate composition of a cohort of fish. Evaluating the energy use of anadromous fishes during migration and reproduction by documenting changes in their proximate composition has received much interest of late (Leonard and McCormick 1999; Hendry and Berg 1999; Hendry et al. 2000; Jonsson et al. 1991; Rand and Hinch 1998). This approach documents changes in sequestered fats and proteins in fish tissues during migration and spawning. Estimates of energy use via sequential proximate analysis will include all the energy used by the animal, including that used for swimming, metabolism, and reproductive behavior and development. We focused our assessment on spring Chinook salmon migrating to the spawning grounds of the Yakima River, Washington and estimated changes in energy density of

this cohort of fish from the time they passed Bonneville Dam—the lowermost dam on the Columbia River—to senescence and death. Specifically, our objectives were to: (1) document changes in the proximate composition of Yakima River-bound spring Chinook salmon during their upstream migration in 2002; (2) assess the influence of different migration histories on energy use in these fish; and (3) assess the efficacy of muscle biopsies and stable isotope analysis (Doucett et al. 1999) as a non-lethal way to obtain nutritional information on fish. We believe our results will increase understanding of the influence of the CRB hydroelectric system on adult salmonid energetics and reproductive success.

Methods

Fish collections.—We obtained tissues for proximate analysis from spring Chinook salmon bound for the Yakima River at three locations during their migration in 2002 (Figure 1; Table 1). First, a sample of fish representing the start of the migration was collected from 14 to 28 April at Bonneville Dam on the Columbia River (rkm 235). Next, we collected a sample of fish from 19 to 26 May at Roza Dam on the Yakima River, which is 510 km upstream of Bonneville Dam. For our last sample, we collected fresh carcasses from 15 to 29 September on the spawning grounds of the Yakima River of fish that had and had not spawned successfully.

At Bonneville Dam, fish ascending the north shore fish ladder were diverted into a trapping and sorting facility. Inside, fish volitionally moved into a flume containing a passive integrated transponder (PIT) tag detector and a series of gates leading to other flumes. Fish with PIT tags were diverted to a large tank containing 50 mg/L clove oil, while those without tags were usually diverted back to the fish ladder to continue their migration. After fish were anesthetized, their origin was determined by passing a hand-held wand over their body to obtain their PIT-tag code. Fish originating from the Yakima River were either implanted with a coded

radio transmitter by personnel from the University of Idaho and released, or they were sacrificed and sampled for proximate analysis. The radio-tagged fish were a primary target of our subsequent sampling because, when coupled with the extensive array of telemetry receivers in the CRB, they can provide a detailed individual migration history. Such history could include total migration time, amount of delay in dam tailraces, and number of fall back events. Our tissue sampling generally followed the passage of fish at Bonneville Dam (Figure 2).

Similar procedures were used to collect fish at Roza Dam, which has facilities that capture all salmonids returning to the Yakima River. Our original intent was to sample fish over the passage season and to focus on fish that had radio or PIT tags in them. However, because of timing and logistical constraints, we sampled fish from the run at large during an early peak of passage (Figure 3). All fish collected at Roza Dam were examined and scanned for tags by personnel from the Yakama Indian Nation before being released into the river or given to us.

Carcasses collected on the spawning grounds of the Yakima River (78-120 km from Roza Dam) provided energy density values of fish that successfully spawned and those that did not. Because of on-going work by other agencies, we were allowed to collect tissues only from carcasses that had radio or PIT tags, thus limiting our ability to sample the run at large. To increase our chances of collecting fresh carcasses that had radio-tags in them, we mobile tracked tagged fish leaving Roza Dam from a truck and a raft until the water levels dropped and spawning commenced (August-September). This tracking, we surmised, would allow us to pinpoint the locations of radio-tagged fish and, later, carcasses. After most spawning had ceased, we floated the river daily to collect carcasses for tissue samples. For each carcass, we estimated how long the fish had been dead by checking for reddish coloration in the gills and examining

the eyes for clarity and recession into the skull. Only carcasses that were considered relatively fresh (i.e., dying within about 24 h) were sampled.

Tissue collections.—At Bonneville and Roza dams, fish to be sampled were deeply anesthetized in clove oil, weighed to the nearest g, and then sacrificed by a blow to the head. Fork length was measured to the nearest 0.1 cm, and we used a 9-cm-long, 14-gauge biopsy needle with a 20-mm throw to remove a small piece of white muscle from the right side of the fish at the mid-point between the anterior insertion of the dorsal fin and the lateral line. A large, rectangular muscle sample was then removed from the left side of the fish, starting just below the dorsal fin and continuing to the center of the abdomen. This muscle sample contained both red and white muscle but did not include the skin or dorsal and ventral fat deposits. Next, the abdominal cavity was opened with a scalpel and the entire gonad and remaining viscera (excluding the kidney) were removed separately. All tissues (except the biopsy) were weighed, homogenized using a commercial blender, sub-sampled and packaged, and then stored at -20°C until proximate analysis. All equipment was washed between each tissue sample. Tissues from carcasses on the spawning grounds of the Yakima River were collected as just described, except that they were frozen whole and processed at a later date.

Analytical procedures and data analysis.—To determine energy content, we estimated the percent water, protein, fat, and ash in each sample by proximate analysis. Like other studies, we ignored carbohydrates because they comprise <0.05% of the somatic tissues of salmonids (Jonsson 1997; Hendry and Berg 1999). To measure water content, the frozen tissue homogenates were thawed and 2 g aliquots were placed in small, tin vessels and dried at 100°C in a mechanical convection oven until they reached constant mass (25-30 h). A second aliquot of each tissue homogenate (~15-20 g) was dried in the same manner to prepare them for lipid and

ash analyses. The large dried samples were sent to Washington State University for determination of lipid (ether extract crude fat analysis; AOAC l965) and ash content. The lipid and ash proportions by dry weight were converted to wet mass by multiplying them by the percent dry solids in the original sample (% lipid or ash dry mass x % dry solids = % lipid or ash wet mass; Hendry and Berg 1999). Protein content of each tissue sample was determined by subtracting ash, lipid and water content from the total sample weight (% protein = 100- % water - % lipid - % ash). This method of determining protein content is usually within a percentage point of results from the Kjeldahl procedure (Hendry and Berg 1999). Lipid and protein contents by wet mass were then multiplied by their energy equivalents (36.4 kJ/g for lipid and 20.1 kJ/g for protein; Brett 1995) to yield mass-specific tissue energy values.

The muscle biopsies were dried at 100°C until they reached constant mass. The dried samples were ground to a fine powder using an aluminum oxide mortar and pestle and 1 mg of the sample was placed into a 4 x 6-mm tin cup. Aliquots of dried and homogenized muscle, viscera, and gonad samples were prepared separately in the same manner. Samples were sent to Northern Arizona University for stable isotope analysis of δN^{15} and δC^{13} ratios (see Doucett et al. 1999).

From the sample of fish at each site, we calculated mean (and SE) energy content values (Kj/g) for each tissue type (muscle, gonad, or viscera) separately by gender. We estimated the total energy content of each tissue by multiplying the rate specific values by the total tissue mass. We estimated mass of the total swimming musculature by assuming it comprised about 60% of the total fish weight (Kizevetter 1971; Webb 1993). To estimate the cost of migration from Bonneville to Roza Dam, we subtracted the mean tissue-specific energy contents of fish at Roza Dam from those of fish at Bonneville Dam. This migration entails about 510 km of swimming

through reservoirs, passage through four major dams, and any delays or fall backs that may have occurred. To assess the influence of different migration histories on energy use, we divided the fish sampled at Roza Dam into two groups: (1) those fish that completed the migration in 27 days or less ("fast" travelers); and (2) those that required more than 27 days to complete the migration ("slow" travelers). Twenty seven days was the median travel time for fish moving from Bonneville to Roza Dam.

We estimated the energy cost of the latter part of the migration and reproduction by subtracting the mean energy contents of fresh carcasses from those of fish at Roza Dam. We did this for fish that successfully spawned (carcasses with <25% of the gonad mass retained) and those that did not (carcasses with >25% of the gonad mass retained). Because the majority of carcasses collected on the spawning grounds had a radio or PIT tag, we used previously collected telemetry data to reconstruct their migration history (e.g., timing, delays, or fall backs) and explore whether different migration histories through the CRB influenced reproductive success.

For our stable isotope data, we plotted the δN^{15} and δC^{13} values for individual fish obtained from the biopsy and the large muscle sample against each other and compared these lines to a 1:1 relation to assess the efficacy of biopsies for estimating stable isotope ratios. We then plotted muscle lipid content against the δC^{13} ratio, protein content against the δN^{15} ratio, and subjected each relation to simple linear regression.

Results

Number of fish sampled

In total, we sampled 19 males and 29 females from Bonneville Dam, 23 males and 25 females from Roza Dam, and 3 males and 19 females from the spawning grounds on the Yakima River (Table 1). At Bonneville Dam, females were slightly longer and weighed more than

males, on average, but at Roza Dam the reverse was true. After traveling from Bonneville Dam to Roza Dam, females lost about 10% of their body weight and males lost about 3%. Compared to fish at Roza Dam, male carcasses on the spawning grounds showed a 32% decrease in weight, whereas females dropped about 46% in weight.

Proximate composition and energy content of fish at Bonneville Dam

Because of an oven malfunction during drying, many of the samples collected at Bonneville Dam were damaged, which lowered the sample sizes for the proximate analyses. Male and female Chinook salmon sampled at Bonneville Dam had similar mean percentages of water, lipid and protein in the swimming musculature and viscera (Table 2). Females, however, had significantly higher levels of lipid and protein in the gonads than males. The gonads of males had a significantly higher water content than females. Energy density (kJ/g wet mass) was greatest in the muscle and did not differ between the sexes (Table 2). Energy density of the viscera was about half the value of muscle and also did not differ between the sexes. The gonads of females had an almost 4-fold higher energy density value when compared to males.

Proximate composition and cost of migration for fish at Roza Dam

Collectively, female Chinook salmon at Roza Dam had slightly lower mean percentages of lipid in the swimming musculature and viscera than did males (Table 2). Protein content in the muscle and viscera was similar between the sexes and females again had significantly higher levels of lipid and protein in the gonads than males (Table 2). Water content in all the tissues followed a similar pattern to that observed for fish from Bonneville Dam.

The median travel time for fish sampled at Roza Dam was 27 d and ranged from 18 to 42 d (Figure 4). The energetic cost of migration for fast and slow traveling fish differed somewhat between the genders. Fast traveling males lost nearly 6% of their energy density in muscle and

showed increases in energy density in the viscera and gonads during the journey from Bonneville to Roza Dam (Table 3). Slow traveling males lost just over 10% of their energy density in muscle and almost 2% in the viscera. Like their fast traveling counterparts, slow moving males gained over 10% in energy density in the gonads. Fast moving females lost almost 10% of their energy density in the muscle and showed increases in energy content of 4-5% in the viscera and gonads during the journey from Bonneville to Roza Dam (Table 3). Slow moving females lost over 17% of their energy density in muscle and 0.2% in the viscera and showed an identical increase in energy density in the gonads to fast moving fish.

Cost of migration and reproduction for fish on the spawning grounds of the Yakima River

We radio tracked 74 fish from Roza Dam to the spawning grounds. The distance from Roza Dam to the main spawning grounds was about 100 km and on average fish spent 114 d traveling to and holding in this area. After spawning had ended, we sampled 22 carcasses; of these, 8 had radio tags, 2 had PIT tags, and 12 were from the general population. Of the 22 carcasses sampled, 15 were from fish that spawned successfully (13 females and 2 males) and 7 were from fish that did not (6 females and 1 male). Male Chinook salmon that successfully spawned and those that did not used similar amounts of energy from the muscle and viscera (Table 2). The single male fish that did not spawn successfully lost about 25% of its gonadal energy density, compared with a mean loss of 14.5% in fish that did spawn. Females that spawned used a similar amount of energy from the muscle and about 5% less energy from the viscera when compared to fish that failed to spawn (Table 2). In contrast, the energy density of gonads in females that spawned was about 24% lower than in fish that failed to spawn .

From the time of passage at Roza Dam to death, males that successfully spawned used, on average, 99.6% and 80.7% of their muscle and visceral lipid stores (Table 2). During this

period, muscular and visceral protein levels in these fish decreased by 30% and 16.4%. The single male that did not spawn used similar amounts of stored muscle lipid and visceral protein and lesser amounts of muscular protein and visceral fat when compared to males that did spawn. The percent decrease of muscle lipid, muscle protein, and visceral protein reserves was similar between females that spawned and those that did not (Table 2). In contrast, females that failed to spawn lost about 13% more of their visceral fat reserves when compared to fish that spawned successfully.

Stable isotope analyses

The concentration of δN^{15} in the biopsy was a good predictor of the level of δN^{15} found in the large muscle sample (Figure 5). However, the biopsy tended to overestimate the level of δC^{13} in the muscle sample (Figure 6). Lipid and protein content in the muscle was poorly correlated with levels of δC^{13} and δN^{15} for fish sampled at Bonneville and Roza Dams (Figures 7 and 8). In carcasses, δC^{13} showed substantial enrichment but δN^{15} levels were similar to live fish sampled at the dams (Figures 7 and 8).

Discussion

The upstream migration of adult Pacific salmonids in the Columbia River Basin has been dramatically altered. For example, the spring Chinook salmon we studied pass through five major hydroelectric dams on their way to spawning grounds on the Yakima River. The ascent of these fish can be affected by delays at dams, fall back over dams, fishway passage, and futile attempts to enter turbine discharges. Further, as stated by Brett (1995), the impoundments above dams have reduced water velocities but expose fish to higher temperatures and contaminants, perhaps expending more energy than is saved by the reduced swimming effort. By using a sequential proximate analysis technique, we estimated the energetic costs of the upstream migration for Yakima River spring Chinook salmon and tried to assess the influence of migration

history on energetics and reproductive success. Our results showed that, on average, fish taking a relatively long time for migration between Bonneville and Roza Dams used from 5 to 8% more energy from the muscle than fish that completed the same distance in a shorter time. Also, slow moving fish showed a net loss of energy from the viscera whereas fast moving fish actually gained energy in the viscera. However, we were unable to assess a potential link between migration history and reproductive success because we did not collect enough carcasses with radio or PIT tags in them that could provide retrospective information on their journey. We noted little difference in the energy content of carcasses from fish that spawned successfully and those that did not. Thus, although a somewhat protracted migration did exact an energetic toll on Yakima River spring Chinook salmon, the question of whether this could influence reproductive success remains equivocal.

At the start of their journey, the energy reserves of Yakima River spring Chinook salmon are remarkably high compared to other species. The high energy content of these fish is consistent with the "interior races" of salmon described by Gilhousen (1980)—i.e., fish that arrive early in the estuary, only partly mature, and migrate over great distances and prolonged times. Compared to "coastal races" of salmon, which store 2-5% somatic lipid reserves to support migration energetics, interior upriver migrants need large amounts of energy for the long migrations and to partition somatic energy to gonadal development (Brett 1995). The energy levels in Yakima River spring Chinook salmon reflect the relatively high percentage of fat in the muscle (18-20%), which is up to 8% higher than other interior races of salmon (see review in Brett 1995). In fact, the only race of salmon that we found to have a higher fat content than those from the Yakima River were Chinook salmon from the Yukon River, which can travel more than 2400 km and have a fat content up to 24% (Iverson 1972). The journey undertaken by

Yakima River Chinook salmon is longer (ca. 845 km) and involves a greater elevation gain (ca. 580 m) than, for example, Pick Creek sockeye salmon (98 km, elevation gain of 22m; Hendry and Berg 1999), Adams River sockeye salmon (483 km, elevation gain of 366m; Gilhousen 1980), or River Drammen Atlantic salmon (~40 km; Jonsson et al. 1997). In contrast, Yakima River Chinook salmon would presumably have a less arduous journey than early Stuart River sockeye salmon (1086 km, elevation gain of 701m; Gilhousen 1980), or Chinook and chum salmon *O. keta* from the Yukon River (see Brett 1995). Thus, the high energy reserves of Yakima River Chinook salmon are necessary for fueling their migration energetics and sustaining a prolonged fresh water holding period during sexual maturation and spawning.

Although Yakima River spring Chinook salmon apparently have sufficient energy reserves at the start of their migration for completion of their journey and successful spawning, excessive delays and protracted migration times can waste energy. For example, females in our study that took a relatively long time to migrate from Bonneville to Roza Dam showed a percentage decrease in energy from the muscle almost twice that of fish that migrated faster. Also, slow, but not fast, moving fish showed some loss of energy from the viscera. However, these energy losses did not affect gonad development since both fast and slow migrating fish showed identical gains in gonadal energy at Roza Dam. Slow moving fish, particularly those that required >30 d to travel from Bonneville to Roza Dam, were not well represented in our samples. Future sampling should target slow moving individuals to provide a greater understanding of the influence of delayed migrations on reproductive success. Current research by personnel from the University of Idaho assessing energy use of spring Chinook salmon migrating from Bonneville Dam to tributaries of the Clearwater River in Idaho could provide further insight. This journey entails a distance of greater than 700 km and passage of 9 dams.

Two questions are salient relative to long migrations and wasted energy: (1) does the amount of energy lost during long migrations influence reproductive success?; and (2) what are the causes of delays and long migration times? Unfortunately, our results provide only moderate insight into these questions. Originally, our intent was to sample fish at Roza Dam and the spawning grounds that had radio tags implanted in them. By using the vast array of telemetry receivers at dams in the CRB, we could have reconstructed an accurate migration history for each fish and assessed the influence of migration history on fish energetics. However, obtaining radio-tagged fish was more difficult than we had anticipated. Our sampling at Roza Dam was constrained by time, logistical, and other agency needs that precluded us from waiting and sampling only radio-tagged fish. On the spawning grounds, despite our mobile tracking of fish, we had problems specifically locating and accessing radio-tagged fish. We did sample many fish that had PIT tags in them, but because PIT tag detectors at dams are not widespread and they have a small detection range, deriving a detailed migration history for fish from PIT tags is questionable. The challenges posed by trying to sample individuals from a cohort that have radio-tags implanted in them are not insurmountable. Future research should: (1) plan for the time needed to be selective about the fish sampled at dams; (2) conduct frequent monitoring of the specific location of radio-tagged fish on the spawning grounds; and (3) use snorkeling or diving to obtain carcasses soon after spawning.

The pattern of energy use by Yakima River spring Chinook salmon was similar to other salmonids. From the time they passed Bonneville Dam to death, these fish, depending on gender, used 97-99% of their muscle and 76-81% of their visceral lipid stores. Also, both sexes used about 32% of their muscular protein reserves and very little of their visceral protein stores. Such changes in the proximate composition of these fish translate into losses of energy content in

the muscle of 69-75%, and 32-37% in the viscera. An almost complete depletion of lipid and a moderate loss of protein have been documented in Atlantic salmon (Jonsson et al. 1997), sockeye salmon (Gilhousen 1980; Hendry and Berg 1999) and other semelparous salmonids (see Brett 1995) from the time of early migration to death. As stated by Hendry and Berg (1999), fat is the primary energy source during the early part of migration and initial gonad development. During final sexual maturation and development of secondary sexual characters, muscle protein is the primary energy source. We sampled our fish at only three points during their migration and, although fat and protein reserves showed the largest decrease during the period from passage at Roza Dam to death, details regarding the partitioning of this energy loss are unknown. For example, we do not know how much of the energy lost during this period (a minimum of 114 d) contributed towards final gonad development. Clearly, more frequent sampling, particularly during the time between passage at Roza Dam and spawning and death, would have provided the most detailed information on energy partitioning of Yakima River spring Chinook salmon.

The naturally occurring stable isotope ratios of δC^{13} and δN^{15} become incorporated into the tissues of salmon during feeding in the marine environment. During the upstream spawning migration of Pacific salmon, when these animals stop feeding and use their lipid and protein stores for energy, the δC^{13} and δN^{15} signatures become enriched in various tissues (see Doucett et al. 1999). We used a small biopsy to estimate the δC^{13} and δN^{15} ratios in the muscle of our fish and correlated those values with lipid and protein content to assess the efficacy of this technique for obtaining nutritional information on fish without killing them. Doucett et al. (1999) explored this idea with Atlantic salmon and were successful in measuring stable isotope ratios during the spawning migration of these fish and correlating them with nutritional information. For example, significant correlations existed between lipid content and δC^{13} in red muscle and

protein content and δN^{15} in liver. However, Doucett et al. (1999) had to sacrifice their fish to obtain this information, which would be unacceptable for any long-term efforts in the Columbia River Basin.

In our study, although the levels of δN^{15} estimated from a muscle biopsy correlated well with values from a large, homogenized muscle sample, the biopsy tended to overestimate δC^{13} values when compared to the muscle sample. This is probably because the biopsy consisted of only white muscle and the large muscle sample was a homogenized mix of red and white fibers. In Atlantic salmon, white muscle had higher δC^{13} values than red muscle during the upstream migration (Doucett et al. 1999) which, if true for our fish, would explain the tendency of a biopsy to overestimate δC^{13} levels. We surmise that an improved correlation between levels of δC^{13} in a biopsy and a large muscle sample would come from sampling only red muscle. In retrospect, we should have taken a biopsy of only red muscle, but chose not to because in a field situation with live fish we thought it would be prudent to avoid damage to the lateral line area. We now realize that the damage sustained from the biopsy procedure is minimal and we could have sampled red muscle from the lateral line area of a fish with minor effects. Despite this oversight, we consider the biopsy a viable technique for obtaining stable isotope ratios in muscle without sacrificing the fish.

The levels of δC^{13} and δN^{15} in the muscle of our fish correlated poorly with lipid and protein content, which is similar to the results of Doucett et al. (1999) from the white muscle of Atlantic salmon. The poor correlation between lipid content and δC^{13} likely stems from sampling mostly white muscle, which does not show the same level of enrichment as red muscle during the upstream migration. Returning salmon rely on aerobic red muscle for sustained swimming (Webb 1993; Bone 1978), which is fueled primarily by lipid reserves and shows a

significant enrichment of δC^{13} as lipid stores are depleted. In contrast, the poorly vascularized white muscle is used for burst swimming events, relies on anaerobic glycolysis for energy, and shows minor enrichment of δC^{13} during the upstream migration. As expected, the greatest enrichment of δC^{13} was seen in the muscle of post-spawn carcasses, which had exhausted almost all of their lipid reserves. Future research should explore the efficacy of red muscle biopsies and stable isotope analysis for obtaining nutritional information on fish.

Despite significant protein losses from the muscle of our fish during the period of migration, spawning, and death, we observed no enrichment of δN^{15} in this tissue. Our results are similar to those reported for Atlantic (Doucett et al. 1999) and sockeye salmon (Kline et al. 1993) and add to the body of evidence that protein catabolism does not cause enrichment of δN^{15} in the muscle of anadromous salmonids. Doucett et al. (1999) offer several possible explanations for the lack of δN^{15} enrichment in muscle, including metabolic reorganization, population effects, and relative ease of migration. Whatever the cause, it does not appear that protein content and δN^{15} levels hold as much promise as lipid content and δC^{13} for obtaining nutritional information on fish as they migrate. .

In summary, we were successful in obtaining energetics information from a specific cohort of spring Chinook salmon during their migration, but were unable to relate energy use and reproductive success to migration history. The variability in proximate composition, travel times, and energy use among individuals coupled with variations in river conditions (e.g., flows, spill levels, and temperatures) suggest that detailed information on the influence of migration history and the hydroelectric system on energetics and reproductive performance will require a multi-year effort. Such an effort should continue to focus on a single cohort and take advantage of the extensive telemetry monitoring system in the CRB to derive individual-based migration

histories. Finally, the use of muscle biopsies and stable isotope analysis, particularly focused on the relation between lipid content and δC^{13} levels, has potential for obtaining nutritional information on fish without sacrificing them.

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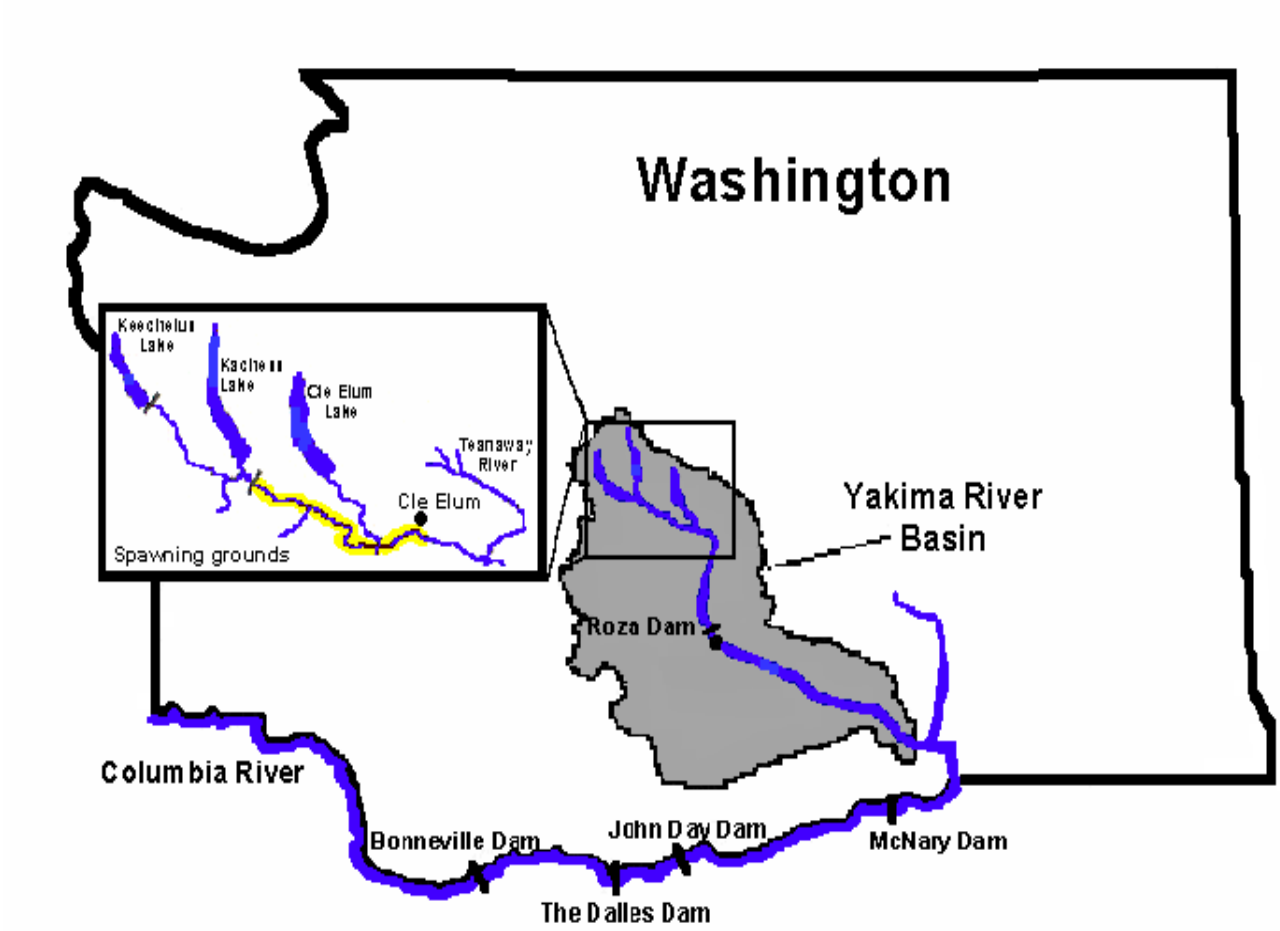

Figure 1.—Map of the migration route for returning Yakima River spring Chinook salmon. Samples were collected at Bonneville dam on the Columbia River, Roza dam on the Yakima River, and the Yakima River spawning grounds represented by the highlighted area.

Table 1.—Sample dates, locations, sample sizes, and mean (± SD) lengths and weights of returning adult Yakima River spring Chinook salmon, 2002. NA = not available.

		Males			Females		
Week	Collection site	N	Length	Weight	N	Length	Weight
April 14	Bonneville Dam	1	66.7	3.60	2	77.2±11.3	6.19±2.5
April 21	Bonneville Dam	4	69.98±6.6	4.59±1.5	7	71.9±3.0	4.84±0.7
April 28	Bonneville Dam	14	69.64±5.4	4.49±1.2	20	70.42±4.9	4.69±1.1
Total		19			29		
May 19	Roza Dam	2	72.5±3.5	4.50±0.3	7	70.71±2.8	4.46±0.8
May 26	Roza Dam	21	70.62±6.8	4.38±1.3	18	69.94±5.4	4.17±0.9
Total		23			25		
September 15	Spawning grounds	1	72.8	2.80	3	69.21±5.6	2.56±0.5
September 22	Spawning grounds	2	74±5.7	3.26±0.93	14	71.04±3.8	2.71±0.6
September 29	Spawning grounds	0	0	0	2	71.0	NA
Total		3			19		

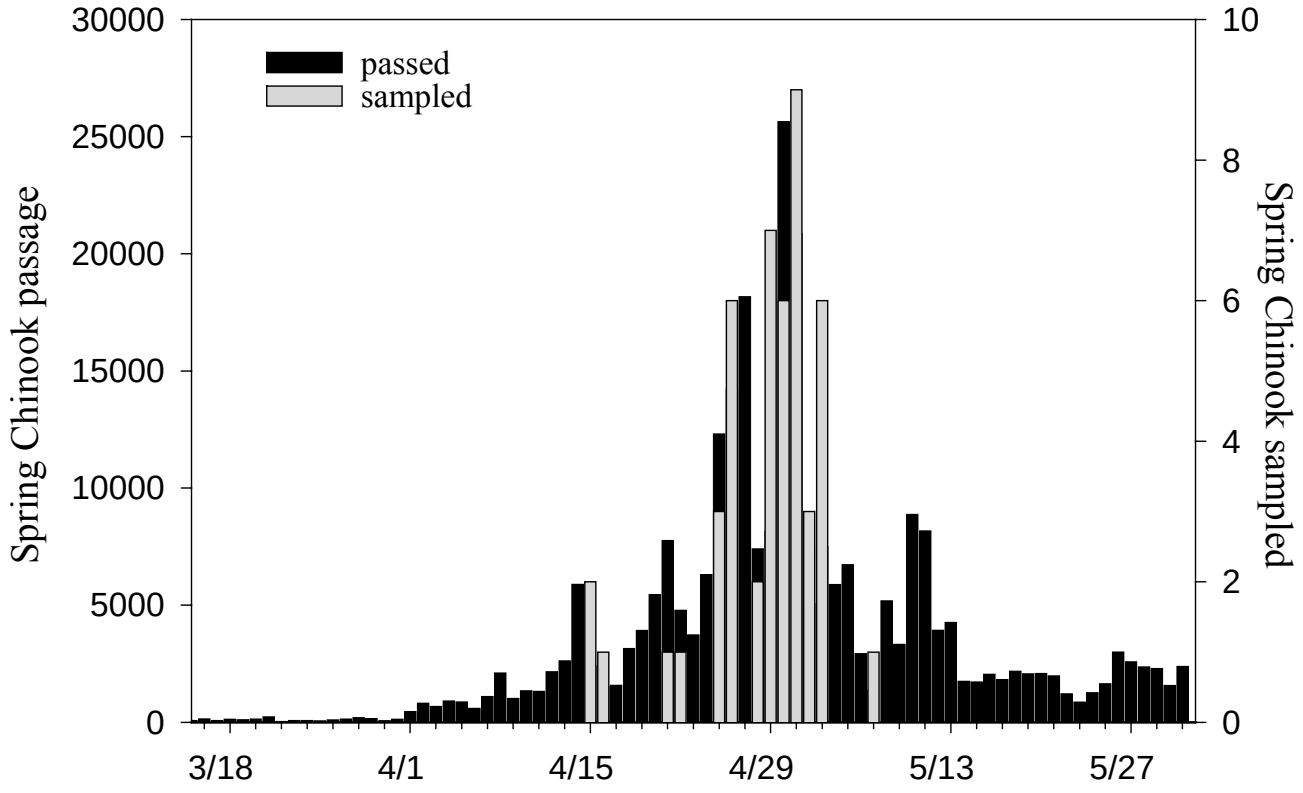

Figure 2.—Adult spring Chinook salmon passage through Bonneville Dam, Columbia River, in 2002, overlayed with the sampling of Yakima River spring Chinook salmon for proximate analysis.

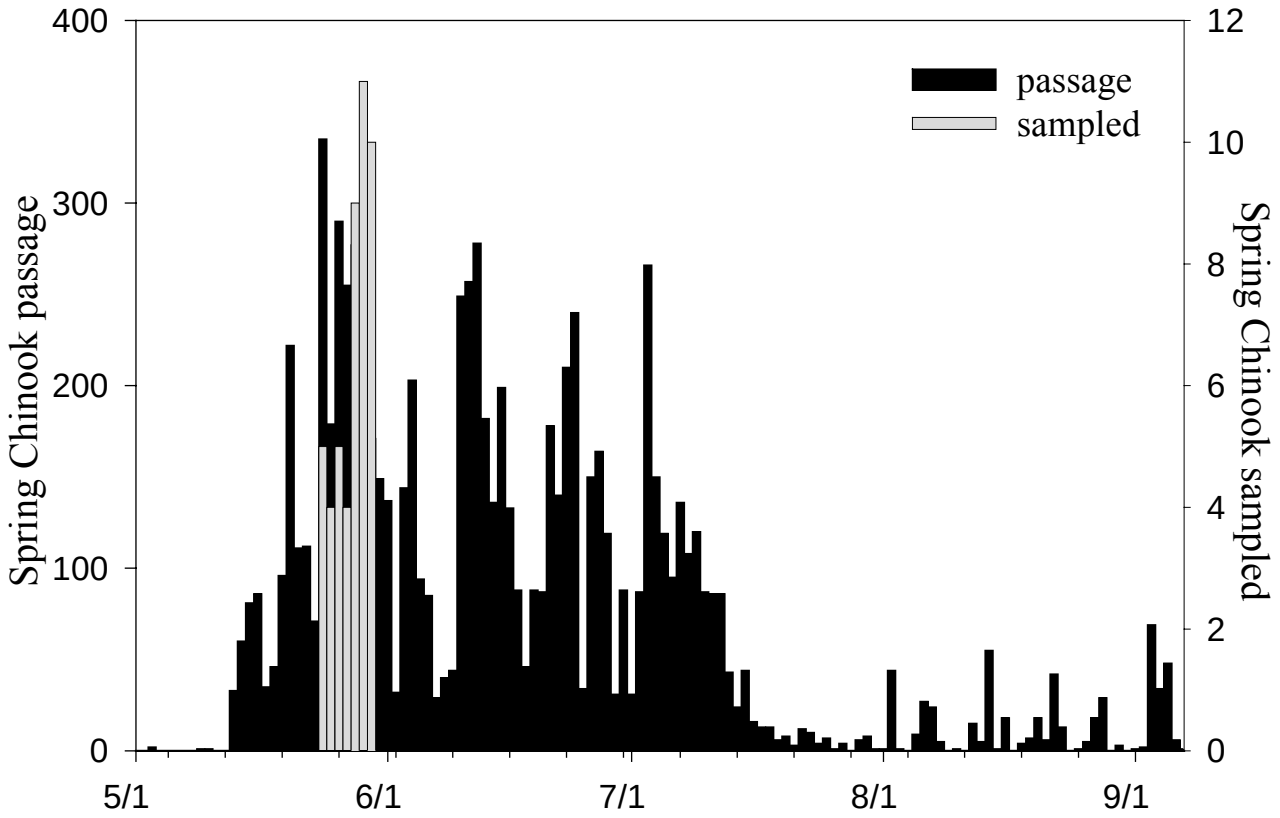

Figure 3.—Adult spring Chinook salmon passage through Roza dam, Yakima River, in 2002, overlayed with the sampling of fish for proximate analysis.

Table 2.—Proximate composition (percent water, lipid and protein by wet mass) and energy content (kJ/g) of the muscle, viscera, and gonad of adult Yakima River spring Chinook salmon at different stages of the migration, 2002. S=successfully spawned, U=did not spawn. Values are the mean±SE.

		Muscle				Viscera				Gonad			
	N	Water	Lipid	Protein	Energy	Water	Lipid	Protein	Energy	Water	Lipid	Protein	Energy
						Females							
Bonn	29	60.2±2.1	19.7±2.0	19.4±1.3	11.1±0.2	75.4±1.9	5.9±1.4	16.8±1.7	5.4±0.2	59.0±2.8	15.3±1.9	24.8±2.4	10.5±0.2
Roza	25	63.0±2.5	15.1±2.9	20.9±1.3	9.7±0.2	74.5±1.8	3.9±1.9	20.4±1.0	5.5±0.1	55.1±1.5	14.5±2.5	28.7±2.6	11.1±0.1
Death													
S	13	85.2±1.6	0.4±1.3	13.2±0.5	2.8±0.5	82.3±1.2	1.6±0.7	15.3±1.4	3.6±0.3	79.2±9.9	5.2±7.6	14.2±4.9	4.8±3.1
U	6	85.1±2.0	0.9±1.9	12.6±1.0	2.9±0.7	83.2±1.2	1.1±0.5	14.7±1.2	3.4±0.3	70.8±4.5	5.0±1.3	22.0±3.0	6.2±1.0
						Males							
Bonn	19	60.3±2.0	18.5±2.3	21.7±1.6	11.1±0.2	76.1±1.8	7.2±1.1	17.0±1.8	5.8±0.1	82.7±1.3	0.3±0.2	15.0±0.8	3.1±0.0
Roza	23	61.8±2.2	16.9±2.6	20.3±1.1	10.2±0.2	74.2±2.5	5.2±2.5	19.6±1.5	5.9±0.2	81.1±1.0	0.1±0.1	17.2±1.1	3.5±0.1
Death													
S	2	84.7±0.9	0.1±0.0	14.2±0.2	2.9±0.0	81.9±0.1	1.0±0.3	16.4±1.3	3.7±0.1	82.1±0.8	1.0±0.3	13.0±2.7	2.9±0.4
U	1	82.5	0.3	16.4	3.4	82.3	1.7	15.8	3.8	83.5	0.2	12.6	2.6

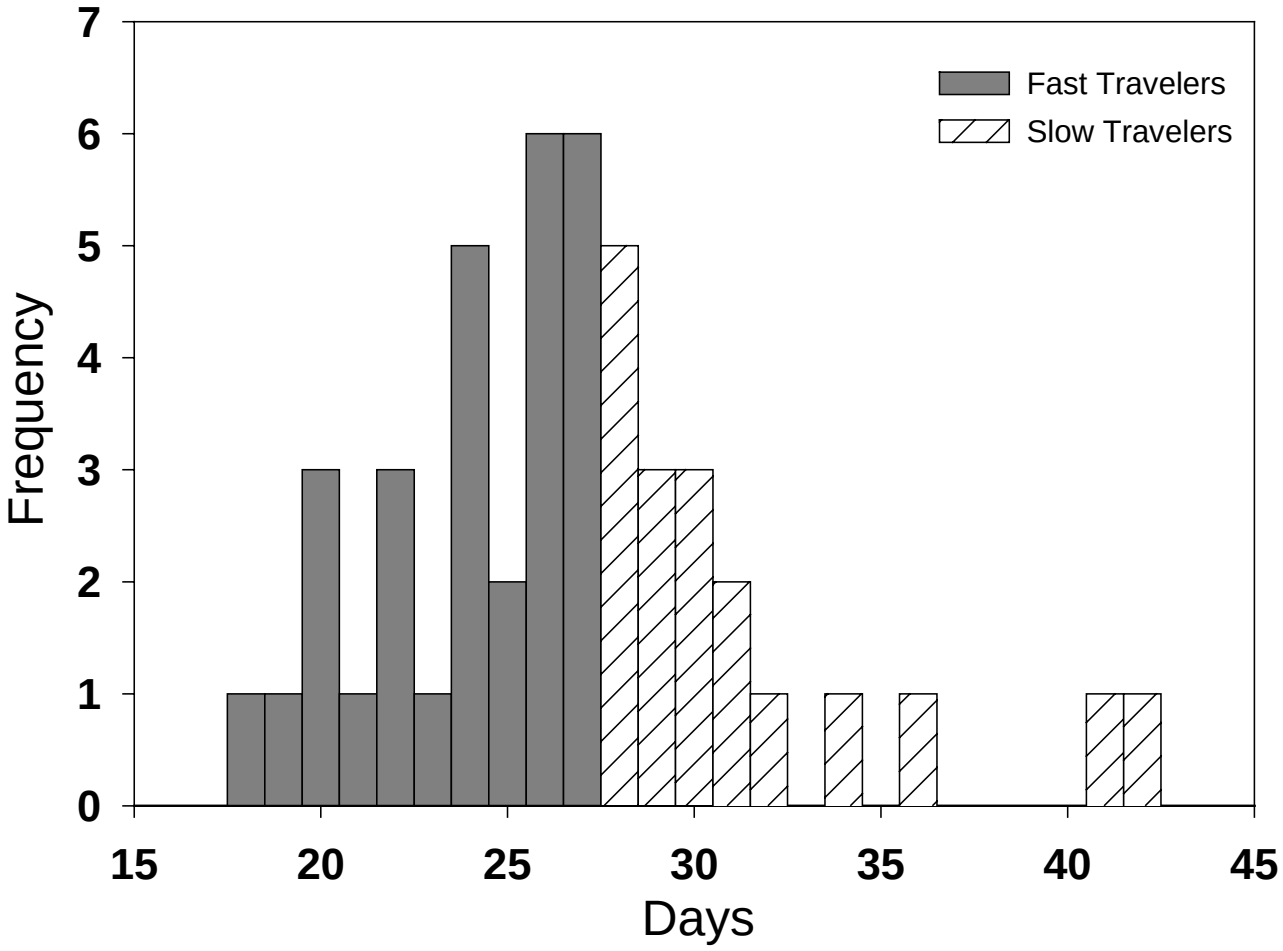

Figure 4.—Travel time distribution of PIT-tagged Yakima River spring Chinook salmon from Bonneville to Roza dam, 2002. Median travel time was 27 d.

Table 3.—Mean (and SE) energy content (kJ/g) in the muscle, viscera, and gonad of adult Yakima River spring Chinook salmon sampled at Bonneville Dam and for fast and slow traveling fish sampled at Roza Dam, 2002. The percent difference is the change in energy content between fish at Bonneville Dam and those at Roza Dam.

	Bonneville	Roza Fast	% Difference	Roza Slow	%Difference
			Males		
Muscle	11.14 ± 0.5	10.49 ± 0.6	**-5.8**	10.00 ± 0.9	**-10.2**
Viscera	5.80 ± 0.2	5.95 ± 1.0	**+2.6**	5.70 ± 0.8	**-1.8**
Gonad	3.10 ± 0.1	3.44 ± 0.2	**+10.9**	3.53 ± 0.3	**+13.9**
			Females		
Muscle	11.09 ± 0.6	10.02 ± 0.6	**-9.6**	9.16 ± 1.2	**-17.4**
Viscera	5.38 ± 0.5	5.58 ± 0.7	**+3.7**	5.37 ± 0.6	**-0.2**
Gonad	10.52 ± 0.8	11.05 ± 0.5	**+5.1**	11.05 ± 0.6	**+5.1**

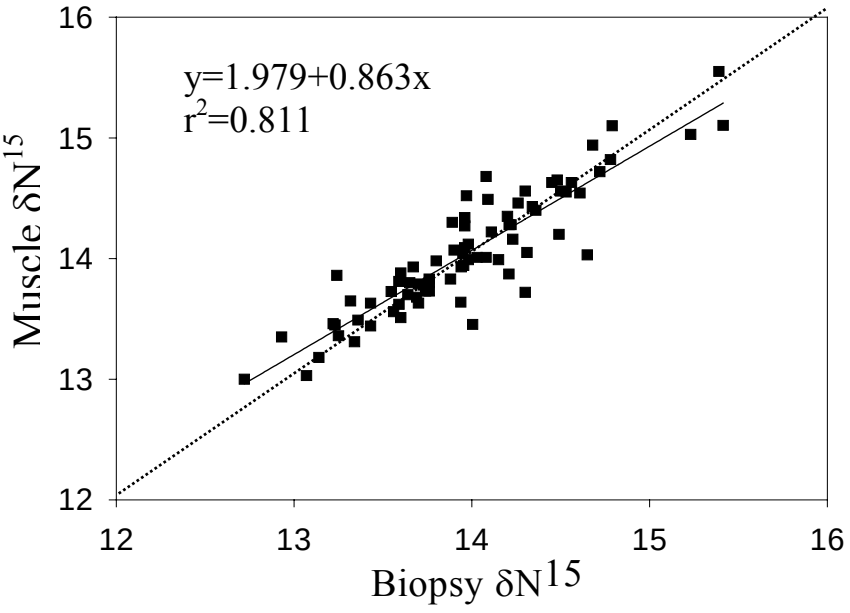

Figure 5.—Relation of white muscle biopsy and homogenized red and white muscle δN^{15} concentrations for all adult Yakima spring Chinook salmon sampled in 2002. Dotted diagonal line represents a 1:1 ratio.

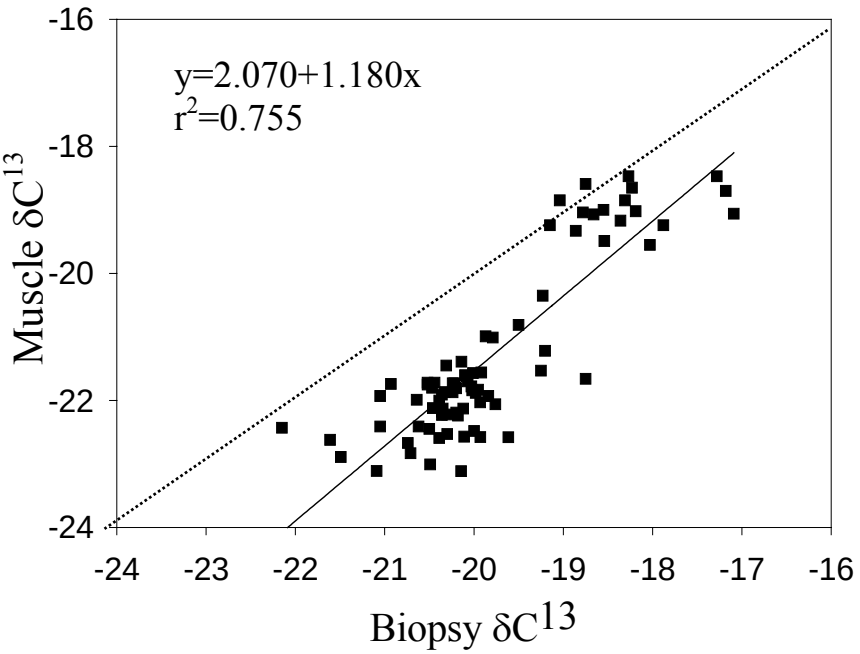

Figure 6.—Relation of white muscle biopsy and homogenized red and white muscle δC^{13} concentrations for all adult Yakima spring Chinook sampled in 2002. Dotted diagonal line represents a 1:1 ratio.

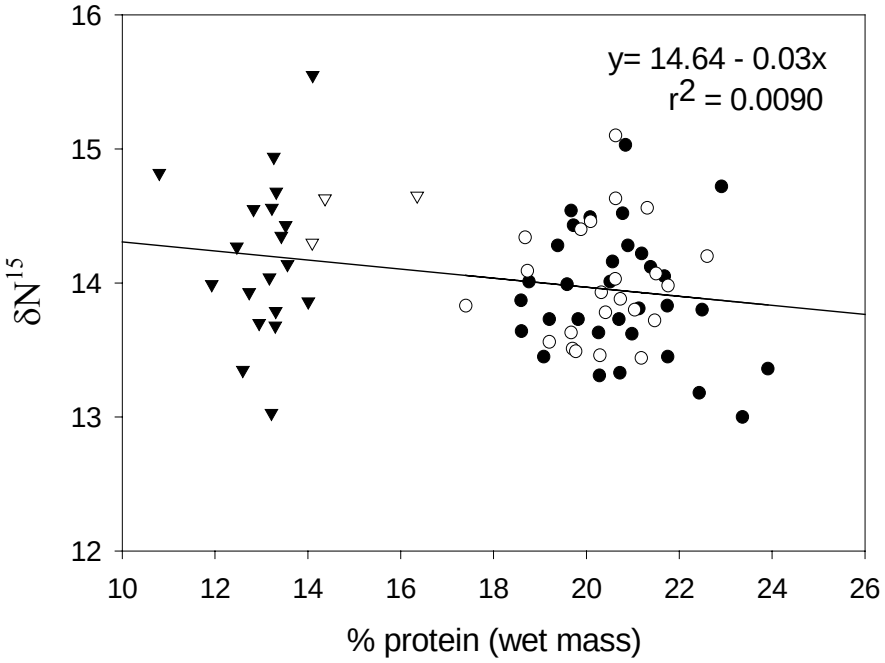

Figure 7.—Relation between concentration of δN^{15} and percent protein in the muscle of Yakima River spring Chinook salmon, 2002.

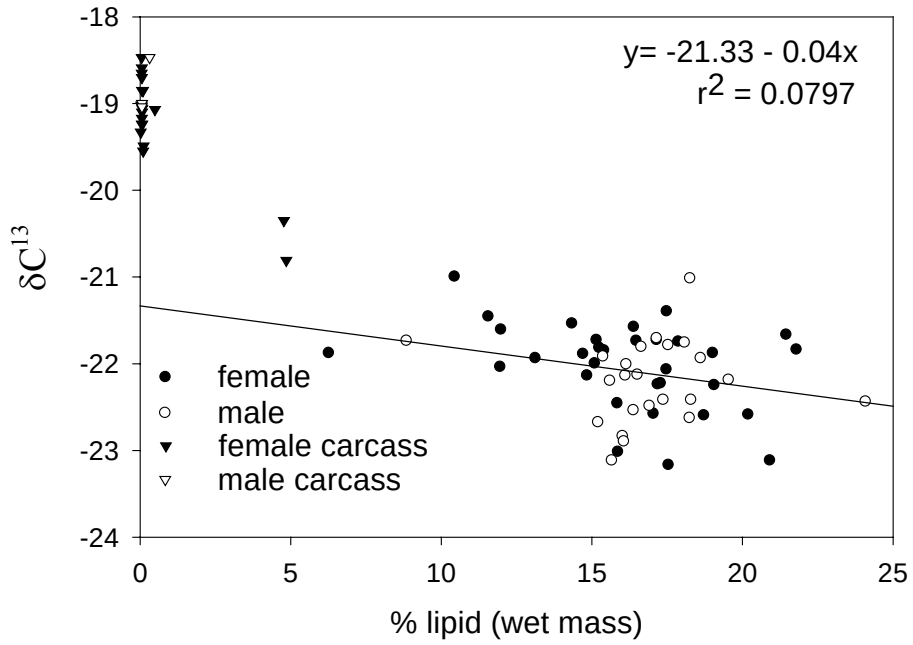

Figure 8.— Relation between concentration of δC^{13} and percent lipid in the muscle of Yakima spring Chinook salmon, 2002.