Lipids in Anadromous Northern Dolly Varden (*Salvelinus malma malma*)

by

Lisa Kulchycki

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Abstract

Anadromous Arctic fish species have adapted to a particular environment by evolving unique lipid cycling strategies such as storing large amounts of lipid during times of high productivity in order to survive long migrations, spawning events, and seasonal variation in food availability. Research on lipid content and storage location in the body is very limited, especially regarding the northern Dolly Varden, a fish species important culturally and for sustenance to the Indigenous Peoples in the western Canadian Arctic that is listed as 'Special Concern' under Species at Risk legislation. Lipid content in anadromous Dolly Varden obtained from two marine (coastal) (summer) and two freshwater (fall) locations were examined and compared to test for differences in percent lipid between locations/seasons. Percent lipid was compared between the muscle and homogenized whole-body of individuals caught in freshwater. Muscle lipid content was significantly different between freshwater locations and one of the marine locations (~34% higher from the marine location). One marine location contained fish with unexpectedly high muscle lipid percent. A weak/moderate linear relationship was found between lipid percent in the muscle tissue and whole-body tissue of the same individuals (r^2= 0.2013 when sex was an added variable; r^2= 0.4204 when reproductive status was an added variable), and reproductive status influenced this relationship. Sex of the individual did not affect lipid content in the muscle nor on the relationship between percent lipids in muscle and whole-body. Changing environmental factors due to climate change such as the timing of the ice melt and phytoplankton blooms can affect energy exchange through the food web, and thus research on the nature of fluctuating energy and lipid levels is needed to aid in conservation efforts of Arctic species.

Acknowledgements

I would like to extend my sincere thanks to my advisors Dr. Lisa Loseto and Dr. Gail Davoren for their patience and guidance in my execution of this project. I'd also like to give special thanks to Colin Gallagher for his mentorship and sharing of expertise, and to Dr. John Markham who generously provided knowledge and feedback. I am also grateful for the lab support team in the Loseto lab for their help in sample processing.

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Introduction

Arctic environments are characterized by substantial seasonal changes in sunlight, ice cover, and solar radiation where very high latitudes can experience a lack of sunlight for up to 4.5 months every winter (Hardie, 2003). Primary production in Arctic marine ecosystems is driven by sunlight and is the most important factor for growth of marine primary producers (Hoppe, 2022). Decreased rates of primary production in an Arctic ecosystem, particularly in winter, will have energetic consequences throughout the entire food chain and species will need to adapt to a variable food supply in order to survive (Blix, 2016). Instability of food sources requires Arctic animals to adapt to efficiently store higher amounts of lipids as energy reserves during periods of low food supply (Blix, 2016). This adaptation is an important factor in the biodiversity of fish, mammals, and birds in the Arctic (Blix, 2016).

Despite having a long winter period with minimal primary production, coastal marine waters in polar areas are among the most productive regions as they draw organic matter from terrestrial and marine sources (Carey et al., 2021), as well as their brief yet intense periods of primary production during spring and summer (Pabi et al., 2008) when sunlight is continuous (i.e., 24-hour period) (Folk et al., 2006). Lipids are biosynthesized by phytoplankton (~10-20% lipids dry mass) that are consumed by herbivorous zooplankton (>50% lipids dry mass) and are rapidly transferred throughout the food web to provide high-caloric energy sources to higher trophic levels (Falk-Petersen et al., 2000; Pomerleau et al., 2014), such as in beluga and bowhead whales who store these as thick layers of blubber (Thiemann et al., 2008; Loseto et al., 2009).

The primary form of stored energy in fish is lipids (Stolarski et al., 2014). Large stores of lipids are necessary to support the annual migration anadromous Arctic salmonid species undertake between freshwater and marine environments (Dermond et al., 2019; Laender et al., 2010). Anadromous Arctic fishes that perform seasonal migrations after rearing in freshwater begin by travelling to the ocean during ice break-up in spring and returning to freshwater in fall to spawn and/or overwinter, which is a period when feeding is largely reduced or absent and movement is limited to conserve energy and improve probability of overwinter survival (Mulder et al., 2018).

Dolly Varden (*Salvelinus malma*) is an iteroparous (i.e., will reproduce repeatedly during its lifetime) salmonid species that is cold-water adapted and whose North American distribution is along the Arctic coast west of the Mackenzie River and south through Alaska down along the Pacific coast of British Columbia and Washington (Redenbach and Taylor, 2002; Carey et al., 2021). They are also distributed on the western side of the Pacific Ocean, from the Chukotsk Peninsula of Russia down to Japan and Korea (Carey et al., 2021). Three subspecies of Dolly Varden are recognized: northern form Dolly Varden (*S. m. malma*), the southern form Dolly Varden (*S. m. lordi*), and the southern Asian Dolly Varden (S. m. *krascheninnikova*) (Dunham et al., 2018). In Canada, the northern form of Dolly Varden have been listed as 'Special Concern' under the Species at Risk Act (DFO, 2019). Northern Dolly Varden is important for the culture and subsistence of the Inuvialuit, Inupiat, and Gwich'in peoples of the Arctic who mainly harvest this species along the coasts of the Beaufort and Chukchi seas in summer and during the upstream/return migration period in the late-summer and fall in rivers (Gallagher et al., 2021). They are considered by co-management partners to be a priority species because populations have experienced declines in abundance and have a small number of geographically limited spawning and overwintering habitats (DFO, 2019). Dolly Varden are a lipid-rich fish, and while there is limited information regarding the role of Dolly Varden as a prey species there is recent evidence as being a food source for American Dipper (*Cinclus mexicanus*) and beluga whales (Gallagher and Lea, 2019; Gallagher et al., 2021).

Anadromous Dolly Varden hatch and remain in natal streams for 2-5 years prior to performing annual seasonal migrations between marine and freshwater habitats (Gallagher et al., 2018). Anadromous individuals enter the Beaufort Sea in approximately mid-June to feed and grow during the summer and return in late-summer and early fall to freshwater to spawn and/or overwinter (Gallagher et al., 2021). Anadromous Dolly Varden will consume almost all their yearly food in the approximately three-month period at sea and will consume very little during their overwintering period (Stolarski et al., 2014). Dolly Varden exhibit a silver colouration in marine environments and will adopt vibrant colouration when spawning (Gallagher et al., 2018). Spawning females change from silver to a dark olive-green dorsal surface with a pink/purple ventral and lateral surface, while males develop a black dorsal surface and bright orange-red ventral surface with secondary sexual characters such as enlarged teeth, kype, and laterally compressed body (Figure 1) (Gallagher et al., 2018).

Figure 1. Photo illustrating phenotypic variation in anadromous (from top) male spawners, female spawners, and non-spawning Dolly Varden (*S. malma malma*) during fall while inhabiting streams used for spawning and overwintering (Source: C. Gallagher).

There is little information regarding lipid dynamics in Dolly Varden; however, there is research on closely related species. The muscle, particularly the myosepta, which is the connective tissue separating muscle fibres (Zhol et al., 1995), is commonly regarded as being a major storage site in salmonids that can make up 1-7% (wet weight) of the muscle mass in wild salmonids (Jobling et al., 1998; Jobling et al., 2002; Nanton et al., 2007). Alternatively, farmed salmonids have higher lipid percentages in the muscle compared to wild ones (Zhol et al., 1995). However, there is some conflicting evidence, as the majority (50%) of body lipids in Arctic char (*S. alpinus*) is contained in the skin and skeletal tissue of the carcass (Jobling et al., 2008). Arctic char muscle tissue tends not to hold more than 5% lipid concentrations (when lipid is extracted from wet tissue) while lipids in viscera account for <5% of the total body lipid and believed to play a minor role as a lipid storage site in Arctic char (Jorgensen et al., 1997). Skeletal lipids may serve as an important storage site in salmonids as the neurocrania and vertebral centra of pre-spawning marine Pacific salmon have been documented containing up to 15% and 7% lipid (wet tissue weight), respectively (Jorgensen et al., 1997), while Atlantic salmon possess lipid-rich skin (18% lipid; Jobling et al., 1998). Mesenteric fat and the gut wall are also important lipid stores in salmonids and are linked to the onset of maturation and spawning (Rowe and Thorpe, 1991).

Lipid cycling is the acquisition, storage, and depletion of body lipids whose strategies differ among species and is influenced by habitat (Fernandes and McMeans, 2019). Inhabiting cold-water environments will lead to increased rates of lipid cycling, as cold-water fish store and deplete lipids more severely than warm-water species given that seasonal changes in food availability are more variable in cold-water environments (Fernandes and McMeans, 2019). Environments characterized by cyclical seasonal contrasts, such as very cold winters, favour fish with the ability to hold vast stores of lipids prior to winter, where fish in an environment with less predictable, mild/moderate seasonal shifts would favour fish with a more constant lipid allocation and storage strategy (Fernandes and McMeans, 2019).

Lipid content in anadromous fishes will fluctuate among seasons due to increased feeding in the summer and near fasting in the winter (Copeman et al., 2022). Arctic char has been known to double in body weight during their marine residency, consequently increasing the proportion of body lipids (Jorgensen et al., 1997). An abundance of lipids is necessary in anadromous fishes as the biannual migration takes a major toll on energy reserves that requires mobilization of stored lipids to meet high metabolic demands (Zimmerman et al., 2002). Lipid content in Arctic char will reduce by 40% in males and 30% in females after migration to freshwater (Jorgensen et al., 1997). If an individual prepares to spawn, lipid stores will deplete further as courtship activity and pre-spawning gonadal development requires a large amount of energy (Penney and Moffitt, 2014). While both sexes deplete energy as a result of spawning, it is for different reasons, as males tend to exert the most energy developing prominent secondary sexual characteristics and while competing with other males for mates, and females will allocate most energy towards creating lipid-rich eggs (Jorgensen et al., 1997; Henderson and Tocher, 1987). In some years an adult will skip-spawning, meaning they will forego spawning that season to save energy for overwintering and the next marine migration (Dutil, 1986). Spawning Arctic char will have a considerably greater depletion of lipid stores relative to non-spawners and will also not be able to replenish their lipid stores to the same degree that non-spawners can during the following marine feeding period (Dutil, 1986). Non-spawning Arctic char lose approximately 30% of their body weight during the ten-month overwintering period and can recover in less than 60 days upon return to the ocean, while post-spawning individuals may weigh up to 46% less than non-spawners of the same length (Dutil, 1986).

Salmonids require a minimum fat content before maturation will be initiated and spawning will be possible (Rowe and Thorpe, 1991). Atlantic salmon, for example, need a minimum of 12% total body lipid in the spring to spawn the subsequent autumn (Rowe and Thorpe, 1991). Specifically, mesenteric fat in Atlantic salmon has been identified as the lipid storage area requiring a high enough lipid content early enough in the year for spawning to occur, as the mesenteric fat becomes mobilized for use of gonadal and secondary sexual characteristic development (Rowe and Thorpe, 1991). Since a minimum fat content is required to spawn, individuals preparing to spawn and those demonstrating skip-spawning may contain different amounts of lipid stores prior to the spawning event. As females hold more lipids in gonadal tissue than males, the location of lipid stores may differ between sexes as well.

Objectives

The objective of this research is to investigate lipid storage by anadromous Dolly Varden. First, I aim to compare the muscle lipid content in Dolly Varden between seasons and habitats (fall/freshwater and summer/coastal). I will test the hypothesis that muscle lipid content in Dolly Varden is influenced by season/habitat and predict that Dolly Varden harvested in coastal marine regions during the summer will have a higher muscle lipid content than those caught in freshwater rivers during the fall. I also predict that lipid content in muscle samples of males will be greater than females, as females devote more lipids to gonadal development than males. My second objective is to determine if lipid content in muscle samples reflect lipid content in the whole body of Dolly Varden. While the limitations of such an extrapolation are recognized, the value of this evaluation serves to address the challenge that Dolly Varden are an important food source to Inuvialuit and thus only a small piece of muscle tissue can be made available for scientific research. As such, I will specifically test the hypothesis that lipid content in muscle predicts lipid content in whole-body samples of Dolly Varden from the same individuals caught in freshwater. I will also test the hypothesis that the relationship between muscle and whole-body lipid content differs between sexes and maturity status (i.e., spawner vs non-spawner). I predict that lipid content in muscle samples from spawning individuals will be lower than muscle samples from non-spawning individuals, due to lipids being used to develop gonads and secondary sexual characteristics. I also predict that females will have lower lipid content in the muscle relative to males, due to the high amount of lipids mobilized and stored in the large female gonads.

Methods

Study Area

The study area is the Babbage River (Fish Hole Creek tributary), Firth River, Shingle Point, and Herschel Island (Pauline Cove), Yukon, Canada (Figure 2) which are located in the Inuvialuit Settlement Region. The Firth and Babbage rivers are inhabited by separate stocks of anadromous Dolly Varden that will mix with other populations during summer while feeding in the Beaufort Sea (Harris et al., 2015). The Babbage and Firth rivers drain into the Beaufort Sea while Shingle Point and Herschel Island are situated along the Beaufort Sea coast (McCart, 1980). The Firth River flows from the British Mountains over 160 km to the Beaufort Sea (Golva and McCart, 1974). The Babbage River is situated between the Barn and British mountains and empties into the Beaufort Sea in Phillips Bay (Gallagher et al., 2018b). Herschel Island and Shingle Point are the primary locations in Canada where Dolly Varden stock from the Firth and Babbage rivers, respectively are harvested during summer (Gallagher et al., 2018b). The study area includes the perennial ground water springs in the Babbage and Firth rivers, which provide freshwater winter flow and overwintering habitat for anadromous Dolly Varden (Golva and McCart, 1974).

The nearshore environment of the southern Beaufort Sea has among the warmest water in the Arctic during summer with temperatures ranging ~10-15°C (Carey et al., 2021). This area contains barrier islands surrounded by relatively shallow lagoons and open coast (Carey et al., 2021). The Mackenzie River terminates in a 13 000 km^2 delta prior to entering the Beaufort Sea (Lesack and Marsh, 2010). It is the longest and largest river in Canada and supplies the most freshwater to the Arctic Ocean in the Western Hemisphere (Rood et al., 2017). During the summer, water along the coast becomes brackish and warm in comparison to the open ocean due to the turbid warmer water from the Mackenzie and other rivers along the coast (Carey et al., 2021). The western channels of the Mackenzie River provide corridors for migration for three known Dolly Varden populations as a route to enter and exit the Beaufort Sea (Gallagher et al., 2021).

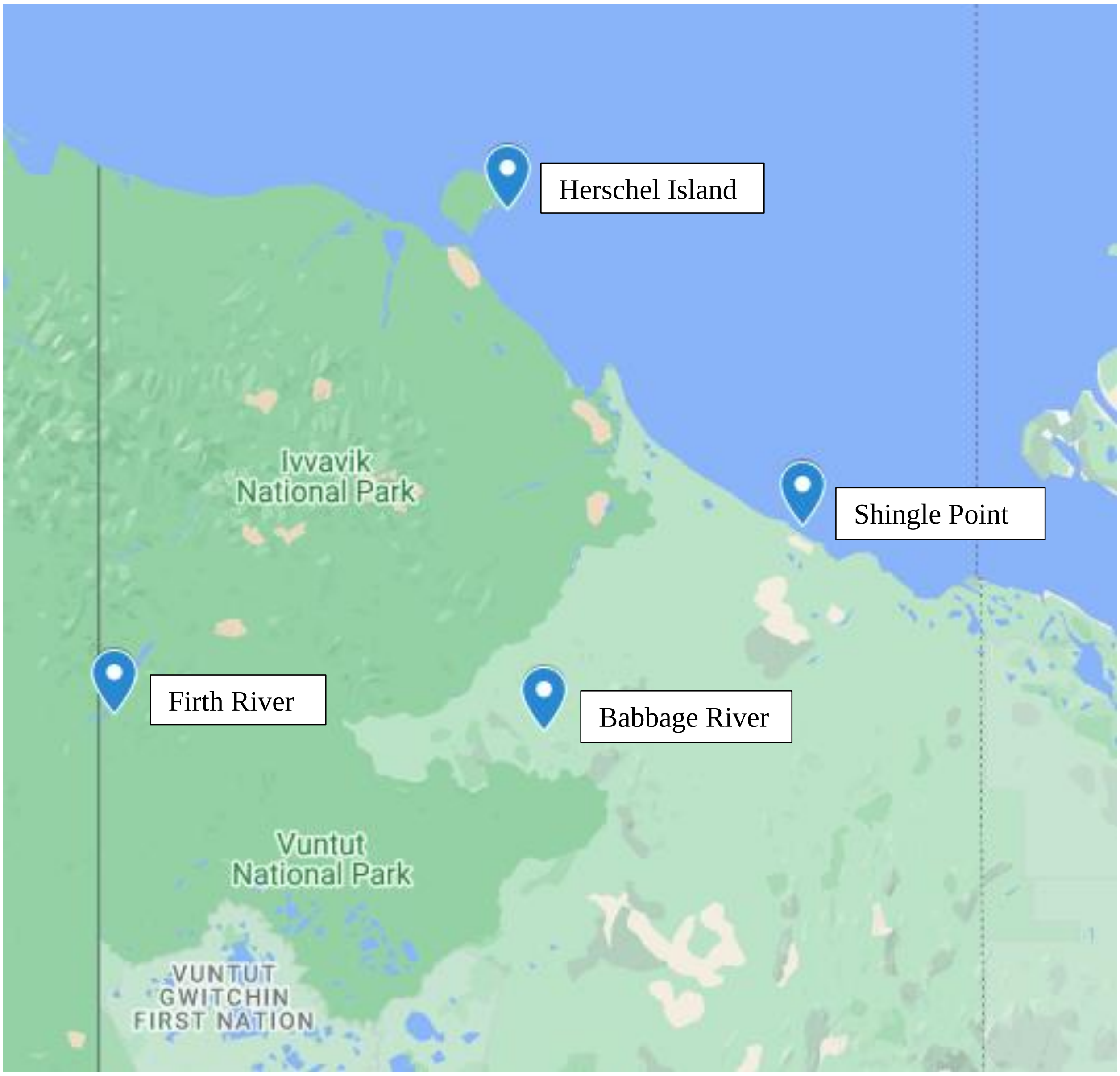

Figure 2. Study area and surrounding landscape. Includes Herschel Island (69.568816°N, -138.915778°W), Shingle Point (68.993817°N, -137.390306°W), Babbage River (68.600387°N, -138.734755°W) and Firth River (68.644773°N, -140.933956°W) (Source: Google Maps, 2023).

Sample collection and study design

Dolly Varden were sampled in marine and freshwater habitats from July to September 2020. Fish from the marine locations were caught in July and August from Herschel Island and Shingle Point using gill nets deployed from subsistence fisheries that had a sample of muscle tissue collected through a fisheries-dependent monitoring program. Sample collection was achieved in partnership with the Aklavik Hunters and Trappers Committee, Herschel Island Territorial Park Rangers, and Parks Canada. Fish from the coastal locations were used for subsistence, therefore only a subsample of dorsal muscle was obtained for research purposes. As a result, marine locations could not be used in the examination of percent lipid in muscle tissue versus whole-body. A total of 41 muscle samples were collected, with 30 samples from Herschel Island, and 11 from Shingle Point; however, four samples were not used in data analysis due to missing sex and maturity data. A total of 37 samples from the coast were used (Table 1). Fish were caught in freshwater in mid- to late September from Babbage and Firth rivers using a seine net, after which the whole body was frozen. A total of 18 and 12 pairs of whole-body/muscle samples were available from the Babbage and Firth rivers, respectively. Data from one sample from Babbage River was discarded, as it produced an unusually high lipid content, likely because of measurement error. Therefore, a total of 58 samples from freshwater were used (Table 1). Biological data from both habitats, including length, weight, age, sex, and reproductive status (i.e., mature, immature, spawner, resting), were recorded at the time of capture prior to freezing.

Table 1. Dolly Varden (*S. malma malma*) muscle (marine and freshwater) and whole-body sample sizes (freshwater) collected and analyzed from each freshwater and marine location in 2020.

	Marine		Freshwater			
Reproductive status	Shingle Pt. Muscle	Herschel Is. Muscle	Babbage R. Muscle	Babbage R. Whole	Firth R. Muscle	Firth R. Whole
Female mature[1]	3	15	5	5	5	5
Male mature[2]	4	15	4	4	5	5
Non-spawning[3]			8	8	2	2
Total	7	30	17	17	12	12

[1] identified as a ‘current year spawner’ in marine and ‘female spawner’ in freshwater
[2] identified as a ‘current year spawner’ in marine and ‘male spawner’ in freshwater
[3] identified a ‘silver’ in freshwater.

Sample processing

At Fisheries and Oceans Canada's Freshwater Institute, whole-body fish were thawed and then processed for biological data (length, weight, gonad weight) and samples including otoliths and muscle tissue were obtained. Subsequently, the entire fish was homogenized using a BN801C 30 Ninja blender before being stored in resealable bags and refrozen. All whole-body and muscle samples were then partially thawed and subsampled prior to being dried in a Labconco FreeZone 18 freeze drier. Once freeze-dried, samples were manually crushed into a powder while keeping the sample free from contamination inside the plastic bag.

A total of 0.2 grams from each dried sample was taken for lipid extraction. Three mL of methanol with 0.01% butylated hydroxytoluene (BHT) (v/v/w) was added to the sample that was subsequently vortexed and allowed to sit for 3 minutes. A total of 6 mL chloroform was added to each sample, which were then vortexed for 30 seconds, flushed with nitrogen, and stored in a freezer overnight. The liquid in the sample (test tube A) was filtered through a glass wool pipette into another test tube (test tube B) and 3 mL 2:1 chloroform-methanol containing 0.01% butylated hydroxytoluene (BHT) (v/v/w) was added to test tube A. Test tube A was then vortexed, the liquid component was filtered through the glass wool pipette, and 7 mL 0.88% NaCl was added to test tube B. The solution sat for 5 minutes before the top layer was discarded. NaSO4 was added to test tube B, which was then shaken manually and allowed to rest for 5 minutes. A third test tube (test tube C) was set up with a glass wool pipette, where the solvent from test tube B was filtered. $NaSO_4$ in test tube B was rinsed with 2 mL chloroform, the test tube was shaken, and the solvent transferred to test tube C. The chloroform rinse and transfer of solvent was repeated once more before test tube C was put in a hot water bath under an

Organomation Associates Inc. Nitrogen Evaporator (N-evap 111) to be evaporated under nitrogen. Total lipid weight was obtained using a Mettler Toledo scale (model AL204) and total lipid content (percent) was calculated by dividing lipid weight by total sample weight (~0.2g). To determine precision of measurements, lipid content was measured in triplicate for all 29 freshwater whole-body samples and in duplicate for a random subset of 21 freshwater and marine muscle samples. Averages were taken from each set of triplicates and duplicates and were used to compare to lipid percent values from the original (i.e., first set of measurements) data set. The average lipid values were used for analyses.

Lipid content in two of the triplicate whole-body samples was measured on wet tissue, while one replicate was measured on dry tissue. Therefore, lipid content from dry tissue was converted to be comparable to lipid content determined from wet tissue. All whole-body samples had 0.2 g subsampled, weighed, and dried using a Heratherm OMS60 oven to determine specific moisture content for each sample. Lipid content measured from dry tissue was converted and compared to lipid content measured from wet tissue as described by Meyer et al. (2017), using the following equation:

Lipid % (Dry Tissue)- ((Percent Moisture/100) * Lipid % Dry Tissue) = Lipid % (Wet Tissue)

The first lipid content measurement for whole body lipid percent had an average percent difference from that of triplicate values of 2.12% and standard deviation of 4.52%. The first lipid content measurement for muscle lipid percent had an average percent difference from that of duplicate values of 4.19% and standard deviation of 3.54%.

Before statistical analysis, one sample was removed from the freshwater whole-body lipid percent dataset because it was unusually high (98%), likely representing measurement error, which was confirmed by the triplicate lipid percent measurements being considerably lower.

Data Analysis

Muscle and whole-body lipid content datasets and biological covariates (age, fork-length, weight) were examined for normality using histograms and Q-Q plots and homogeneity of variance was examined using a Levene's test to determine whether these data met the underlying assumptions of parametric statistical tests. Although there were some slight departures from normality and heterogeneity of variance, we continued to use parametric statistics as they are robust to minor violations in assumptions (Erceg-Hurn and Mirosevich, 2008). As lipid content was expressed as a percentage, these data were arcsine transformed (Ahrens et al., 1990). Age, fork-length, and weight were considered as covariates of lipid content and the correlations among these covariates with lipid content (muscle and whole-body separately) were assessed prior to testing hypotheses. For the first hypothesis, a two-way ANOVA was conducted on muscle percent lipids (dependent variable) with habitat/season and sex as independent variables to confirm whether habitat/season and sex have an effect on lipid content in muscle tissue. For the second hypothesis, two ANCOVAs were conducted. The first examined the relationship between whole-body lipid content and muscle lipid content, and maturity status was included as a factor, along with the interaction, to compare the relationship (i.e., y-intercept and slope) between spawning and non-spawning individuals. The second examined the relationship between whole-body lipid content and muscle lipid content with sex included as a factor, along with the interaction, to compare the relationship between males and females. The two ANCOVAs were performed separately due to low sample sizes within each sex/maturity category.

Results

Visual inspection of muscle tissue samples post-freeze-drying demonstrated differences between samples from Shingle Point and the other three locations. Tissue samples from Shingle Point were a darker red-brown colour, oilier, and more difficult to homogenize due to the gummier texture than muscle samples from Herschel Island, and Babbage and Firth rivers, which were a lighter, off-white colour, and homogenized easily into individual muscle fibres and loose powder (Appendix: Figure 3). The cause of this difference was unknown.

Correlations were not significant between muscle lipid percent and age ($p= 0.9662$, $r= -0.01$), fork length ($p= 0.6098$, $r= -0.06$), or weight ($p= 0.5989$, $r= -0.07$; Figure 4). No correlations were found between whole-body lipid percent and age ($p= 0.7160$, $r= -0.07$), fork length ($p= 0.8281$, $r= 0.04$), and weight ($p= 0.1702$, $r= 0.26$; Figure 5). Covariates had significant relationships to one another ($p < 0.0001$ for all combinations of covariates), with fork length and weight showing the strongest correlation ($r = 0.94$, $p < 0.0001$).

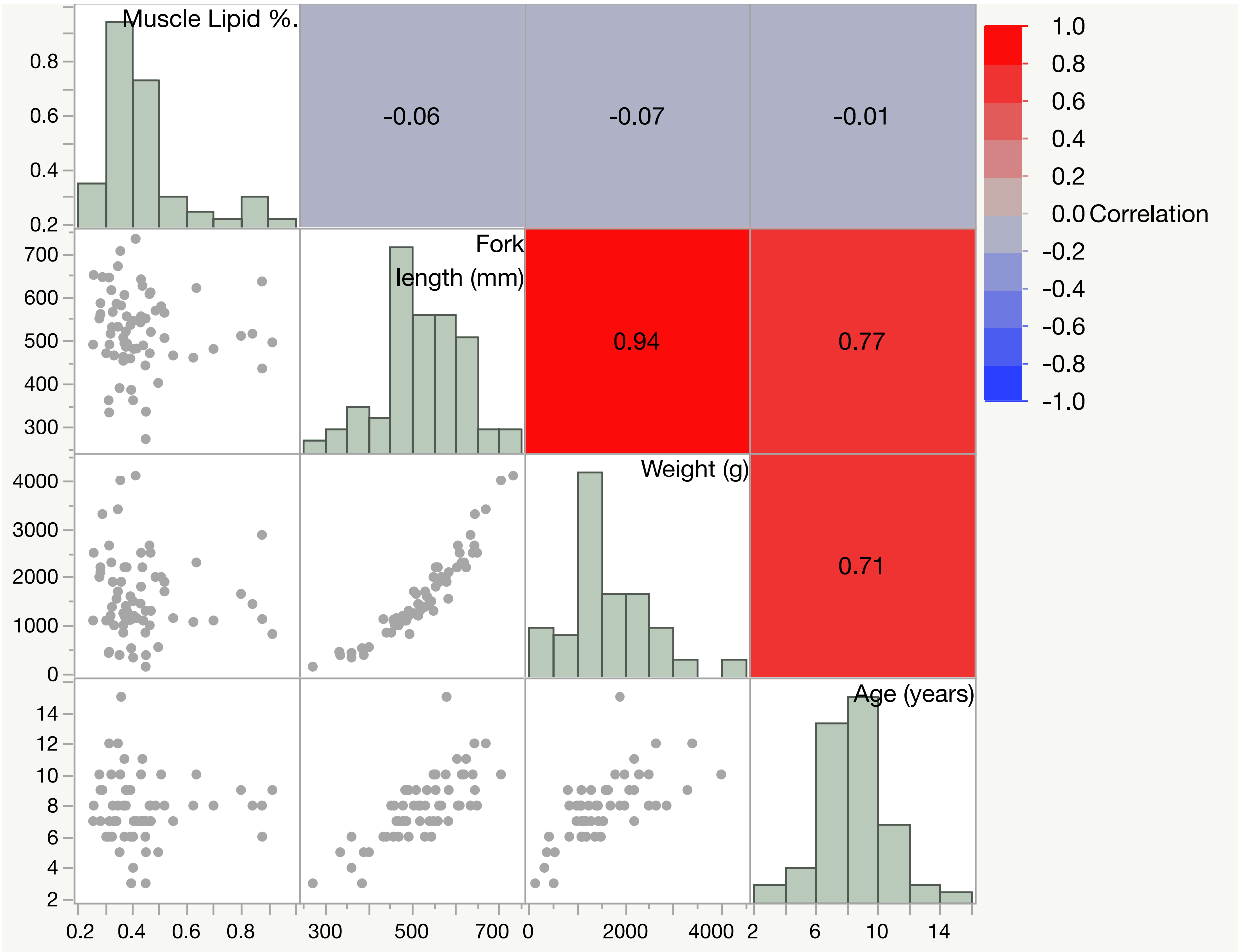

Figure 4. Correlation matrix showing histograms, scatterplots, and heat map showing correlation values (R) between muscle lipid percent (dry weight) and age (years), fork length (millimetres), and weight (grams) performed on arcsine transformed lipid percent data from Dolly Varden (*Salvelinus malma malma*) collected from freshwater and marine locations. Fork length, weight, and age data are not transformed.

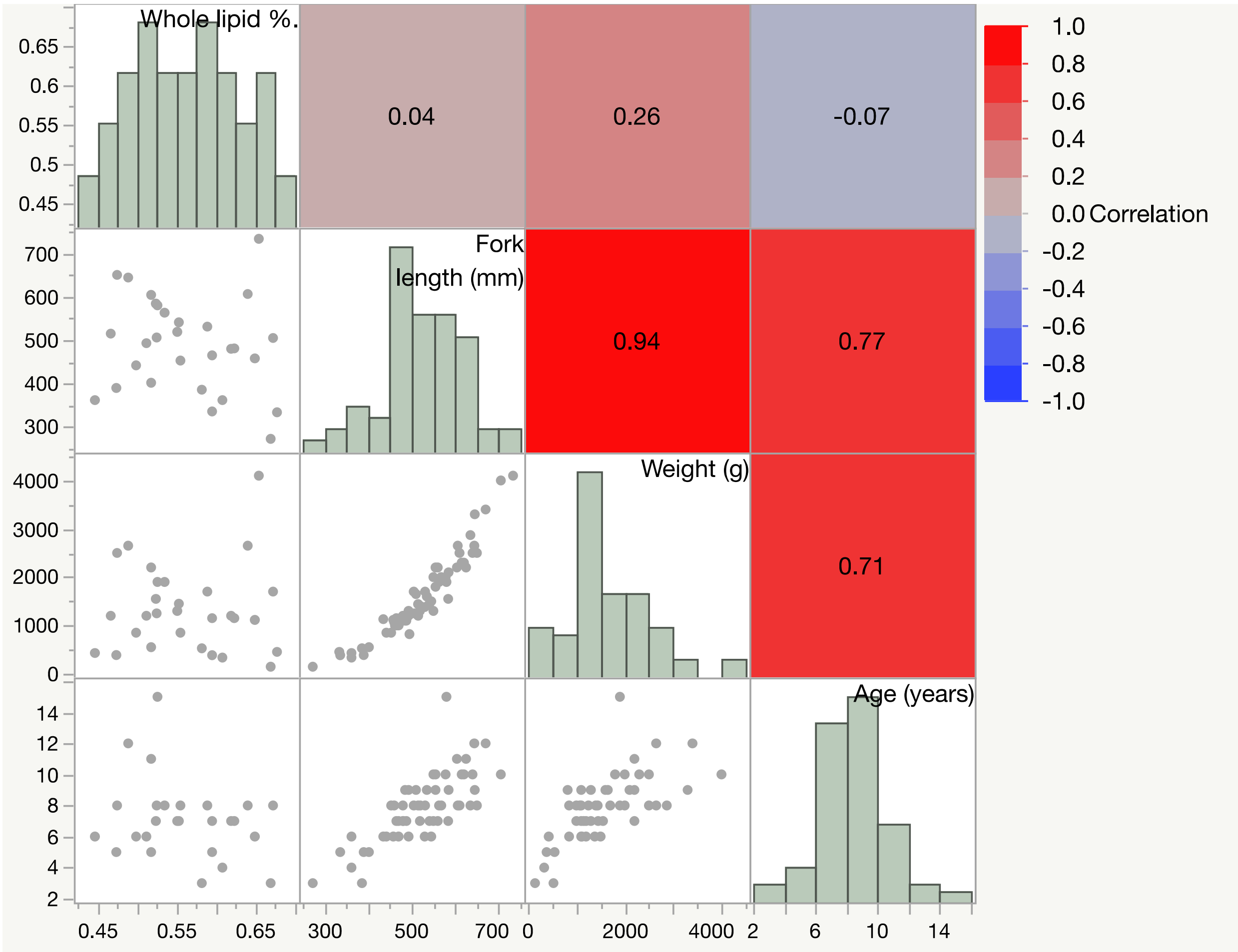

Figure 5. Correlation matrix showing R-values, histograms, scatterplots, and heat map showing correlation values between whole-body lipid percent (dry weight) and age (years), fork length (millimetres), and weight (grams) performed on arcsine transformed lipid content data collected from Dolly Varden (*Salvelinus malma malma*) collected from freshwater locations. Fork length, weight, and age data are not transformed.

During exploratory analyses, differences in freshwater and marine muscle lipid contents between sampling locations were examined to assess if sites within each habitat could be pooled. The lipid content of the two freshwater locations were not significantly different (p= 0.4941), but lipid content significantly differed between the marine locations (p <0.0001; Figure 6). Thus, in analyses comparing lipid content in fish from freshwater versus marine sources, the two freshwater locations were pooled, while the two marine locations were kept separate. Therefore, three habitats/locations were used in the analysis.

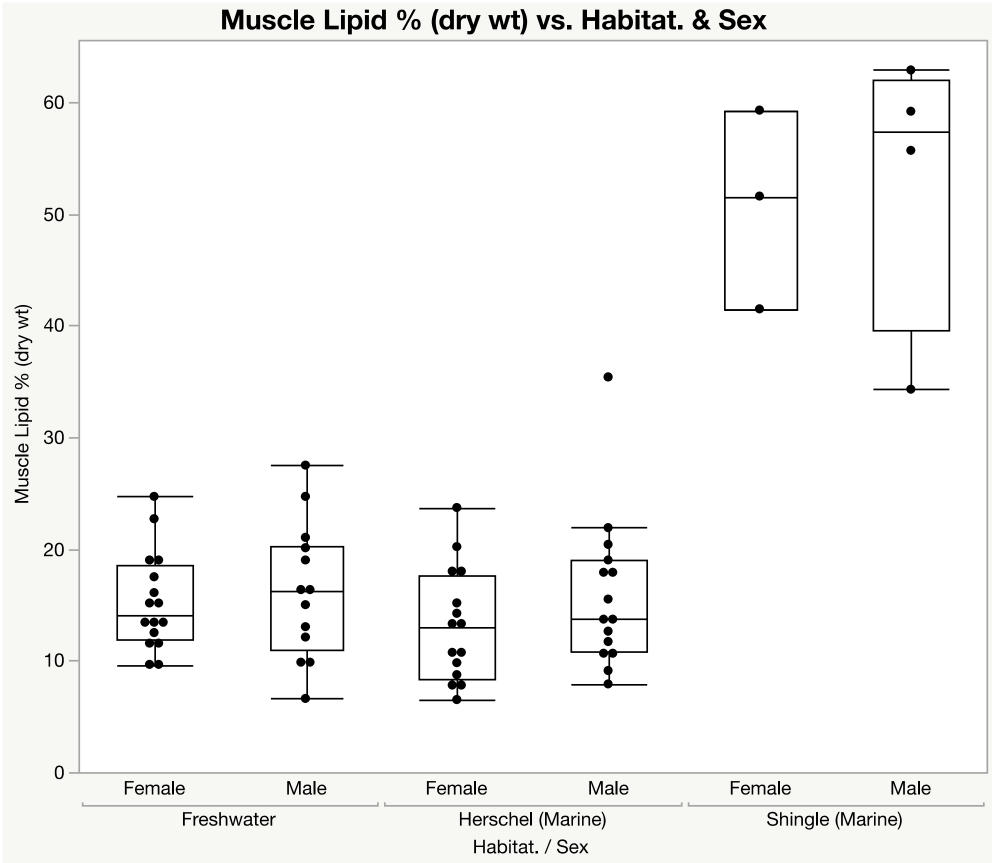

Figure 6. Boxplot of muscle lipid percent in Dolly Varden (*Salvelinus malma malma*) data sets grouped by habitat (three locations) and sex.

Muscle lipid percent differed between habitats ($F(2, 61)= 92.5103$, $p< 0.0001$), but not between sexes ($F(1, 61)= 0.0276$, $p= 0.8686$), nor was the interaction significant ($F(2, 61)= 1.0513$, $p= 0.3557$; Figure 6). Post-hoc tests revealed that muscle lipid content did not differ between the freshwater locations and Herschel Island (marine) although Shingle Point was significantly different compared to all locations (p-values < 0.05). Differences in muscle lipid content between sexes within each location were not significantly different (freshwater: $p= 0.9999$; Shingle: $p= 0.9999$; Herschel: $p= 0.5213$).

Table 2. Mean, standard deviation, and sample size (N) of muscle lipid percent from non-transformed data in Dolly Varden (S*alvelinus malma malma*) from all individuals grouped together by habitat, by sex, and grouped together by habitat and sex.

	Total	Freshwater	Marine	Female	Male	Freshwater Female	Freshwater Male	Marine Female	Marine Male
Mean Muscle Lipid %	19.9	15.7	23.2	19.3	20.6	15.2	16.2	22.7	23.7
Standard Deviation	15.1	5.1	19.0	15.9	14.4	4.4	6.1	20.9	17.5
N	67	29	38	35	32	16	13	19	19

There was a moderate and statistically significant positive relationship between muscle and whole-body lipid percent ($F(1)= 6.7901$, $p= 0.0152$, $r^2= 0.4204$; Figure 7) when examining differences between reproductive categories. The interaction was not significant ($F(1)= 0.4256$, $p= 0.5201$), indicating that the slope of the relationship did not differ significantly between spawners and non-spawners. However, non-spawners had a significantly higher overall whole-body lipid content relative to spawning individuals (i.e., higher y-intercept; ($F(1)= 9.6515$, $p= 0.0047$); Table 3).

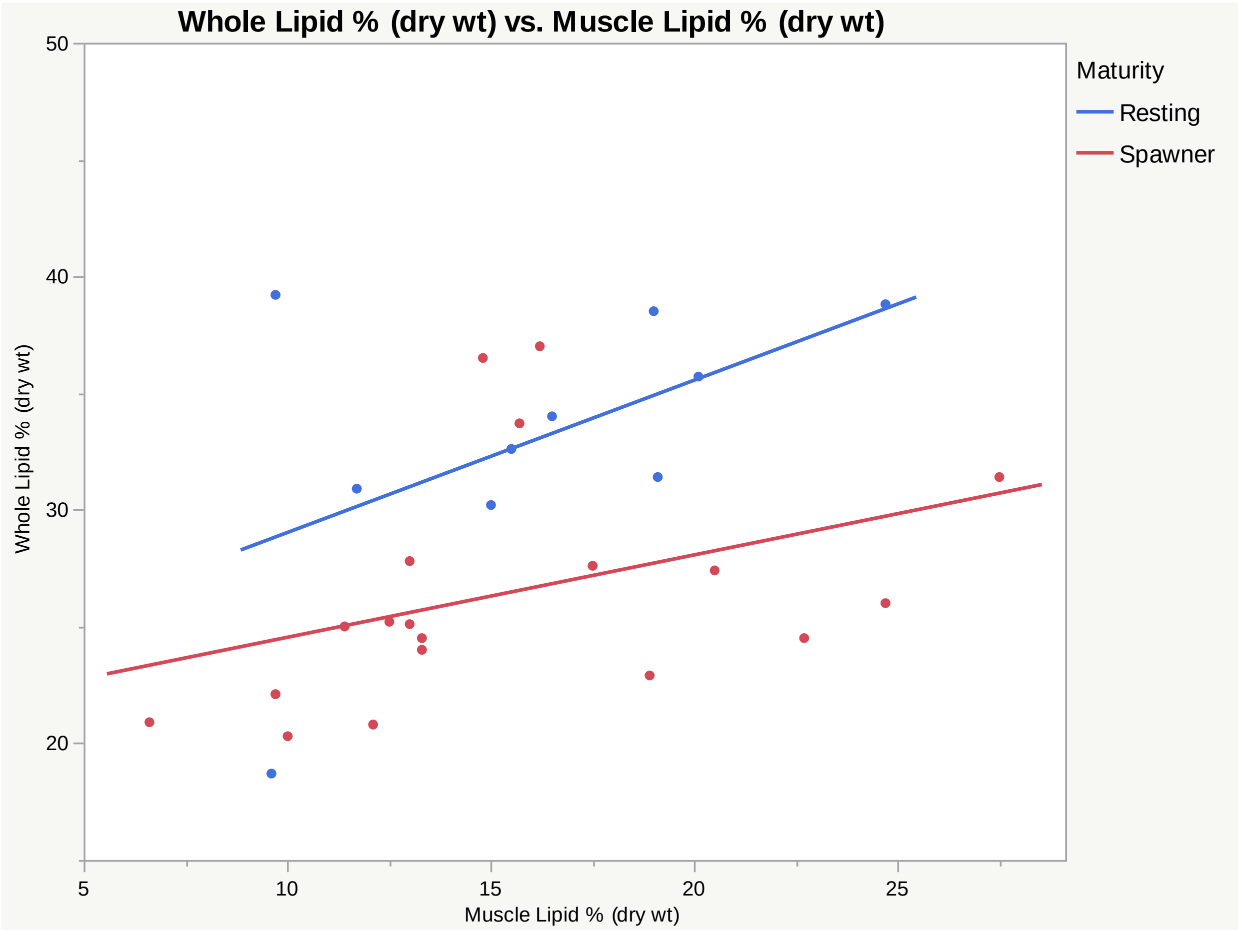

Figure 7. Muscle lipid percent vs whole-body lipid percent taken from the same individuals of spawning and non-spawning Dolly Varden (*Salvelinus malma malma*) from freshwater habitats during fall spawning. (Prediction Expression: Whole Lipid Percent (dry weight) (Resting)= 22.51 + 0.6522 X Muscle Lipid Percent (dry weight)); Whole Lipid Percent (dry weight) (Spawner)= 21.02 + 0.3527 X Muscle Lipid Percent (dry weight).

There was also a weak albeit significant positive relationship between muscle and whole-body lipid percent (($F(1)= 4.7064$, $p= 0.0398$, $r^2= 0.2013$; Figure 8) when examining differences between sexes. The interaction was not significant ($F(1)= 0.5598$, $p= 0.4613$), indicating that the slope of the relationship did not differ between sexes. Additionally, males and females did not differ in whole-body lipids (i.e., y-intercept; $F(1)= 0.0757$, $p= 0.7854$).

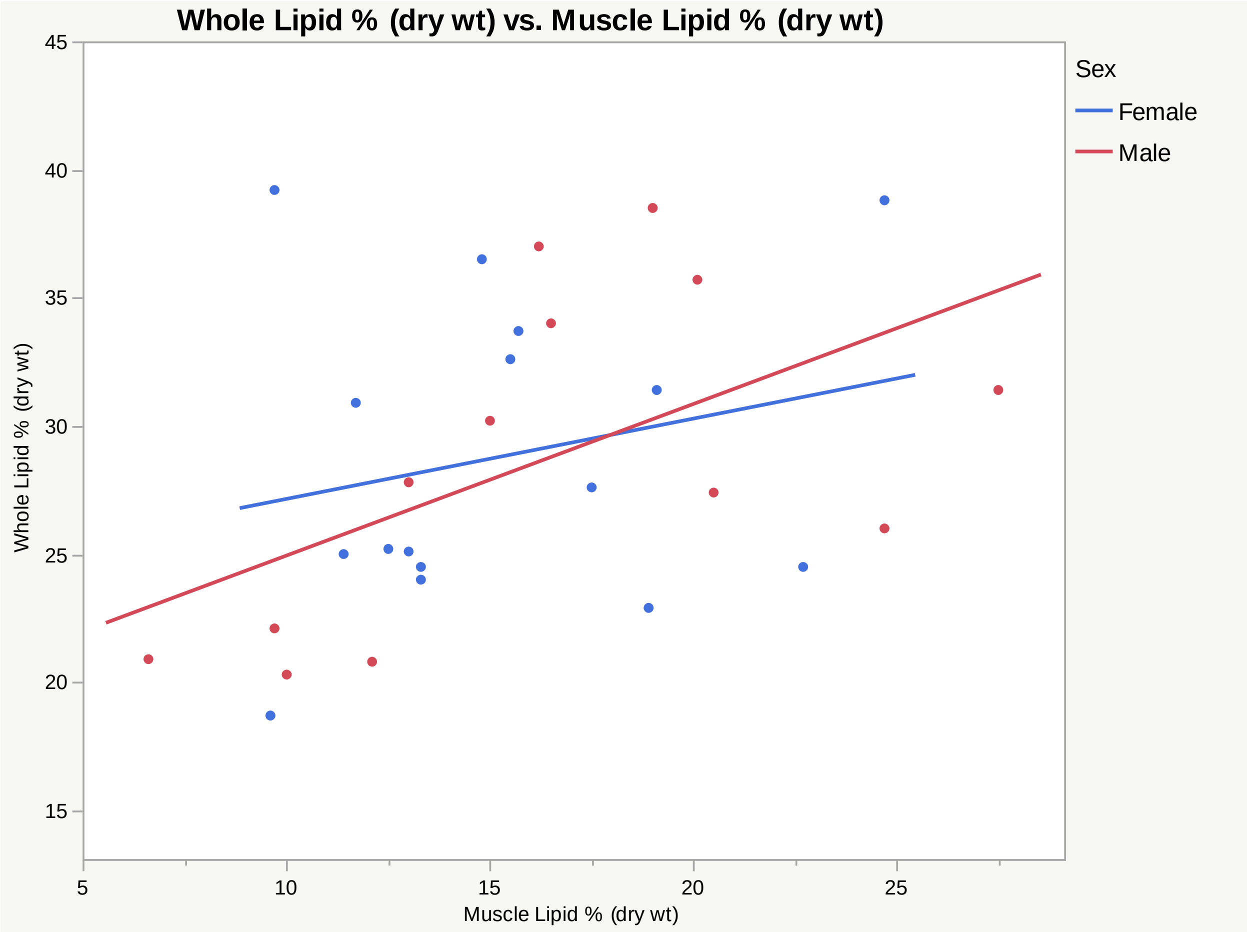

Figure 8. Muscle lipid percent vs whole-body lipid percent taken from the same individuals of male and female Dolly Varden (*Salvelinus malma malma*) from freshwater habitats during fall spawning. (Equation: Whole Lipid Percent (dry weight) (Female) = 24.03 + 0.313 X Muscle Lipid Percent (dry weight)); Whole Lipid Percent (dry weight) (Male) = 19.04 + 0.5908 X Muscle Lipid Percent (dry weight).

Table 3. Mean, standard deviation, and sample size of analyzed freshwater muscle and whole-body lipid percent of Dolly Varden (*Salvelinus malma malma*), including individuals grouped by sex and maturity.

	Total	Whole-body	Female Whole-body	Male Whole-body	Female Muscle	Male Muscle	Spawner Muscle	Non-spawner Muscle	Spawner Whole-body	Non-spawner Whole-body
Mean Lipid %	15.7	28.7	28.8	28.6	15.2	16.2	15.4	16.1	26.5	33.0
Standard Deviation	5.1	6.1	6.1	6.4	4.4	6.1	5.4	4.8	5.0	6.1
N	29	29	16	13	16	13	19	10	19	10

Discussion

I tested whether lipid content in anadromous northern Dolly Varden differed between seasons/habitat (summer and fall/ marine and freshwater), reproductive status (spawner and non-spawner), sex (male and female), and tissue type (muscle and whole-body). Season/habitat had an influence on lipid content in the muscle tissue. Muscle lipid content was higher in fish from Shingle Point compared to fish from the freshwater locations, although fish from Herschel Island had lipid content similar to those from the freshwater locations. A statistically significant linear relationship was found between muscle lipid percent and whole-body lipid percent, suggesting that muscle lipid content can be used to predict whole body lipid percent. Although the relationship was moderate, this finding is important because if reliable predictions about whole-body lipid percent can be calculated using muscle tissue, smaller tissue samples can be collected, shipped, and stored, as opposed to requiring the entire body of a fish. Interestingly, non-spawning individuals had higher whole-body lipids than spawning individuals, but sexes did not differ in whole-body and muscle lipid content. No prediction was made regarding differences in whole-body lipids between reproductive status, but the lack of difference between sexes was contrary to my prediction that males would have higher muscle lipids than females.

Seasons/Habitat

As predicted, the season/habitat of capture impacted lipid in the muscle of anadromous Dolly Varden; however, only one of the marine locations, Shingle Point, was significantly higher relative to the freshwater locations, whereas Herschel Island was not. Indeed, this higher lipid content was noticed when processing samples as muscle tissue was visibly oilier and darker than tissue samples from the other locations (Appendix: Figure 3). The higher lipid content in fish from one marine site (Shingle Point) relative to the other (Herschel Island) was unexpected as harvest at both marine locations are comprised of multiple stocks that are mixed, meaning the fish originated from different rivers and mixed together at both locations. Genetic mixed-stock analyses have revealed that the Babbage River stock contributes to the harvest at Shingle Point and Herschel Island while the Firth River stock is predominantly harvested at Herschel Island. I predicted both marine locations would have fish with higher lipid content than those from freshwater due to the high feeding intensity during marine residency in the summer (Stolarski et al., 2014) and because fish in freshwater have recently performed an energy-intensive migration and are not actively feeding until the following summer (Jorgensen et al., 1997). Although marine fish sample size was small in this study, lipid percent values were consistently high among fish from Shingle Point. Larger sample sizes and further study is required to evaluate the lipid content of Dolly Varden from the other populations that contribute to the harvest at Shingle Point (e.g., Big Fish River and Rat River) to determine if their lipid content is considerably higher. Diet of fish using Shingle Point as a summer habitat is not well understood (Brewster et al., 2016). Stable isotope analysis or fatty acid analysis are potential methods that could be used to help determine feeding ecology and habitat use of the individual locations (Brewster et al., 2016). Speculative reasons for the large differences between Shingle Point and Herschel Island may be related to distance between locations (~100km), available prey, or an unknown occurrence relating to Dolly Varden feeding between the time of sampling at Herschel Island and Shingle Point. It is also known that air temperature at Herschel Island is cooler than Shingle Point during the summer, and about 1ºC warmer in the winter (Burn and Zhang, 2009). This may affect prey species residing in the area. Inuvialuit harvesters claim that char from Herschel Island are typically bigger in size and that the water at Herschel Island is saltier than at Shingle Point (Papik et al. 2003). More research is needed to determine the cause of these differences.

Findings from our results underscore the notion that two different relatively nearby locations may be assumed to be ecologically similar (in our case, both summer feeding, marine habitat for northern Dolly Varden), yet contain underlying factors that may drastically affect the outcome of the desired variable. Spatial consideration is important when discussing any area, but especially one as variable as the ocean, and it is important to partake in preliminary analysis before assuming two locations are statistically similar.

Relationship between Lipid in Muscle Tissue and Whole Body

I hypothesized that muscle lipid content could predict the lipid content of the whole body of an anadromous Dolly Varden. A positive relationship was found to be significant in both ANCOVAs although the extent of the strength of the relationship differed when accounting for reproductive status and sex. There was no difference in the slopes of the relationship between maturity levels, however, whole body lipid percent was significantly higher in resting individuals than in spawners (Table 3). I correctly predicted that lipid content in muscle from spawning individuals would be lower than non-spawning individuals. This is consistent with the findings from Dutil (1986) who found that post-spawning Arctic char contained 35-46% less energy reserves than non-spawning individuals.

Although the relationship between muscle lipid percent and whole-body lipid percent is significant, it may not be strong enough for practical application to use a sample of muscle tissue as an estimate for whole-body lipid percent. The r^2 values between muscle and whole-body lipids while accounting for maturity status and sex demonstrate that a low amount of variation in whole-body lipid percent is accounted for by muscle lipid percent. As expected, my results indicate that lipids are distributed unevenly throughout the body. Overall muscle lipid percent (15.7%) was lower than whole body lipid percent (28.7%) in fish caught from freshwater when all maturity groups and sexes were combined, indicating that organs and tissues other than muscle hold large stores of lipids in northern Dolly Varden. This is consistent with what is reported in the literature, which illustrates that certain organs and tissues act as larger lipid storage sites than others (Jobling et al., 2008; Nanton et al., 2007).

The mean muscle lipid percent for all locations and individuals was 19.1%, which is much higher than the 2-7% (wet weight) found in wild anadromous salmonids in the literature (Jobling et al., 2002) and is closer to the >15% found in farmed salmonids (Jobling et al., 2002). Even omitting the marine data sets, average muscle lipid percent of the fish caught in freshwater was 15.7%, which is a larger value than expected. To contrast this with other fish species, Brook trout (*Salvelinus fontinalis*) and Lake trout (*Salvelinus nayamcush*), relatives of the Dolly Varden, have been found to contain approximately 3.4% and 1.9-19.4% lipid in the muscle tissue, respectively (Henderson and Tocher, 1987). Fishes in these studies were not from anadromous populations, which is important to note as this would presumably play a role in the amount of lipids found in the muscle tissue, depending on the time of the year.

Another interesting finding was that neither muscle nor whole-body lipids were correlated with the covariates (age, length, weight). This contradicts findings from other studies that have shown body size can affect tissue composition. For example, changes in body size can affect the ratio of protein, water, ash, and lipid in the body of fish (Breck, 2014; Sutton et al., 2011).

Sex and Lipid Content

I predicted that lipid content in the muscle of males would be greater than females in both freshwater and marine locations, as females tend to invest more lipid for gonadal development than males (Penney and Moffitt, 2014). Lipid content in the testes is always lower than the ovaries, despite stage of the sexual cycle (Henderson and Tocher, 1987). My findings here did not support my prediction, as sex did not significantly influence the level of muscle lipid content among locations, indicating that males do not store more lipid in the muscle tissue than females. Lipid content in muscle tissue of males was also predicted to be greater than females when comparing between muscle and whole-body tissue of Dolly Varden in freshwater. Again, there was no difference when accounting for sex. Zimmerman et al. (2022) found that female Steelhead and Rainbow Trout contained higher somatic lipid content than males, however, this was only found in open-ocean-feeding individuals, not those sampled from coastal or freshwater environments. However, consistent with our findings, Jonsson et al. (1991) documented no differences between somatic lipid reserves between sexes in Atlantic salmon. Based on my findings, accounting for sex is not necessary when comparing lipid content between Dolly Varden, or when predicting whole-body percent lipids using data from muscle.

Much of the literature pertaining to lipids in fish do not examine the general lipid percent found in different tissue types among seasons or between sexes or reproductive statuses but is often looking at the fatty acid composition (Doucett et al., 1999; Olsen et al., 1991; Ulrich, 2013). A large portion of the literature is from a food science viewpoint (Ng, 2007; Sushchik et al., 2020; Skonberg et al., 1994) especially when regarding lipids in salmonids, as this is a common food source for human consumption given that the fatty acids found in the tissue of salmonids are linked to positive health benefits in humans (Turchini et al., 2011).

Conclusion

Arctic food webs are particularly vulnerable to the effects of climate change (Kortsch et al., 2015). Reductions in Arctic sea ice coverage and increased ocean temperature due to ice-albedo effect (Rantanen et al., 2022) has the potential to create a substantial restructuring of marine food webs (Sallon et al., 2011). There has already been evidence of generalist, migratory fish moving poleward, entering arctic marine habitats (Perry et al., 2005; Kortsch et al., 2015; Spies et a., 2019; Copeman et al., 2022;). Shifting species distributions will establish novel interactions with endemic species that can lead to food web reorganizations and altered ecosystem functions (Kortsch et al., 2015). With newly interacting species potentially competing for resources, it’s crucial to understand energy flow within Arctic food webs to inform conservation efforts of endemic species (Gallagher et al., 2021b). Characterizing which habitats provide lipid-rich energy sources, as well as understanding the natural variation in lipids based on life history using lipid content analysis is relevant for protecting at-risk species such as the northern Dolly Varden.

Determining whether muscle samples can act as an accurate representative for whole-body lipid content in Dolly Varden can be important for monitoring the stock status of energetic investment for this species of management concern. For example, if a muscle sample could accurately represent whole-body lipid content, there would be no need to sample the entire body when analyzing lipid and fatty acid content. This would save time, money, and space when transporting samples from the field site to the lab and would allow subsistence fisheries to keep more of the animal for food. However, whole-body lipids can be highly variable, and the relationship between muscle lipid percent and whole-body lipid percent in Dolly Varden is not overly strong, therefore using muscle tissue as a predictor for whole-body lipids is unadvised. As information on lipid dynamics in Dolly Varden is extremely limited, more research is needed to help solidify the findings of this study, as well as to find more effective sampling techniques of these fishes.

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Appendix

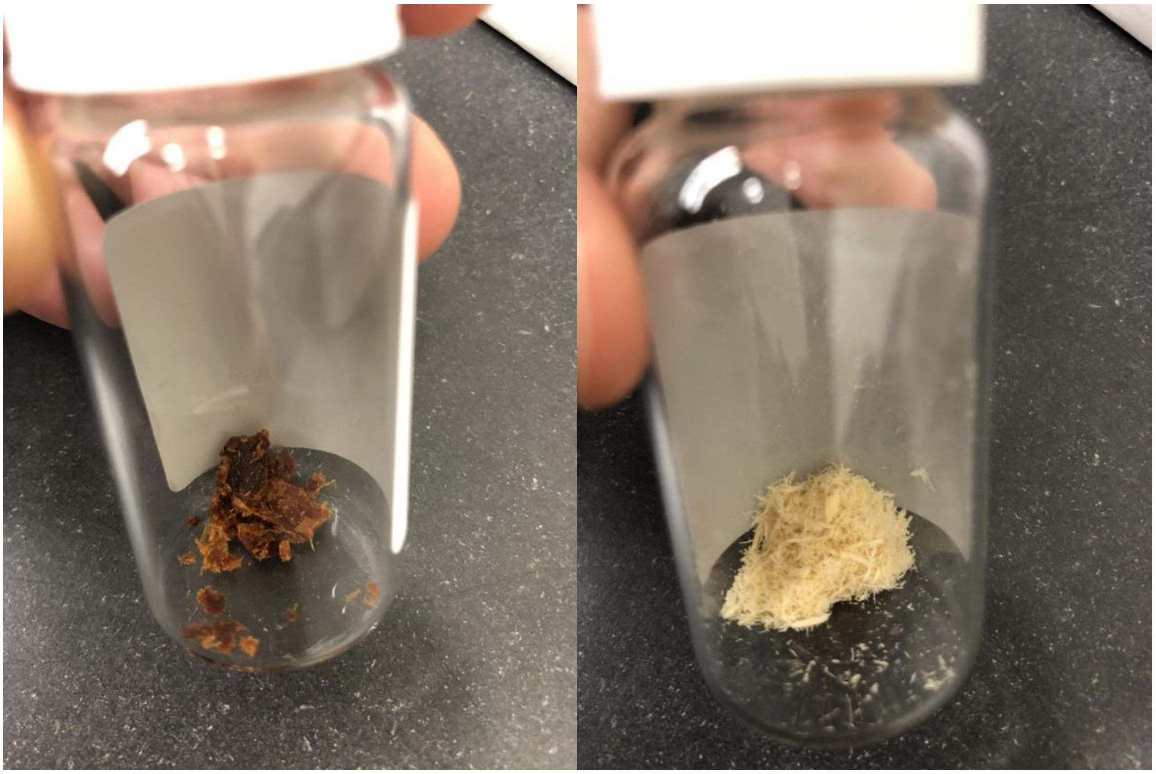

Figure 3. Freeze-dried muscle tissue from a sample of Dolly Varden (*S. malma malma)* from Shingle Point (left) and Babbage River (right) (Source: L. Kulchycki, 2022).