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Sex Ratio and Maturation Characteristics of Adult Pacific Lamprey at Willamette Falls, Oregon

Laurie L. Porter, Peter F. Galbreath, Brian J. McIlraith, and Jon E. Hess

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EXECUTIVE SUMMARY

Returns of anadromous Pacific lamprey *Entosphenus tridentatus* to the Columbia River have declined dramatically, with hydrosystem development and passage barriers identified as major factors contributing to these declines. Concurrent with interagency efforts to address issues associated with hydrosystem passage, the Columbia River treaty tribes have initiated adult translocation programs to supplement spawner numbers in interior streams, to rebuild natural production in the basin. The translocation programs involve collection of adults within fish ladders of lower mainstem dams, transportation of the fish to tribal facilities for holding over winter (during which time the fish undergo final sexual maturation), and release of the fish the following spring into rivers and tributaries within their ceded territories where the lamprey were previously abundant but are now diminished in abundance or extirpated. Previous research on in-migrating Pacific lamprey in the Willamette River, however, indicated that sex-ratios and maturation status of the fish may vary over the migration season. Inclusion of fish with a significant skew in sex ratio (especially if towards males) or holding of fish for overwintering that are already mature, could compromise the boost to natural production that is anticipated from the translocation programs. To obtain greater clarification of any trends in sex ratio and maturation status of migrating adult Pacific lamprey, in 2016 we sampled 269 returning fish at Willamette Falls, Oregon City OR, that were collected as part of the annual tribal harvest. The fish were collected on one day per month in June, July and August – the same months during which adults are captured at the Columbia mainstem dams for the tribal translocation projects. Length, weight and dorsal fin gap measures were recorded for each fish, then they were dissected to identify sex, to record liver and gonad weight, and to make a visual assessment of gonadal development. Results indicated a sex ratio of 1:1 in all three samples (49F:51M; 34F:35M; 50F:50M, respectively). Gonadosomatic index (GSI) among males averaged 2.4% (range 0.4% to 5.7%). GSI for females was larger, averaging 7.2% (range 1.0% to 20.1%). A trend for decreased size and dorsal fin gap over time was observed for both sexes, as expected for fish initiating maturation following reentry into freshwater. Nonetheless, even the lamprey with the highest GSI values were not yet mature and would require at least one overwintering period before being ready to spawn. During the sampling process we also collected tissue samples from the fish for eventual use in a study to identify a sex-linked DNA marker, and heads from a random sub-sample were frozen, pending eventual extraction of the statoliths for microchemical analysis and examination to possibly determine ocean age.

INTRODUCTION

Populations of lamprey species (Order Petromyzontiformes) have been in decline globally (Renaud 1997 and 2011; Maitland et al. 2015) including those of anadromous Pacific lamprey *Entosphenus tridentatus* across their historic range in the Pacific Northwest (Murauskas et al. 2016). Reduction in runs of Pacific lamprey over the last half century is due to restricted or blocked passage associated with human-made barriers (e.g., road culverts, irrigation dams, hydroelectric dams), rotenone treatments used by ODFW for the control of invasive or nuisance fish species (Close et al. 1995), climate change impacts at both the freshwater and ocean stages (Close et al. 1995; CRITFC 2011; Luzier et al. 2011; Wade and Beamish 2016), and other causes. As a result, Pacific lamprey are currently listed as a species of moderate concern in the state of California (https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=104268&inline), as a state sensitive species at risk of extinction in Oregon (http://www.dfw.state.or.us/fish/ONFSR/docs/final/11-other/summary-pacific-lamprey.pdf), as endangered by the state of Idaho (http://fishandgame.idaho.gov/ifwis/cwcs/pdf/Pacific%20Lamprey.pdf), and a species of concern in Washington (https://www.fws.gov/wafwo/species/fact%20sheets/pacific_lamprey_final.pdf).

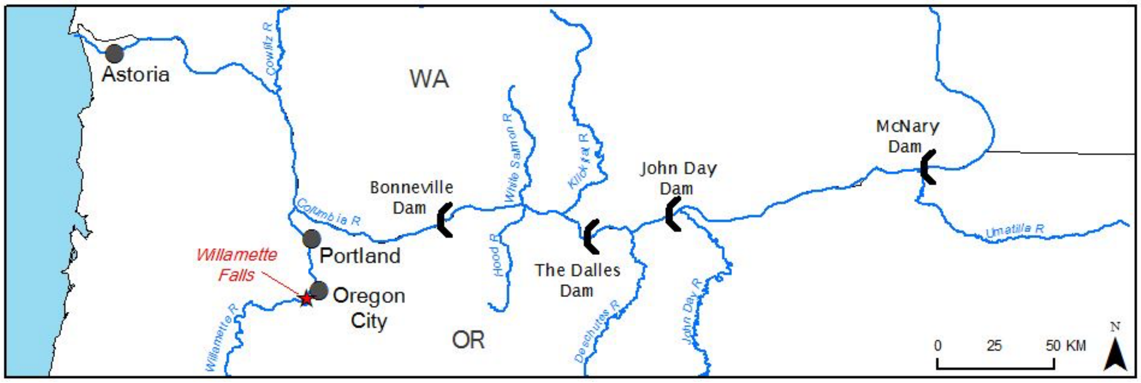
In 2003, the US Fish and Wildlife Service (USFWS) was petitioned to place Pacific lamprey on the endangered species list. However, in the 90-day findings it was concluded that the petition did not contain sufficient scientific or commercial information to warrant listing at the time (USFWS 2004). This was due in part to an apparent lack of a tributary homing instinct and the associated lack of sub-division of Pacific lamprey into distinct population segments (DPSs), as based on analyses of neutral genetic markers (Goodman et al. 2008; Lin et al. 2008; Spice et al. 2012; Hess et al. 2013). The fish were therefore viewed by the USFWS as members of one large range-wide population, whose overall number was deemed sufficiently elevated to not merit listing, despite the dramatic declines in river-specific return numbers across the species' range (USFWS 2004). However, consideration of Pacific lamprey as a single panmictic population may be an over-simplification. A recent study of adult Pacific lamprey sampled across the migration season in the Willamette River Basin in two years, indicated three genetically distinguishable groups of fish characterized by both temporal (between and within year) and migration distance differences (Clemens et al. 2017), and an assessment of Pacific lamprey sampled from rivers from California to British Columbia with a suite of neutral and potentially adaptive genetic markers, revealed variation related to geography and life history (Hess et al. 2013). Much remains to be learned regarding the patterns of dispersion in the ocean and return to freshwater of Pacific lamprey, how these behaviors are affected by host species population dynamics, and how the ocean life histories of Pacific lamprey affect population genetics of the species (Murauskas et al. 2013; Hess et al. 2013).

Given the historic abundance of these anadromous fish, Pacific lamprey likely had a substantial impact on the freshwater aquatic ecosystems they inhabited. The carcasses of post-spawning adults would have contributed large amounts of marine derived nutrients to the freshwater systems. Additionally, during their freshwater residence, the filter feeding larvae burrow in the sediments, facilitating cycling of the nutrients within the streambed and increasing stream productivity (Beamish 1980; Close et al. 1995; Mundahl et al. 2005; Nislow and Kynard 2009; Weaver et al. 2015). For example, results from experiments conducted with Arctic lamprey (*Lethenteron camtschaticum*) involving treatment versus control (no larvae) enclosures in the Oshirarika River, Hokkaido, Japan, concluded that lamprey larvae

increased oxygen, maintained sediment softness and increased surface fine particulate organic matter of the streambed ecosystem (Shirakawa et al. 2013). The decline of Pacific lamprey and their associated influences on freshwater aquatic ecosystems has no doubt had negative repercussions on productivity of species with which they share these habitats (Close et al. 2002; Luzier et al. 2011), e.g., during lamprey spawning surveys, salmonids have been observed feeding on lamprey eggs (Brumo 2006); and, Steller sea lions (*Eumetopias jubatus*), white sturgeon (*Acipenser transmontanus*), double-crested cormorants (*Phalacrocorax auritus*), Caspian terns (*Hydroprogne caspia*), gulls (*Larus sp.*) and other species have been observed preying on adult Pacific lamprey, sometimes it is thought, in lieu of preying on the culturally and economically important salmonids (*Oncorhynchus spp*.; Roffe and Mate 1984; Wolf et al. 1989; Close et al. 2002; Riemer et al. 2011; Sepulveda et al. 2013).

Beyond their ecological roles, Pacific lamprey have historically been a significant nutritional and cultural resource for native American tribes and First Nations. While lamprey abundance is currently reduced, and many traditional fishing locations have been lost due to inundation by hydrosystem development, lamprey nonetheless continue to have an important role in tribal ceremonial, medicinal, and subsistence activities (Close et al. 2002; Petersen-Lewis 2006; Sheoships 2014). The tribes have fished for lamprey since time immemorial, and incorporating traditional ecological knowledge into lamprey rehabilitation and restoration efforts is critical. Indeed, it has been the tribes who have been at the forefront of efforts to protect and restore Pacific lamprey in the region (Jackson and Kissner 1997; Petersen 2006; CRITFC 2011; Sheoships 2014).

Recent research was conducted on adult lamprey captured at Willamette Falls (rkm 43) on the Willamette River, (Oregon City, Oregon), a tributary to the Columbia River whose confluence is downstream of the mainstem dams (Figure 1). Within the Columbia River Basin, Willamette Falls remains the only location of significant lamprey harvest for Columbia Basin tribes. The Willamette River drains approximately 29,138 km^2, flowing 474 km north from the confluence of the Middle Fork and Coast Fork Willamette Rivers to the river's confluence with the Columbia River, just downstream from Portland, Oregon (Sedell and Froggatt 1984). Willamette Falls is the second largest waterfall by volume in North America. For millennia, large numbers of tribal fishers and their families gathered at the falls annually to harvest salmon and Pacific lamprey. While tribal harvest of salmon at the falls has essentially disappeared, due to development activities that severely reduced their abundance, returns of Pacific lamprey have remained sufficient to support a modest level of tribal harvest for ceremonial and subsistence purposes. Harvest also provides fishers the opportunity to transmit to tribal youth their knowledge of traditional fishing practices and of the cultural role that lamprey has played for the tribes.



1A.

1B.

FIGURE 1. Map of the lower Columbia River basin showing the location of Willamette Falls on the Willamette River, and of the four lower mainstem hydroelectric dams (1A), and a satellite photo of Willamette Falls showing the location of the T. W. Sullivan Powerhouse and fish ladder on the west side of the falls, and the east side of the falls where the Pacific lamprey were collected for this study.

Pacific lamprey is a semelparous anadromous species, which has been estimated to spend 1-4 years in the ocean before returning to freshwater for spawning. In the Columbia River Basin, fish return from the ocean in late winter through summer, with peak returns from April to July (Clemens et al. 2011; McIlRaith et al. 2015). The fish migrate upstream through the mainstem Columbia River and into the

various tributaries, although dams in the tributary rivers upstream are an obstacle to successful passage to much of the original spawning habitat in the basin (Moser and Close 2003; Moser et al. 2010; Keefer et al. 2010; 2012). In the fall, Pacific lamprey seek areas of cover and attachment (e.g., boulders or large wood) where they will remain through the winter, before finishing the sexual maturation process the following spring and continuing their upstream migration to the spawning grounds (Robinson and Bayer 2005; Clemens et al. 2011 and 2012). Observations on timing of migration and spawning of Pacific lamprey in Oregon coastal streams were similar to those made in the Columbia River (Brumo et al. 2009; Gunckel et al. 2009; Luzier 2011; Starcevich et al. 2013). There is also some evidence that a small percentage of Pacific lamprey may require overwintering for a second season prior to reaching full maturity (Clemens et al. 2011 and 2016; J. Hess, Columbia River Inter-Tribal Fish Commission, personal communication). This has also been documented in Fifteenmile creek and the Deschutes River (Baker et al. 2015).

To promote rebuilding of Pacific lamprey abundance in the Columbia basin, the four member tribes of the Columbia River Inter-Tribal Fish Commission (CRITFC) developed the Tribal Pacific Lamprey Restoration Plan (2011), with the goal to restore abundance of the species across the basin and in sufficient numbers to provide for "ecological, tribal cultural, and harvest values". Over a similar period, the USFWS led the interagency development of the Pacific Lamprey Conservation Agreement (2012), involving representatives from regional tribes, federal agencies, states, and other governmental agencies. The purpose of the agreement is to promote coordinated implementation of conservation measures for Pacific lamprey across the 14 Regional Management Units spanning five states (Washington, Oregon, Idaho, California, and Alaska) within the species' range.

Under guidelines described in the Tribal Pacific Lamprey Restoration Plan (2011), the four CRITFC member tribes have led many of the Pacific lamprey conservation and restoration efforts in the Columbia River basin; efforts which include enacting several adult translocation programs (Ward et al. 2012). CRITFC commissioners review collection plans annually for these programs prior to the beginning of the migration season, and they set allocation numbers for each of the participating tribes (CRITFC 2011). In-migrating adults are captured at lower mainstem Columbia River dams - Bonneville, The Dalles and John Day (Figure 1) - and the fish are transferred to various tribal facilities for overwintering, during which time the fish continue the process of gonadal maturation. The following spring the fish are released into streams within tribal ceded territories to supplement, or reintroduce where extirpated, the naturally spawning populations*.* The long-term goal is to return the populations to self-sustaining and harvestable levels (Close 1999; CRITFC 2011; Ward 2012), to ensure their survival, and to reinforce use of the fish for tribal cultural and harvest purposes. In addition to translocation programs, the Confederated Tribes of the Umatilla Indian Reservation and the Confederated Tribes and Bands of the Yakama Nation have begun artificial propagation programs to provide larvae for research and supplementation purposes (Lampman et al. 2016).

Recent research conducted on Pacific lamprey collected at Willamette Falls during the adult migration indicated that sex ratios may be skewed from a presumed 1:1 ratio over the course of the migration season (Clemens et al. 2013). Also, it was noted that some fish were sexually mature, presumably because they had already overwintered in locations downstream of the falls (Clemens et al. 2013). While conducting carcass surveys in the Coquille River, Oregon, Brumo (2006) observed an increased residence time of males at spawning areas and a male skewed ratio (2:1) among carcasses. Clemens (2011) reported differences in sex ratio of Pacific lamprey captured at Willamette Falls over the course of the

migration season in two years, though towards an increase in females in one year, and males in a second. Both a skewing in sex ratio (especially towards males) and an elevated proportion of already sexually mature lamprey among the adults held for overwintering would have negative implications on the productivity boost anticipated from the tribes' translocation programs. A greater understanding of lamprey biology was therefore needed for management of these tribal programs, as it is for restoration and reintroduction efforts in general (Ward et al. 2012; IUCN 1998).

In 2016, we conducted a study involving capture of in-migrating adults at Willamette Falls and examination of their sex ratio and maturation characteristics. Lamprey were harvested by hand once per month in June, July and August 2016. These are the same months that the tribes collect adults at the Columbia River mainstem dams for the translocation. A variety of external and internal measurements were recorded, and following data collection the fish were cleaned and donated to the tribes for consumption.

Objectives for the study were to:

1) Collect morphometric information, including liver and gonad weight for comparison between sexes and across the migration season.
2) Use visual observation of the gonads to identify phenotypic sex and to estimate sex ratio.
3) Use gondadosomatic index (GSI) and visual observation to categorize each fish as sexually mature or immature.
4) Collect tissue samples from each lamprey for eventual use in a study to identify a sex-linked DNA marker.
5) Collect heads from a random sub-sample of the fish for eventual extraction of the statoliths and microchemical analysis and examination to determine ocean age, as possible.

METHODS

Fish Collection

While our interest was in describing characteristics of in-migrating Pacific lamprey captured at Columbia River mainstem dams for the tribal translocation programs, additional permits would have been required to trap and sacrifice the number of fish required. Instead, we chose to sample fish at Willamette Falls, presuming these fish would resemble those captured at the mainstem dams. Willamette Falls is located at a distance from the mouth of the Columbia River similar to that for Bonneville Dam, the first of the mainstem dams – 204 km and 235 km, respectively (Figure 1A). There is a tribal fishery for Pacific lamprey that occurs annually at the falls, and our data were recorded on fish that were already going to be sacrificed as part of the tribal harvest, thus requiring no additional permits.

Pacific lamprey were harvested by tribal fishermen at Willamette Falls on three separate days in 2016: June 17, July 8, and August 9. Water temperature and flow for each date were 65°C and 10,000 cfs, 72 °C and 7,270 cfs, and 73 °C and 6,290 cfs, respectively

(http://www.dfw.state.or.us/fish/fish_counts/willamette%20falls.asp). The fishermen approached the falls in a boat from downstream, anchoring the boat at the base of the east side of the falls (Figure 1B). Proceeding then on foot and by swimming to the face of the falls, the lamprey were collected by hand from the rocks to which they were adhered and placed into moist burlap sacks. Upon departure, creel staff from the Confederated Tribes of the Warm Springs Reservation of Oregon (CTWSRO) stationed at the Clackamette Park boat ramp, Oregon City, recorded the number of fish harvested, scanned each for PIT tags (possible recaptures of fish implanted with PIT tags as part of a separate CTWSRO study), and recorded length and weight on a subset of fish according to their normal monitoring practices. The fish were then transported to the CRITFC Troutdale workshop, Troutdale OR, for processing. Travel time to the Troutdale workshop from Clackamette Park was approximately 20 minutes.

The original study design included a sample to be collected in May 2016. Each year when river flow decreases to below 8,000 cfs, Portland General Electric, the utility that operates the Sullivan Hydroelectric Plant on the west side of Willamette Falls, places dam boards across the falls to divert the water towards the turbine intakes and fish ladder, maintaining flow there through the summer months (Figure 1). Diversion of the water facilitates access to the east side of the falls for tribal harvesters. In 2016, however, water flows remained high into June and sampling of fish in May was abandoned due to safety concerns.

Data Collection

At the Troutdale workshop, fish were held in tubs filled with ice water. The fish were measured individually for whole body weight (g), length (mm), and dorsal fin gap (DFG, mm). DFG is the distance between the posterior end of the front dorsal fin and the anterior end of the rear dorsal fin (Clemens 2011). A clip of fin tissue (approximately 0.5 cm^2) from the edge of the caudal fin was collected and adhered to a cell within a pre-printed grid on a sheet of filter paper. The fish were then dissected to identify sex via presence of testes or ovaries; only as they approach full sexual maturity do Pacific lamprey exhibit external characteristics that differentiate phenotypic sex. The gonads and liver were removed, blotted on a towel to remove excess blood and water, and weighed (0.1 g). During processing of the samples in June, it was noted that unlike the liver, the gonads could not be readily separated from associated connective tissue, visceral and gonadal adipose tissue, and intestine; therefore, “gonad weight” represents a composite of all of these tissues. During processing of the next sample in July, efforts were made with the first half of the fish to tease away these additional tissues from the gonads. However, doing so proved overly difficult and time-consuming. Therefore, as for the June samples, the remaining samples in July and those in August again included these connected tissues. The resulting overestimate for actual gonad weight is greater for males than females, due to the smaller size of the testes relative to the ovaries. For a random subset of approximately 25 fish per sample day, the head was removed and frozen. Processing time was approximately 5 minutes per fish. Following dissection, the fish were rinsed, vacuum packed and frozen, and subsequently distributed to CRITFC member tribes for tribal ceremonial and subsistence purposes.

Using the measures recorded, the following metrics were derived for each individual as follows (GSI and HSI according to Clemens et al. 2013):

Condition Factor (K): $K = \frac{weight}{length^{\wedge}3} * 100{,}000$

Dorsal fin gap per unit whole body length (%): $\text{DFG/Length} = \frac{DFG*100}{length}$

Gonadosomatic Index (GSI, %): $\text{GSI} = \frac{gonad\ weight*100}{(Body\ weight - gonad\ weight)}$

Hepatosomatic Index (HSI, %): $\text{HSI} = \frac{liver\ weight\ *100}{(body\ mass - liver\ weight)}$

RESULTS and DISCUSSION

Morphometric comparisons between sexes

Summary statistics for the morphometric data and derived metrics are provided below in Table 1. The information is arranged for comparisons between females and males within each of the three sample dates, and includes results from single factor ANOVA tests for differences between sexes. Individual measures and derived metrics, plus graphical illustrations of relationships among characters are provided in the Appendices.

Length and weight of female fish were significantly, or nearly so, larger than for male fish within sample dates, and females exhibited significantly (except in August) higher condition factors. DFG and DFG/length measures were similar between sexes. Ovary weight and GSI for females were significantly greater than testes weight and GSI for males (recall that these values overestimate actual gonad weights and GSI values, due to the inability to separate the connective tissue, visceral adipose tissue and intestine tissues that were intimately connected with the gonads). Conversely, liver weight and HSI for males were significantly greater than for females.

The larger gonad size for females was expected. Clemens et al. (2013) found mean GSI in Pacific lamprey females categorized as ‘immature’ was 3.9% and ‘mature’ was 10.5% (n=59). Manion (1972) collected data on fecundity of sexually mature sea lamprey collected in the Chokolay River, Michigan, and found the average total egg weight as a percentage of body weight was 17.2 % (n=7) for a sample taken in May and 19.5% (n=22) for a sample taken in June.

Liver weight and HSI values were similar to those observed for Pacific lamprey by Clemens et al. (2013), as was larger liver size and HSI for males relative to females.

TABLE 1. Summary statistics for morphometric measures and derived metrics recorded for female and male adult Pacific lamprey captured at Willamette Falls one day per month in June, July and August 2016, with results for ANOVA analysis for differences between sexes within sample dates.

Date		Weight (g)	Length (mm)	K Factor	DFG (mm)	DFG/Length (%)	Gonad (0.1g)	Liver (0.1g)	GSI (%)	HSI (%)
June 17										
Females (n=49)										
	Avg:	371.0	579.7	0.188	22.9	3.91	23.2	4.1	7.04	1.12
	StDev:	80.3	41.1	0.014	6.8	0.95	8.3	1.1	2.99	0.18
Males (n=51)										
	Avg:	328.8	565.3	0.180	23.3	4.10	8.9	4.4	2.73	1.37
	StDev:	76.7	45.9	0.018	5.2	0.70	3.5	1.0	0.76	0.24
		p=0.008 **	p=0.10	p=0.013 *	p=0.73	p=0.24	p<0.001 ***	p=0.15	p<0.001 ***	p<0.001 ***
July 8										
Females (n=34)										
	Avg:	346.2	581.9	0.173	22.5	3.85	16.3	4.0	5.37	1.17
	StDev:	79.0	40.7	0.013	4.7	0.69	6.5	1.2	2.83	0.16
Males (n=35)										
	Avg:	303.9	569.5	0.163	20.6	3.6	5.9	4.3	1.93	1.44
	StDev:	70.2	42.4	0.022	4.2	0.6	3.2	1.1	0.85	0.22
		p=0.038 *	p=0.33	p=0.022 *	p=0.08	p=0.12	p<0.001 ***	p=0.37	p<0.001 ***	p<0.001 ***
August 9										
Females (n=50)										
	Avg:	306.9	555.3	0.177	18.8	3.35	19.7	3.8	7.37	1.24
	StDev:	61.6	40.8	0.017	4.4	0.72	8.7	0.9	4.31	0.19
Males (n=50)										
	Avg:	255.7	526.7	0.173	17.4	3.27	5.6	3.7	2.10	1.51
	StDev:	62.5	42.9	0.022	5.6	0.93	3.1	0.9	0.79	0.26
		P<0.001 ***	p=0.001 **	p=0.31	p=0.16	p=0.66	p<0.001 ***	p=0.94	p<0.001 ***	p<0.001 ***

Morphometric comparisons over time

The information provided in Table 1 was rearranged to facilitate comparison of values across sample dates within sexes, including ANOVA results for differences over time and presented below in Table 2.

TABLE 2. Summary statistics for morphometric measures and derived metrics recorded for female and male adult Pacific lamprey captured at Willamette Falls one day per month in June, July and August 2016, with results for ANOVA analysis for differences between sample dates within sexes. Note – due to bias resulting from differences in sampling procedures for measuring gonad weight in July, a second ANOVA comparing June versus August only data was conducted for gonad weight and GSI.

	Females						Males				
	(n=49) June 17	(n=34) July 8	(n=50) August 9				(n=51) June 17	(n=35) July 8	(n=50) August 9		
Weight (g)											
Avg:	371.0	346.2	306.9	p<0.001	***	Avg:	328.8	303.9	255.7	p<0.001	***
StDev:	80.3	79.0	61.6			StDev:	76.7	70.2	62.5		
Length (mm)											
Avg:	579.7	581.9	555.3	p=0.004	**	Avg:	565.3	569.5	526.7	p<0.001	***
StDev:	41.1	40.7	40.8			StDev:	45.9	42.4	42.9		
K Factor											
Avg:	0.188	0.173	0.177	p<0.001	***	Avg:	0.180	0.163	0.173	p=0.001	**
StDev:	0.014	0.013	0.017			StDev:	0.018	0.022	0.022		
DFG (mm)											
Avg:	22.9	22.5	18.8	p<0.001	***	Avg:	23.3	20.6	17.4	p<0.001	***
StDev:	6.8	4.7	4.4			StDev:	5.2	4.2	5.6		
DFG/Length (%)											
Avg:	3.91	3.85	3.35	p=0.002	**	Avg:	4.10	3.60	3.27	p<0.001	***
StDev:	0.95	0.69	0.72			StDev:	0.70	0.60	0.93		
Gonad (0.1g)											
Avg:	23.2	16.3	19.7	p<0.001	***	Avg:	8.9	5.9	5.6	p<0.001	***
StDev:	8.3	6.5	8.7	(p=0.040 Jun & Aug)		StDev:	3.5	3.2	3.1	(p<0.001 Jun & Aug)	
Liver (0.1g)											
Avg:	4.1	4.0	3.8	p=0.28		Avg:	4.4	4.3	3.7	p=0.004	**
StDev:	1.1	1.2	0.9			StDev:	1.0	1.1	0.9		
GSI (%)											
Avg:	7.04	5.37	7.37	p=0.030	*	Avg:	2.73	1.93	2.10	p<0.001	***
StDev:	2.99	2.83	4.31	(p=0.066 Jun & Aug)		StDev:	0.76	0.85	0.79	(p<0.001 Jun & Aug)	
HSI (%)											
Avg:	1.12	1.17	1.24	p=0.003	**	Avg:	1.37	1.44	1.51	p=0.021	*
StDev:	0.18	0.16	0.19			StDev:	0.24	0.22	0.26		

Length, weight and condition factor measures within sexes all showed significant differences among sample dates, with a general decrease for each over time. DFG and DFG/length measures also decreased significantly from June to August. Similarly, Clemens et al. (2013) observed decrease in body length and DFG measures for Pacific lamprey collected at Willamette Falls over the same months. Adult Pacific lamprey cease feeding following reentry into freshwater, utilizing lipid and protein stores in the muscle and visceral tissues to support general metabolic needs and to initiate gonadal maturation processes. Being cartilaginous, the result is that not only does body weight decrease, length also decreases, with an average decrease of approximately 20% and up to as much as 30% (Beamish 1980, Clemens et al. 2009; 2011). Beamish (1980) reported greater shrinkage in females (23%) compared to males (15%). Lampman et al. (2016) observed that from the time of collection in 2013 at Columbia River mainstem dams to the time of artificial spawning approximately one year later, average reduction in total length for male and female adult Pacific lamprey was 23.3% and 27.1%, respectively, and average reduction in total weight was 42.9% and 40.2%, respectively. Decrease in length is apparently occurs disproportionately in the middle portion of the body; Lampman et al. (2016) observed that just prior to artificial spawning, average DFG for females diminished to only 0.6 mm, and for males to -2.9 mm (the two fins actually overlap).

We did not, however, observe an increase in gonad weight over time, as would be expected for fish progressing in gonadal maturation. In fact, average gonad weight (as measured with the additional connective tissues) for both sexes sampled in August was significantly lower than for fish sampled in June. (Note – we have excluded consideration of measures made for fish sampled in July, due to bias associated with efforts to tease away non-gonadal tissue prior to recording gonad weight.) However, it is possible that actual weight of the gonads did in fact increase over time, but that the increase was surpassed by reduction in weight of the associated visceral and gonadal adipose tissue, due to metabolism of the latter during this period of non-feeding. This possibility is supported by a near-significant increase in GSI for females in August relative to June. In contrast, there was a significant decrease in GSI in August for males, although as indicated previously, the proportion of actual testes weight in the recorded gonad weight for males was lower than for females, and an increase in testes size could have been masked by a relatively larger decrease in weight of the associated adipose tissues.

While liver size tended to decrease over time (significant for males), HSI showed a significant increase for both sexes, associated with the highly significant decrease in average body size for both sexes over the summer sampling dates.

Sex Ratio

The number of females (F) and males (M) within each sample date are provided below (Table 3). Sex ratio never differed significantly from 1:1 (Chi-Square test, $p<0.05$).

TABLE 3. Number of females and males and sex ratio of adult Pacific lamprey captured at Willamette Falls one day per month in June, July and August 2016.

	Number and ratio per 2016 sample date		
Sex	June 17	July 8	August 9
Female	49	34	50
Male	51	35	50
F:M ratio	0.96 : 1.04	0.97 : 1.03	1.00 : 1.00

Among the 360 fish collected at Willamette Falls in 2007 and 2008 by Clemens (2011), the overall sex ratio within years was not significantly different from 1:1. However, in both years there was a trend for an increase in frequency over time for one sex relative to the other. For lamprey sampled from April through September 2007 there was a weak trend for an increase in the proportion of females. In contrast, from April through August 2008 there was a strong trend for an increase in the proportion of males. How much these trends are real versus an artifact of small sample size for several of the collection dates, and/or related to a major die-off of fish at the falls due to high water temperatures in August 2008 that may have affected females preferentially is unclear.

Most fish species, as well as mammal and bird species, are gonochoristic (individuals develop only as males or females) and sex determination is monogenic and associated with a XX/XY or ZZ/WZ sex determining system resulting in 1:1 sex ratios (though, unlike in mammals, karyotypic differences in sex chromosomes are typically not apparent). However, polygenic sex determination has also been observed in several fish species, resulting in variability in sex ratio among populations within species. Additionally, various fish species demonstrate a substantial degree of lability in gonadal development, and environmental factors have been shown to alter population sex ratios in some cases (Devlin and Nagahama 2002). Dawson et al. (2015) reviewed several studies that reported sex ratios skewed from 1:1 for lamprey species (though not Pacific lamprey). In these studies, the influence of temperature, pH and/or larval density during the protracted (1-3 years) period of larval sexual indeterminacy, was proposed to have altered gonadal development towards one sex. A study recently published by Johnson et al. (2017) proposed variation in growth rate as having altered the sex ratio in developing sea lamprey in productive versus unproductive habitats. On the other hand, Dawson et al. (2015) also cite studies in which equal proportions of males and females in sampled populations were observed, and various laboratory studies that reported treatments applied to developing larvae were unsuccessful in altering sex ratio from 1:1. While not discounting the possibility of environmentally influenced lability in sex determination in Pacific lamprey, our observation of a 1:1 sex ratio in each of the June, July and August 2016 samples collected at Willamette Falls, leads us to hypothesize that environmental sex determination is not playing a significant role and that we can expect that Pacific lamprey collected during these summer months at the Columbia River mainstem dams for tribal translocation programs will exhibit similar proportions of males and females.

Maturation status

None of the fish collected in 2016 freely expressed eggs or milt, and none of the females showed the distended abdomen and presence of a pseudoanal fin characteristic of females at full maturity (Lampman et al. 2016). Upon dissection, the testes and ovaries appeared to be only partially developed. Testes in the males were a pinkish tan in color and lobular in form (Figure 2A; includes the liver). Average GSI for males per sample date ranged from 2.0% to 2.7%, with an overall range for individuals from 0.4% to 5.7%. Ovaries in females were larger than the testes and with a similar magnitude of variation in size among individuals (Figure 2B). Average GSI per sample date ranged from 5.4% to 7.4%, with an overall range for individuals from 1.0% to 16.0% (plus one individual at 20.1%). Individual oocytes were apparent upon non-magnified visual examination, and whitish-pink in color. We hypothesize that all of the lamprey examined would require overwintering for a year (or more) prior to reaching full maturity and spawning.

2A 2B

FIGURE 2. Gonads from Pacific lamprey sampled in June 2016: testes (plus liver) from a male (2A), and ovaries from two females, the larger of which was from a fish with a GSI of approximately 15% (2B; lower magnification than 2A), note presence of associated connective tissue, visceral and gonadal adipose tissue, and intestine.

In contrast to our observations, Clemens et al. (2013) observed a small percentage of fish collected at Willamette Falls that were in a relatively advanced state of maturation. The females among these fish had ovaries that had gone through vitellogenesis and were approaching maturity, and the males exhibited testes in relatively advanced stage of spermatogenesis. However, with just a few exceptions

that involved fish sampled in June, all of these near-mature fish were ones collected in April and May, during the early portion of the run. It is thought that these fish with maturing gonads had entered the Columbia as immature fish the year prior, overwintered at locations downstream of Willamette Falls, and begun the final upstream migration run to seek spawning grounds when they were captured. Baker and McVay (2015) observed that average size among fish captured in the fish ladder at Willamette Falls early in the return migration season (mid-March through May) was smaller than for fish captured in June and later. They believe this to be due to inclusion of a number of individuals in the early samples that had already overwintered, had decreased in length relative to their size upon re-entry the year before, and were approaching full maturity.

Over the period since the translocation programs were initiated, tribal biologists have also observed that a limited number of the lamprey collected at the Columbia mainstem dams had relatively small DFG measures and soft distended bellies. These fish were presumed to have already reached sexual maturity and typically were re-released to the river instead of being kept for overwintering (Ralph Lampman, and Aaron Jackson, personal communications). Because the number of these putatively mature fish was small, and because all of the 267 fish collected in our 2016 samples were confirmed to be immature, we believe program managers are safe in presuming that essentially all lamprey transferred to their facilities for translocation will indeed require at least one year of overwintering prior to release.

Tissue collections for additional studies

During the dissection process, we collected fin clips from all fish, and heads from a sub-sample of the fish. The fin clips and associated biodata, including phenotypic sex identification, were sent to the CRITFC molecular genetics laboratory at the Hagerman Fish Culture Extension Station, Hagerman, Idaho. There, DNA will be extracted from each sample, and the DNA will be used in a search for a sex-specific DNA marker. If such a marker can be found, it would provide a means to identify sex in a non-lethal manner.

In addition to the fin clip, heads from a subsample of the fish were removed and frozen with an accompanying individual identification number. We have initiated discussions with other laboratories experienced with microchemical analysis of fish otoliths and lamprey statoliths, regarding the possibility of ascertaining age during the freshwater and the salt water phases, and/or location of residence during these two phases.

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Appendix 1. Biodata and metrics (sorted by GSI) for female Pacific lamprey captured at Willamette Falls on June 17, 2016.

	Weight (g)	Length (mm)	K Factor	DFG (mm)	DFG/Length (%)	Gonad (0.1g)	Liver (0.1g)	GSI (%)	HSI
	445	621	0.186	21	3.38	14.8	4.8	3.44	1.09
	431	602	0.198	22	3.65	15.2	4.5	3.66	1.06
	365	566	0.201	28	4.95	13.2	4.1	3.75	1.14
	395	597	0.186	21	3.52	15.4	3.9	4.06	1.00
	378	587	0.187	24	4.09	15	5.3	4.13	1.42
	614	682	0.194	40	5.87	25.2	6.3	4.28	1.04
	314	608	0.140	28	4.61	12.9	4.6	4.28	1.49
	399	608	0.178	30	4.93	16.4	4.1	4.29	1.04
	341	561	0.193	19	3.39	14.3	4.4	4.38	1.31
	462	613	0.201	20	3.26	19.5	5.8	4.41	1.27
	595	690	0.181	43	6.23	25.3	7.9	4.44	1.35
	425	600	0.197	32	5.33	18.1	4.5	4.45	1.07
	552	665	0.188	29	4.36	23.8	6.4	4.51	1.17
	427	606	0.192	28	4.62	18.7	3.8	4.58	0.90
	329	553	0.195	18	3.25	14.6	3.3	4.64	1.01
	357	579	0.184	16	2.76	16.6	4	4.88	1.13
	405	605	0.183	30	4.96	19.3	4.4	5.00	1.10
	393	593	0.188	22	3.71	19.1	3.8	5.11	0.98
	430	586	0.214	28	4.78	21.3	4.2	5.21	0.99
	405	593	0.194	28	4.72	20.4	4.6	5.30	1.15
	367	578	0.190	19	3.29	19.7	4.7	5.67	1.30
	317	545	0.196	16	2.94	17.8	3.6	5.95	1.15
	484	635	0.189	36	5.67	27.7	5.4	6.07	1.13
	334	575	0.176	19	3.30	20.1	3.7	6.40	1.12
	372	590	0.181	24	4.07	23.1	3.1	6.62	0.84
	302	541	0.191	19	3.51	19	3.3	6.71	1.10
	372	580	0.191	19	3.28	23.7	4	6.80	1.09
	247	518	0.178	20	3.86	16.3	3.5	7.07	1.44
	267	546	0.164	14	2.56	18.4	3.6	7.40	1.37
	377	574	0.199	28	4.88	26.1	4.1	7.44	1.10
	366	584	0.184	18	3.08	25.5	4.1	7.49	1.13
	353	570	0.191	28	4.91	26	3.9	7.95	1.12
	329	576	0.172	20	3.47	24.3	4	7.98	1.23
	320	568	0.175	20	3.52	24	3.2	8.11	1.01
	338	560	0.192	20	3.57	25.4	3.9	8.13	1.17
	312	546	0.192	21	3.85	24	3.4	8.33	1.10
	339	605	0.153	25	4.13	26.9	3.2	8.62	0.95
	303	546	0.186	20	3.66	24.1	2.9	8.64	0.97
	349	576	0.183	20	3.47	27.9	3.5	8.69	1.01
	271	522	0.191	7	1.34	21.7	4.2	8.70	1.57
	427	633	0.168	31	4.90	34.5	6	8.79	1.43
	341	554	0.201	21	3.79	27.9	3.3	8.91	0.98
	250	514	0.184	19	3.70	23.4	3	10.33	1.21
	300	527	0.205	21	3.98	28.6	2.7	10.54	0.91
	302	543	0.189	14	2.58	29.9	2.5	10.99	0.83
	409	571	0.220	20	3.50	47.3	4.5	13.08	1.11
	220	468	0.215	10	2.14	27.4	2.5	14.23	1.15
	421	581	0.215	22	3.79	55.2	2.9	15.09	0.69
	327	562	0.184	24	4.27	43.5	2.5	15.34	0.77
Average	371.0	579.7	0.188	22.9	3.91	23.2	4.1	7.04	1.12
StDev	80.3	41.1	0.014	6.8	0.95	8.3	1.1	2.99	0.18

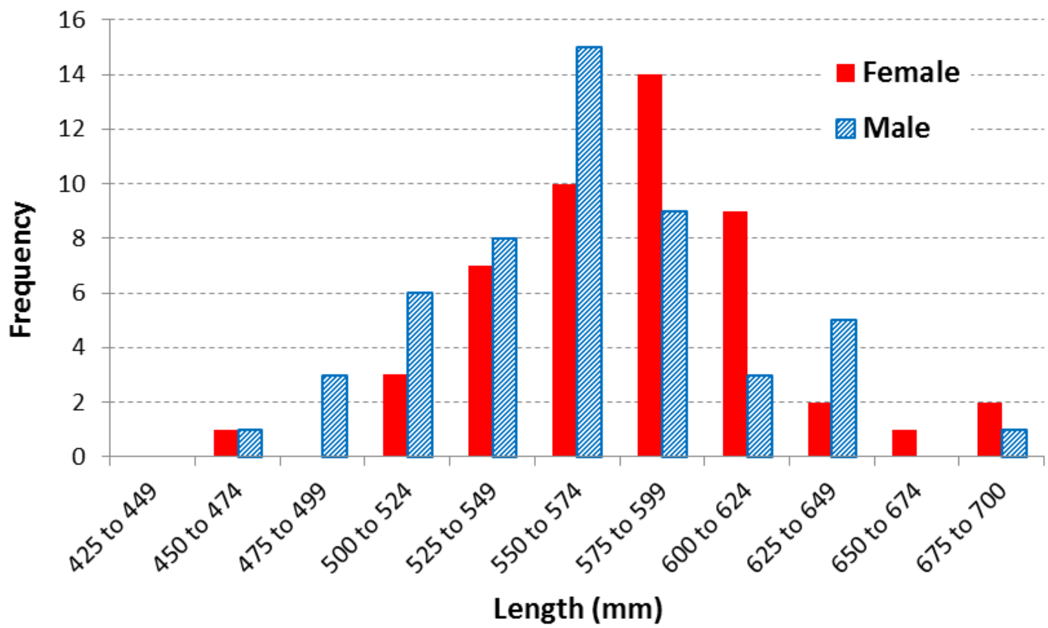
Appendix 2. Biodata and metrics (sorted by GSI) for male Pacific lamprey captured at Willamette Falls on June 17, 2016.

	Weight (g)	Length (mm)	K Factor	DFG (mm)	DFG/Length (%)	Gonad (0.1g)	Liver (0.1g)	GSI (%)	HSI
	258	491	0.218	20	4.07	2.5	3.2	0.98	1.26
	275	552	0.163	21	3.80	4.3	4	1.59	1.48
	277	517	0.200	21	4.06	4.7	4.1	1.73	1.50
	301	544	0.187	27	4.96	5.3	3.5	1.79	1.18
	275	545	0.170	20	3.67	5.2	5.2	1.93	1.93
	315	575	0.166	28	4.87	6.1	5	1.97	1.61
	231	498	0.187	18	3.61	4.5	3.9	1.99	1.72
	343	574	0.181	16	2.79	6.8	5.9	2.02	1.75
	239	515	0.175	19	3.69	4.9	3.2	2.09	1.36
	376	586	0.187	21	3.58	8.1	4.3	2.20	1.16
	287	534	0.188	18	3.37	6.2	3.5	2.21	1.23
	244	506	0.188	14	2.77	5.3	2.9	2.22	1.20
	365	622	0.152	29	4.66	8	4.4	2.24	1.22
	376	612	0.164	26	4.25	8.3	5.7	2.26	1.54
	204	466	0.202	20	4.29	4.7	3.1	2.36	1.54
	323	578	0.167	27	4.67	7.5	4.8	2.38	1.51
	294	591	0.142	19	3.21	6.9	5.4	2.40	1.87
	307	571	0.165	20	3.50	7.3	4.5	2.44	1.49
	277	520	0.197	14	2.69	6.6	3.2	2.44	1.17
	285	549	0.172	23	4.19	6.8	3.6	2.44	1.28
	219	497	0.178	20	4.02	5.3	4.3	2.48	2.00
	362	569	0.197	18	3.16	8.8	3.8	2.49	1.06
	243	520	0.173	20	3.85	6	3.3	2.53	1.38
	315	555	0.184	20	3.60	7.8	5.4	2.54	1.74
	369	592	0.178	26	4.39	9.3	3.9	2.59	1.07
	317	597	0.149	22	3.69	8	4.5	2.59	1.44
	324	559	0.185	27	4.83	8.3	4.7	2.63	1.47
	283	541	0.179	20	3.70	7.7	3.5	2.80	1.25
	224	518	0.161	20	3.86	6.2	3.3	2.85	1.50
	411	596	0.194	23	3.86	11.4	4.9	2.85	1.21
	328	554	0.193	19	3.43	9.1	3.5	2.85	1.08
	480	647	0.177	29	4.48	13.4	5.8	2.87	1.22
	338	556	0.197	22	3.96	9.5	3.8	2.89	1.14
	316	570	0.171	27	4.74	9	3.9	2.93	1.25
	262	526	0.180	20	3.80	7.5	3.8	2.95	1.47
	407	629	0.164	36	5.72	11.8	5.2	2.99	1.29
	281	531	0.188	22	4.14	8.2	3.1	3.01	1.12
	298	551	0.178	20	3.63	9.1	4.2	3.15	1.43
	490	645	0.183	22	3.41	15	6.7	3.16	1.39
	502	648	0.184	31	4.78	15.4	5.2	3.16	1.05
	501	691	0.152	40	5.79	15.5	6.4	3.19	1.29
	339	560	0.193	22	3.93	10.7	4.4	3.26	1.32
	490	628	0.198	28	4.46	15.5	6.6	3.27	1.37
	438	621	0.183	32	5.15	14	4.1	3.30	0.94
	369	567	0.202	29	5.11	11.9	4.4	3.33	1.21
	382	569	0.207	28	4.92	13	4.8	3.52	1.27
	279	526	0.192	28	5.32	9.6	3.3	3.56	1.20
	317	571	0.170	24	4.20	11.5	3.8	3.76	1.21
	427	599	0.199	25	4.17	16.9	6.2	4.12	1.47
	350	558	0.201	23	4.12	14.4	4.7	4.29	1.36
	255	592	0.123	25	4.22	13.7	4.4	5.68	1.76
Avg:	328.8	565.3	0.180	23.3	4.10	8.9	4.4	2.73	1.37
StDev:	76.7	45.9	0.018	5.2	0.70	3.5	1.0	0.76	0.24

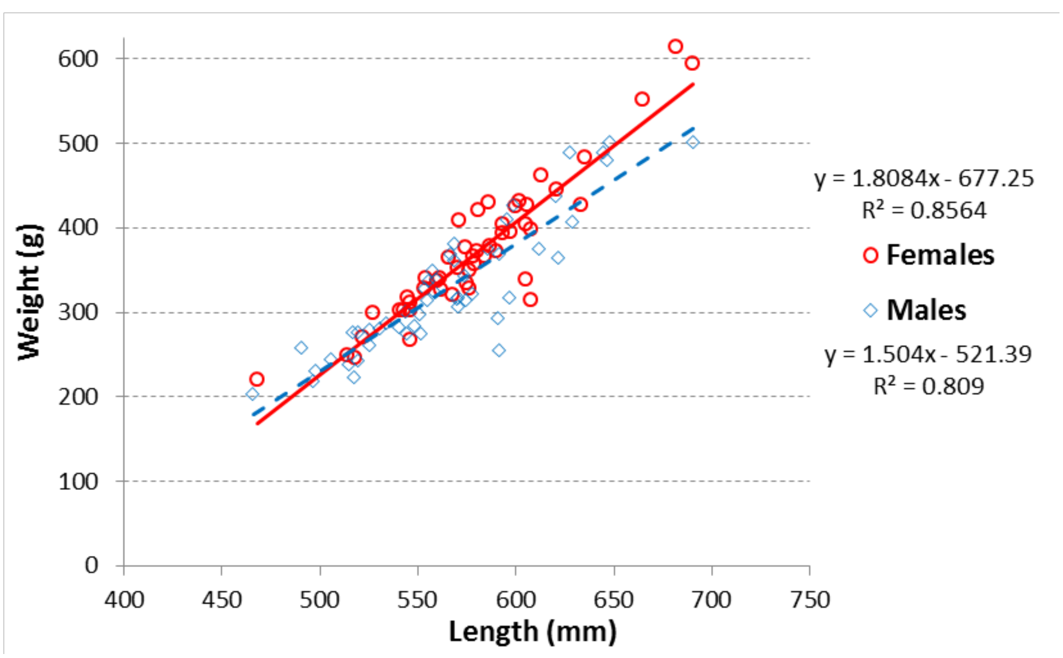
Difference Females : Males, and Significance Level:

	Weight (g)	Length (mm)	K Factor	DFG (mm)	DFG/Length (%)	Gonad (0.1g)	Liver (0.1g)	GSI (%)	HSI
	p=0.008	p=0.103	p=0.013	p=0.732	p=0.243			p<0.000	p<0.000
	**		*					***	***

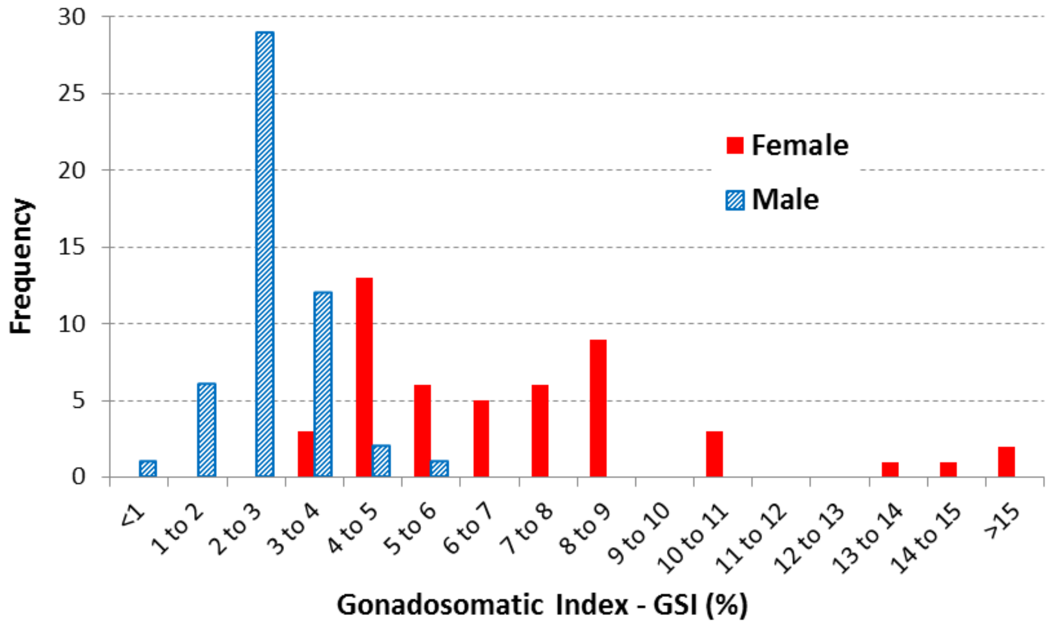
Appendix 3. Length (mm) frequency distribution for female and male Pacific lamprey captured at Willamette Falls on June 17, 2016.



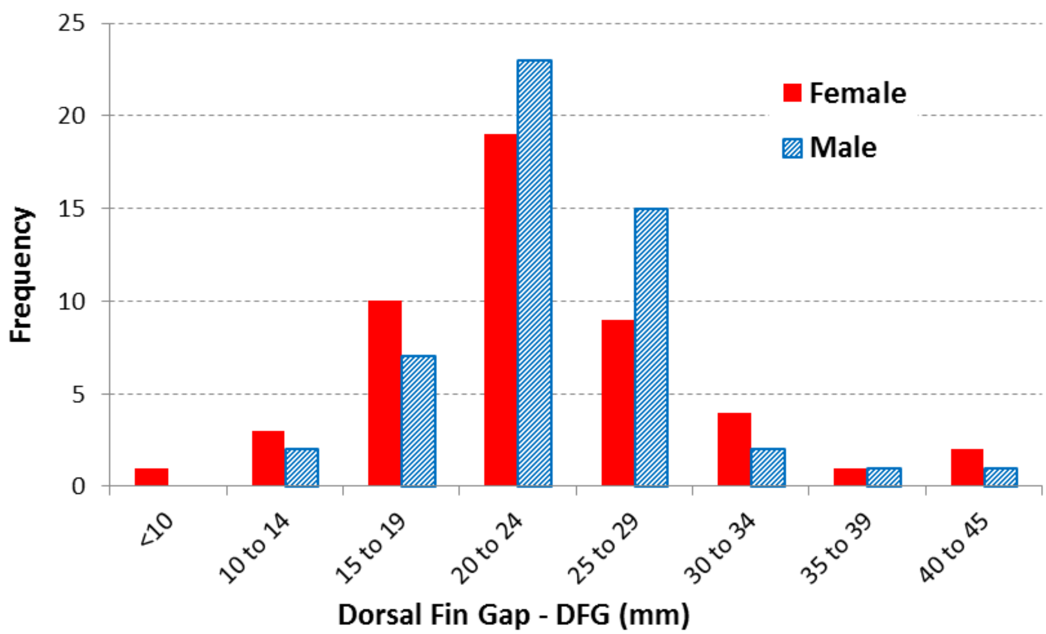
Appendix 4. Relationship of Weight (g) to Length (mm) for female and male Pacific lamprey captured at Willamette Falls on June 17, 2016.



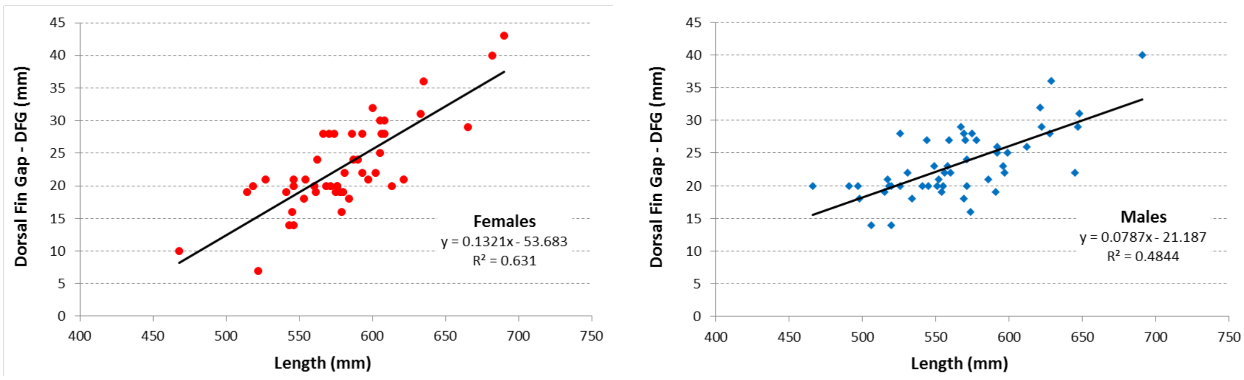
Appendix 5. Gonadosomatic Index - GSI (%) frequency distribution for female and male Pacific lamprey captured at Willamette Falls on June 17, 2016.



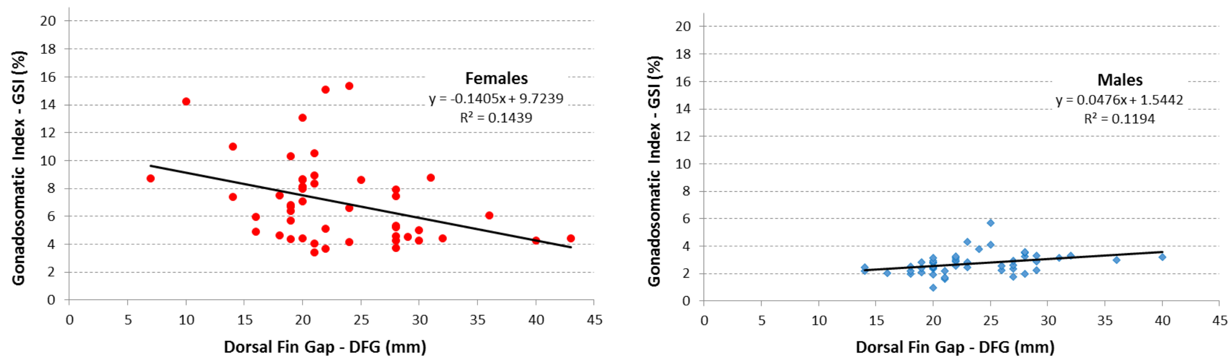
Appendix 6. Dorsal fin gap – DFG (mm) frequency distribution for female and male Pacific lamprey captured at Willamette Falls on June 17, 2016.



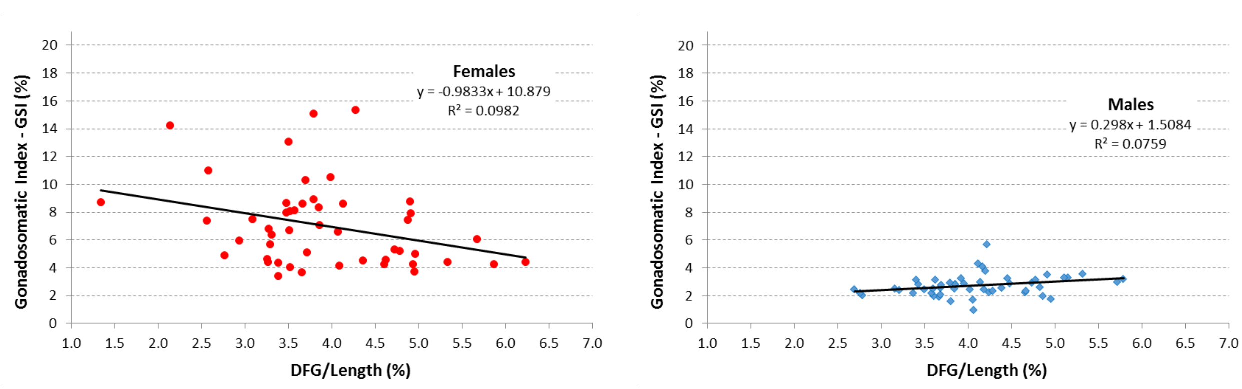
Appendix 7. Relationship of Dorsal Fin Gap - DFG (mm) to Length (mm) for female and male Pacific lamprey captured at Willamette Falls on June 17, 2016.



Appendix 8. Relationship of Gonadosomatic Index - GSI (%) to Dorsal Fin Gap – DFG (mm) for female and male Pacific lamprey captured at Willamette Falls on June 17, 2016.



Appendix 9. Relationship of Gonadosomatic Index - GSI (%) to Dorsal Fin Gap/Length (%) for female and male Pacific lamprey captured at Willamette Falls on June 17, 2016.



Appendix 10. Biodata and metrics (sorted by GSI) for female Pacific lamprey captured at Willamette Falls on July 8, 2016.

	Weight (g)	Length (mm)	K Factor	DFG (mm)	DFG/Length (%)	Gonad (0.1g)	Liver (0.1g)	GSI (%)	HSI
	574	686	0.178	30	4.37	6.3	7.5	1.11	1.32
	444	602	0.204	23	3.82	8.8	6.1	2.02	1.39
	311	569	0.169	22	3.87	6.2	3.8	2.03	1.24
	400	628	0.162	30	4.78	10.5	6.0	2.70	1.52
	475	640	0.181	30	4.69	13.5	5.2	2.93	1.11
	422	630	0.169	23	3.65	12.3	4.6	3.00	1.10
	389	594	0.186	21	3.54	11.7	4.2	3.10	1.09
	352	590	0.171	25	4.24	11.0	4.5	3.23	1.29
	438	646	0.162	25	3.87	13.7	4.4	3.23	1.01
	305	560	0.174	19	3.39	9.9	3.2	3.35	1.06
	329	595	0.156	22	3.70	10.9	3.7	3.43	1.14
	340	587	0.168	27	4.60	12.0	4.3	3.66	1.28
	329	590	0.160	23	3.90	11.8	4.0	3.72	1.23
	381	613	0.165	19	3.10	13.9	4.3	3.79	1.14
	353	580	0.181	20	3.45	13.4	3.0	3.95	0.86
	375	602	0.172	31	5.15	15.9	4.0	4.43	1.08
	312	551	0.187	20	3.63	13.4	3.8	4.49	1.23
	358	561	0.203	16	2.85	15.6	4.1	4.56	1.16
	258	552	0.153	24	4.35	11.3	2.6	4.58	1.02
	356	592	0.172	17	2.87	16.3	5.5	4.80	1.57
	250	509	0.190	21	4.13	12.8	2.7	5.40	1.09
	523	653	0.188	30	4.59	27.5	6.4	5.55	1.24
	259	549	0.157	19	3.46	14.7	3.1	6.02	1.21
	331	580	0.170	19	3.28	20.2	4.1	6.50	1.25
	312	566	0.172	22	3.89	19.3	3.6	6.59	1.17
	383	598	0.179	28	4.68	27.2	4.8	7.64	1.27
	271	554	0.159	27	4.87	20.0	3.1	7.97	1.16
	255	533	0.168	25	4.69	19.7	2.9	8.37	1.15
	318	565	0.176	20	3.54	24.9	3.3	8.50	1.05
	313	590	0.152	20	3.39	25.5	4.1	8.87	1.33
	255	542	0.160	17	3.14	21.0	2.6	8.97	1.03
	262	525	0.181	23	4.38	23.6	3.1	9.90	1.20
	266	514	0.196	13	2.53	28.5	2.2	12.00	0.83
	272	540	0.173	14	2.59	29.4	2.4	12.12	0.89
Avg:	346.2	581.9	0.173	22.5	3.85	16.3	4.0	5.37	1.17
StDev:	79.0	40.7	0.013	4.7	0.69	6.5	1.2	2.83	0.16

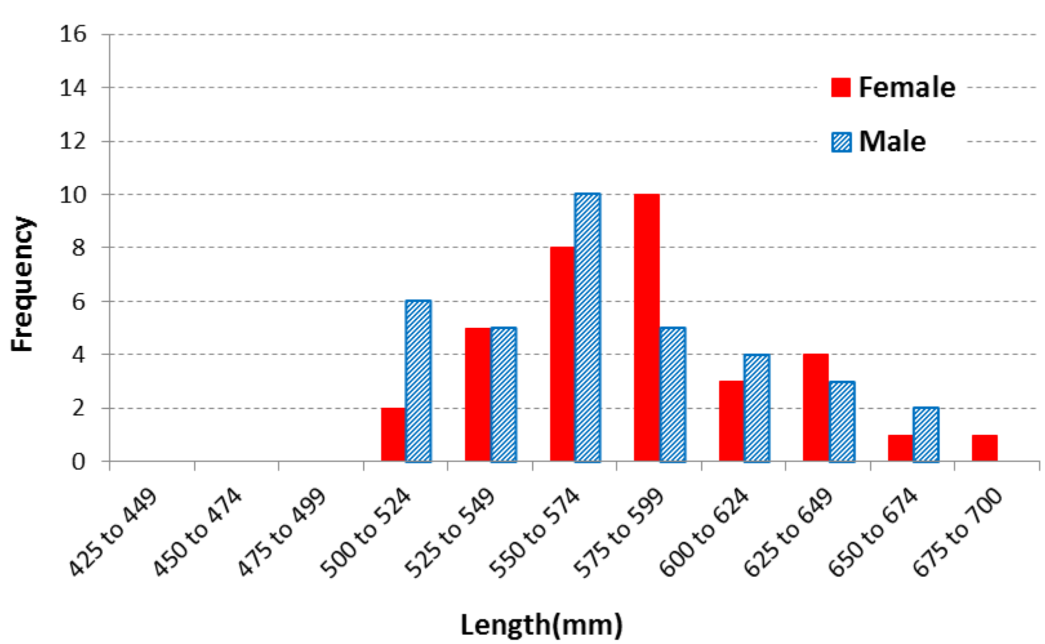
Appendix 11. Biodata and metrics (sorted by GSI) for male Pacific lamprey captured at Willamette Falls on July 8, 2016.

	Weight (g)	Length (mm)	K Factor	DFG (mm)	DFG/Length (%)	Gonad (0.1g)	Liver (0.1g)	GSI (%)	HSI
	333	580	0.171	24	4.14	1.4	5.3	0.42	1.62
	351	610	0.155	19	3.11	2.1	4.9	0.60	1.42
	281	548	0.171	27	4.93	2.0	2.8	0.72	1.01
	277	553	0.164	22	3.98	2.1	3.3	0.76	1.21
	217	504	0.169	18	3.57	1.7	2.8	0.79	1.31
	226	535	0.148	23	4.30	1.8	3.4	0.80	1.53
	259	566	0.143	20	3.53	2.8	4.8	1.09	1.89
	240	519	0.172	14	2.70	2.7	4.5	1.14	1.91
	237	551	0.142	17	3.09	2.9	3.3	1.24	1.41
	292	559	0.167	15	2.68	3.6	3.9	1.25	1.35
	178	520	0.127	24	4.62	2.5	3.1	1.42	1.77
	252	550	0.151	18	3.27	3.6	4.1	1.45	1.65
	353	594	0.168	20	3.37	5.1	4.3	1.47	1.23
	457	635	0.178	27	4.25	7.4	5.4	1.65	1.20
	222	522	0.156	17	3.26	3.8	2.4	1.74	1.09
	318	600	0.147	21	3.50	5.8	4.8	1.86	1.53
	200	510	0.151	16	3.14	3.8	3.4	1.94	1.73
	247	531	0.165	20	3.77	4.8	3.7	1.98	1.52
	270	529	0.182	18	3.40	5.5	3.8	2.08	1.43
	457	652	0.165	30	4.60	9.4	7.7	2.10	1.71
	359	522	0.252	22	4.21	7.4	4.8	2.10	1.36
	232	561	0.131	19	3.39	5.1	2.9	2.25	1.27
	260	534	0.171	15	2.81	5.9	3.7	2.32	1.44
	349	606	0.157	23	3.80	8.2	4.8	2.41	1.39
	320	578	0.166	20	3.46	8.1	4.8	2.60	1.52
	400	642	0.151	23	3.58	10.4	5.4	2.67	1.37
	345	594	0.165	23	3.87	9.2	4.5	2.74	1.32
	375	569	0.204	19	3.34	10.0	5.3	2.74	1.43
	322	634	0.126	27	4.26	8.6	5.6	2.74	1.77
	400	657	0.141	29	4.41	10.8	5.5	2.77	1.39
	297	555	0.174	15	2.70	8.2	3.4	2.84	1.16
	407	620	0.171	19	3.06	11.3	5.8	2.86	1.45
	312	575	0.164	23	4.00	8.9	3.9	2.94	1.27
	300	566	0.165	14	2.47	10.1	3.9	3.48	1.32
	293	553	0.173	20	3.62	10.2	4.0	3.61	1.38
Avg:	303.9	569.5	0.163	20.6	3.6	5.9	4.3	1.930	1.439
StDev:	70.2	42.4	0.022	4.2	0.6	3.2	1.1	0.852	0.216

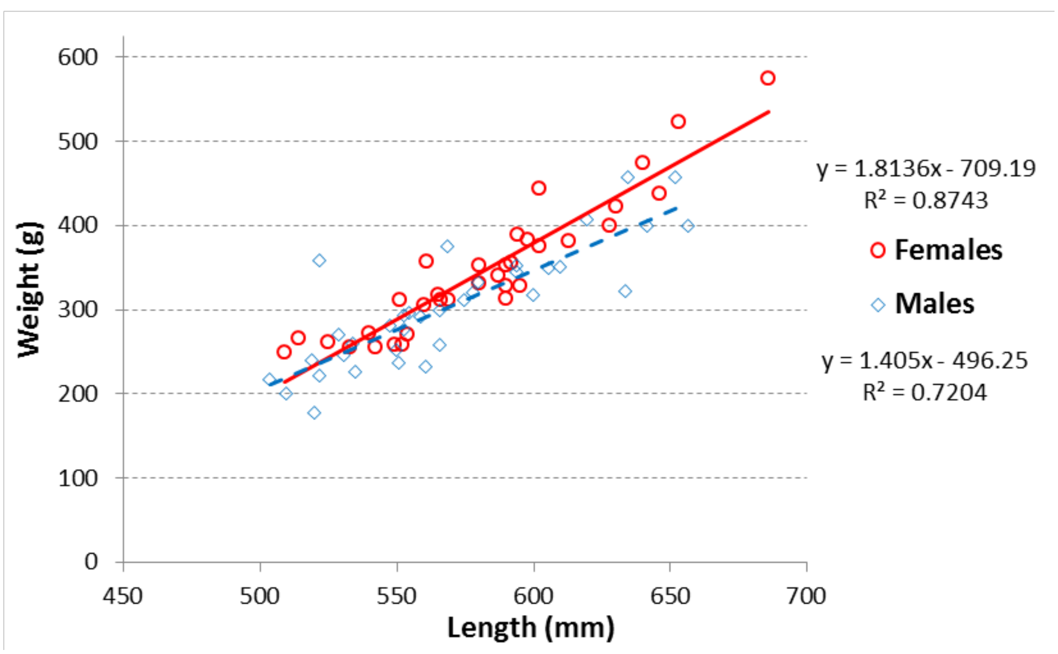
Difference Females : Males, and Significance Level:

	Weight (g)	Length (mm)	K Factor	DFG (mm)	DFG/Length (%)	Gonad (0.1g)	Liver (0.1g)	GSI (%)	HSI
	p=0.038*	p=0.333	p=0.022	p=0.081	p=0.120			p<0.001	p<0.001
	*		*					***	***

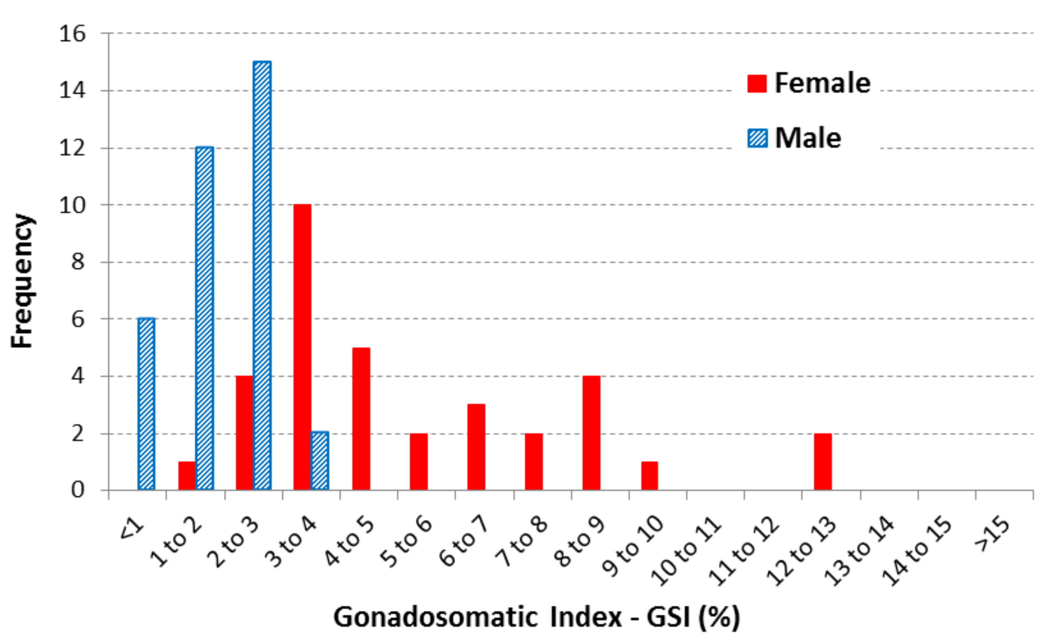
Appendix 12. Length (mm) frequency distribution for female and male Pacific lamprey captured at Willamette Falls on July 8, 2016.



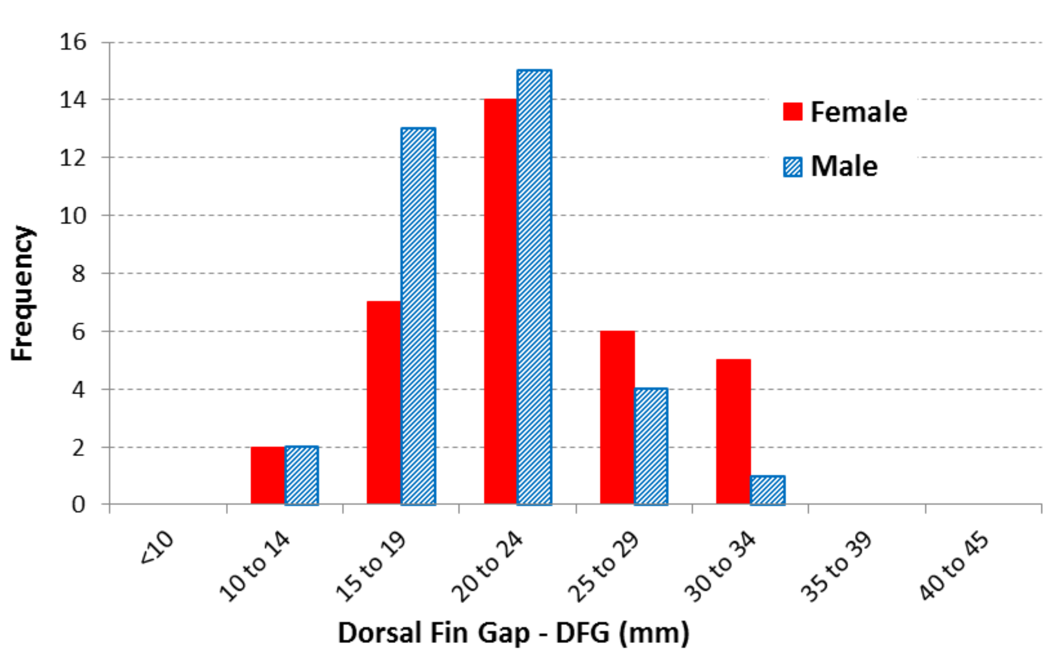
Appendix 13. Relationship of Weight (g) to Length (mm) for female and male Pacific lamprey captured at Willamette Falls on July 8, 2016.



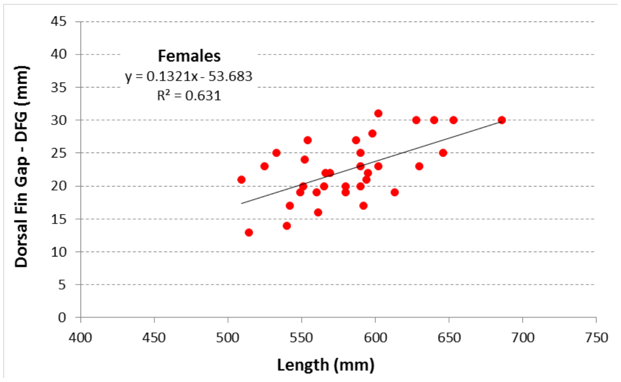
Appendix 14. Gonadosomatic Index - GSI (%) frequency distribution for female and male Pacific lamprey captured at Willamette Falls on July 8, 2016.

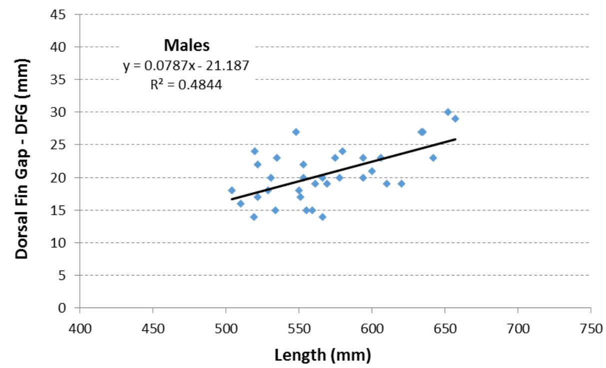


Appendix 15. Dorsal fin gap – DFG (mm) frequency distribution for female and male Pacific lamprey captured at Willamette Falls on July 8, 2016.

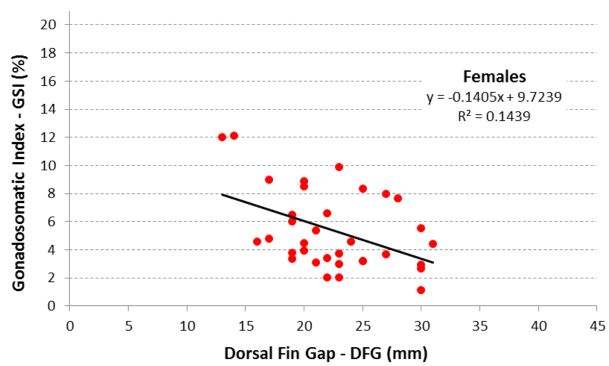


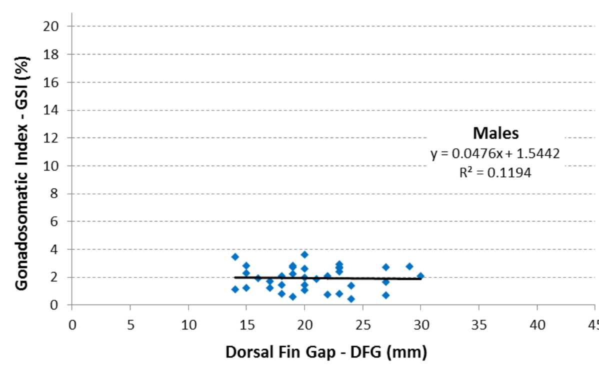
Appendix 16. Relationship of Dorsal Fin Gap - DFG (mm) to Length (mm) for female and male Pacific lamprey captured at Willamette Falls on July 8, 2016.



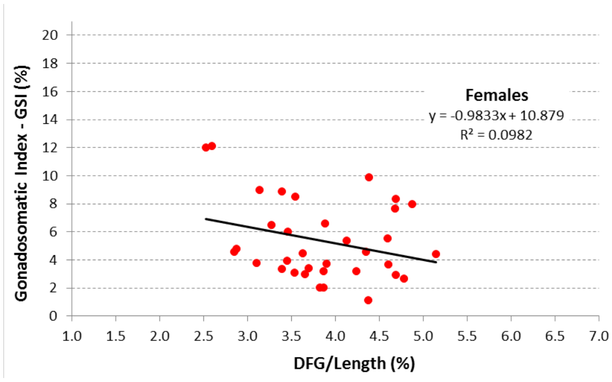


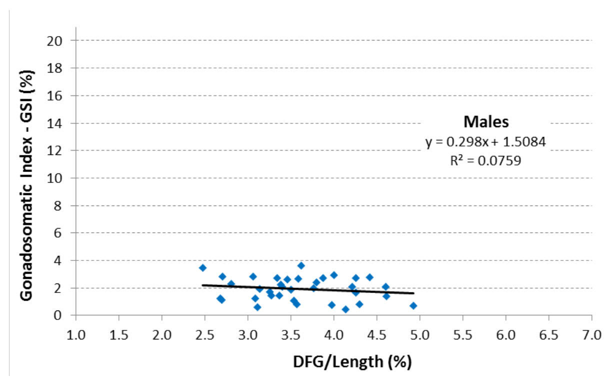
Appendix 17. Relationship of Gonadosomatic Index - GSI (%) to Dorsal Fin Gap – DFG (mm) for female and male Pacific lamprey captured at Willamette Falls on July 8, 2016.





Appendix 18. Relationship of Gonadosomatic Index - GSI (%) to Dorsal Fin Gap/Length (%) for female and male Pacific lamprey captured at Willamette Falls on July 8, 2016.





Appendix 19. Biodata and metrics (sorted by GSI) for female Pacific lamprey captured at Willamette Falls on August 9, 2016.

	Weight (g)	Length (mm)	K Factor	DFG (mm)	DFG/Length (%)	Gonad (0.1g)	Liver (0.1g)	GSI (%)	HSI
	375	633	0.148	19	3.00	8.5	4.7	2.32	1.27
	270	536	0.175	20	3.73	8.0	3.2	3.05	1.20
	322	566	0.178	20	3.53	10.0	3.8	3.21	1.19
	382			24		12.4	4.4	3.35	1.17
	250	528	0.170	22	4.17	8.4	3.2	3.48	1.30
	247	536	0.160	14	2.61	8.3	3.0	3.48	1.23
	281	549	0.170	23	4.19	9.7	3.4	3.58	1.22
	426	616	0.182	26	4.22	15.0	4.5	3.65	1.07
	277	588	0.136	16	2.72	10.0	4.1	3.75	1.50
	331	565	0.184	16	2.83	12.9	3.2	4.06	0.98
	370	590	0.180	19	3.22	14.6	4.8	4.11	1.31
	476	639	0.182	23	3.60	20.1	5.3	4.41	1.13
	278	573	0.148	24	4.19	11.8	3.7	4.43	1.35
	278	529	0.188	26	4.91	11.9	3.8	4.47	1.39
	407	606	0.183	22	3.63	17.6	4.9	4.52	1.22
	319	564	0.178	20	3.55	14.0	4.1	4.59	1.30
	380	597	0.179	12	2.01	17.0	5.3	4.68	1.41
	254	518	0.183	14	2.70	11.4	3.5	4.70	1.40
	346	573	0.184	14	2.44	15.7	4.3	4.75	1.26
	326	575	0.171	25	4.35	14.8	3.6	4.76	1.12
	232	536	0.151	18	3.36	10.6	3.8	4.79	1.67
	225	489	0.192	14	2.86	10.3	2.7	4.80	1.21
	324	553	0.192	15	2.71	15.5	5.1	5.02	1.60
	296	560	0.169	32	5.71	14.3	3.9	5.08	1.34
	289	541	0.183	15	2.77	14.0	3.3	5.09	1.16
	398	590	0.194	22	3.73	19.6	6.5	5.18	1.66
	334	615	0.144	22	3.58	17.1	3.7	5.40	1.12
	305	571	0.164	16	2.80	16.0	4.1	5.54	1.36
	294	555	0.172	15	2.70	16.7	3.8	6.02	1.31
	339	569	0.184	22	3.87	19.6	4.3	6.14	1.28
	409	605	0.185	22	3.64	23.8	4.0	6.18	0.99
	364	586	0.181	17	2.90	22.7	5.4	6.65	1.51
	388	589	0.190	20	3.40	25.9	4.9	7.15	1.28
	247	554	0.145	17	3.07	16.8	3.3	7.30	1.35
	323	553	0.191	20	3.62	23.1	3.3	7.70	1.03
	299	562	0.168	16	2.85	30.3	3.4	11.28	1.15
	302	569	0.164	18	3.16	30.9	3.7	11.40	1.24
	280	544	0.174	23	4.23	28.8	3.4	11.46	1.23
	307	551	0.184	15	2.72	31.9	4.0	11.60	1.32
	218	496	0.179	12	2.42	22.8	1.9	11.68	0.88
	332	595	0.158	24	4.03	36.2	2.7	12.24	0.82
	309			21		35.2	2.9	12.86	0.95
	231	492	0.194	15	3.05	26.9	3.4	13.18	1.49
	231	484	0.204	13	2.69	27.0	2.9	13.24	1.27
	256	487	0.222	12	2.46	30.8	2.5	13.68	0.99
	235	517	0.170	19	3.68	28.8	2.9	13.97	1.25
	301	547	0.184	22	4.02	37.3	3.7	14.14	1.24
	221	493	0.184	16	3.25	28.0	2.7	14.51	1.24
	256	506	0.198	14	2.77	35.2	3.2	15.94	1.27
	205	465	0.204	14	3.01	34.3	1.8	20.09	0.89
Avg:	306.9	555.3	0.177	18.8	3.35	19.7	3.8	7.37	1.24
StDev:	61.6	40.8	0.017	4.4	0.72	8.7	0.9	4.31	0.19

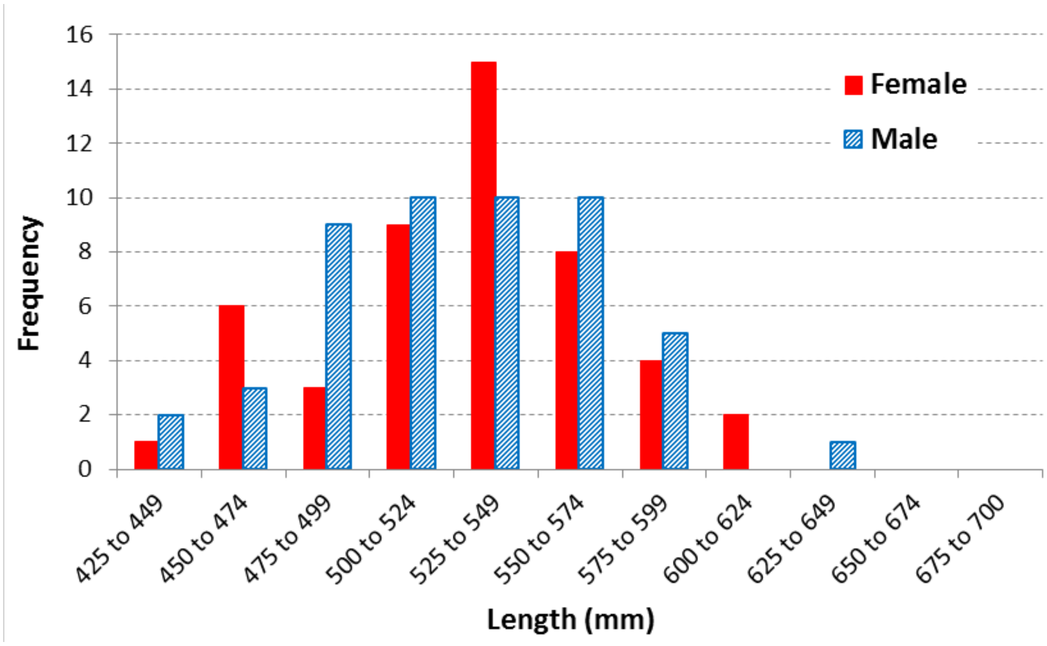
Appendix 20. Biodata and metrics (sorted by GSI) for male Pacific lamprey captured at Willamette Falls on August 9, 2016.

	Weight (g)	Length (mm)	K Factor	DFG (mm)	DFG/Length (%)	Gonad (0.1g)	Liver (0.1g)	GSI (%)	HSI
	199	506	0.154	14	2.77	1.3	3.0	0.66	1.53
	212	498	0.172	6	1.20	1.4	3.6	0.66	1.73
	192	496	0.157	15	3.02	1.4	3.4	0.73	1.80
	215	509	0.163	19	3.73	2.0	2.7	0.94	1.27
	208	475	0.194	19	4.00	2.2	3.4	1.07	1.66
	148	437	0.177	12	2.75	1.7	2.2	1.16	1.51
	254	557	0.147	16	2.87	3.5	4.6	1.40	1.84
	181	455	0.192	15	3.30	2.5	2.5	1.40	1.40
	198	506	0.153	22	4.35	2.8	3.2	1.43	1.64
	301	556	0.175	20	3.60	4.3	4.9	1.45	1.65
	213	492	0.179	16	3.25	3.1	2.7	1.48	1.28
	170	482	0.152	11	2.28	2.5	2.3	1.49	1.37
	198	491	0.167	15	3.05	3.0	4.0	1.54	2.06
	195	504	0.152	18	3.57	3.2	2.9	1.67	1.51
	229	516	0.167	8	1.55	3.8	3.0	1.69	1.33
	247	546	0.152	21	3.85	4.1	4.5	1.69	1.86
	222	521	0.157	13	2.50	3.7	4.3	1.69	1.98
	226	516	0.164	14	2.71	3.8	3.0	1.71	1.35
	253	525	0.175	16	3.05	4.5	3.7	1.81	1.48
	275	544	0.171	14	2.57	4.9	4.1	1.81	1.51
	189	491	0.160	13	2.65	3.4	2.7	1.83	1.45
	205	501	0.163	13	2.59	3.9	4.3	1.94	2.14
	236	536	0.153	18	3.36	4.5	3.7	1.94	1.59
	321	569	0.174	20	3.51	6.3	4.8	2.00	1.52
	239	509	0.181	15	2.95	4.8	4.3	2.05	1.83
	174	455	0.185	15	3.30	3.5	2.4	2.05	1.40
	178	487	0.154	9	1.85	3.6	3.0	2.06	1.71
	315	552	0.187	9	1.63	6.4	3.9	2.07	1.25
	214	513	0.159	10	1.95	4.4	2.9	2.10	1.37
	189	478	0.173	13	2.72	3.9	2.0	2.11	1.07
	231	472	0.220	15	3.18	4.8	3.1	2.12	1.36
	260	448	0.289	22	4.91	5.7	3.7	2.24	1.44
	281	561	0.159	18	3.21	6.4	3.7	2.33	1.33
	291	546	0.179	18	3.30	6.9	4.3	2.43	1.50
	375	570	0.202	22	3.86	9.0	3.4	2.46	0.91
	316	571	0.170	27	4.73	7.7	5.1	2.50	1.64
	247	541	0.156	22	4.07	6.1	4.1	2.53	1.69
	337	597	0.158	33	5.53	8.5	4.2	2.59	1.26
	320	572	0.171	19	3.32	8.1	5.3	2.60	1.68
	265	529	0.179	15	2.84	6.9	4.7	2.67	1.81
	382	596	0.180	30	5.03	10.2	6.2	2.74	1.65
	288	539	0.184	30	5.57	7.9	4.7	2.82	1.66
	270	544	0.168	20	3.68	7.6	4.2	2.90	1.58
	335	584	0.168	19	3.25	9.7	3.9	2.98	1.18
	310	580	0.159	15	2.59	9.1	3.6	3.02	1.17
	405	625	0.166	24	3.84	12.2	4.8	3.11	1.20
	372	596	0.176	21	3.52	12.1	4.6	3.36	1.25
	307	562	0.173	22	3.91	10.8	4.4	3.65	1.45
	269	525	0.186	15	2.86	9.8	2.8	3.78	1.05
	330	553	0.195	22	3.98	13.7	4.5	4.33	1.38
Avg:	255.7	526.7	0.173	17.4	3.27	5.6	3.7	2.10	1.51
StDev:	62.5	42.9	0.022	5.6	0.93	3.1	0.9	0.79	0.26

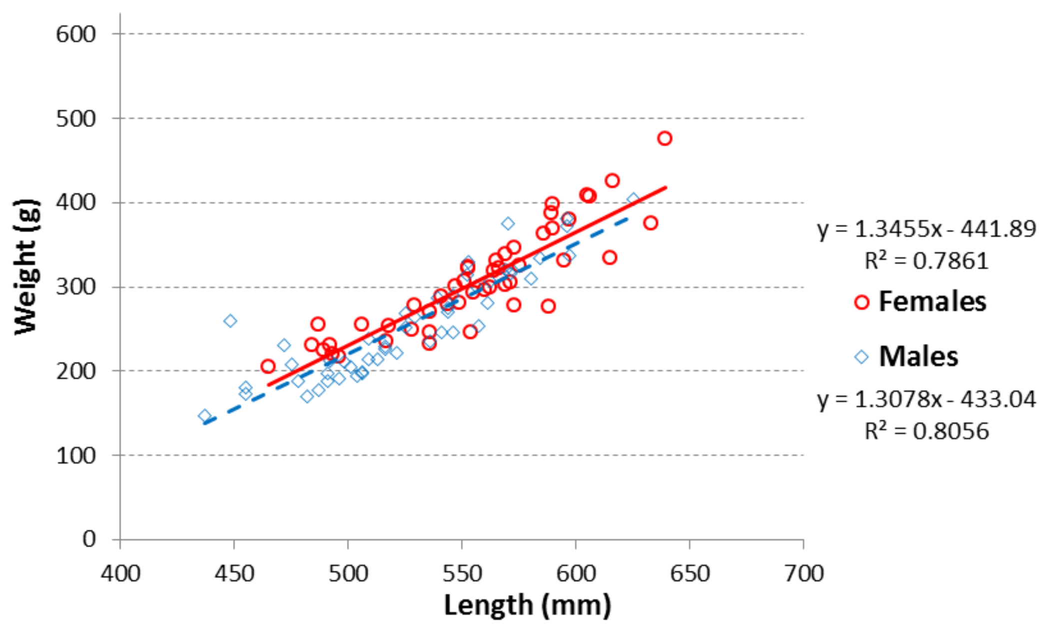
Difference Females : Males, and Significance Level:

	Weight (g)	Length (mm)	K Factor	DFG (mm)	DFG/Length (%)	Gonad (0.1g)	Liver (0.1g)	GSI (%)	HSI
	$p < 0.001$	$p = 0.001$	$p = 0.31$	$p = 0.16$	$p = 0.66$			$p < 0.001$	$p < 0.001$
	**	*						***	***

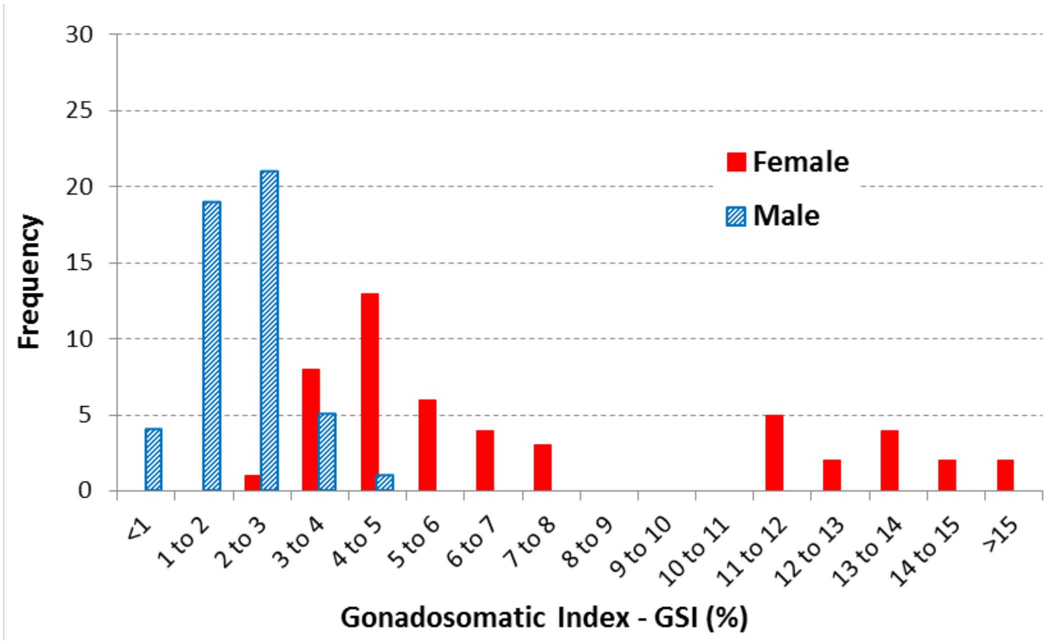
Appendix 21. Length (mm) frequency distribution for female and male Pacific lamprey captured at Willamette Falls on August 9, 2016.



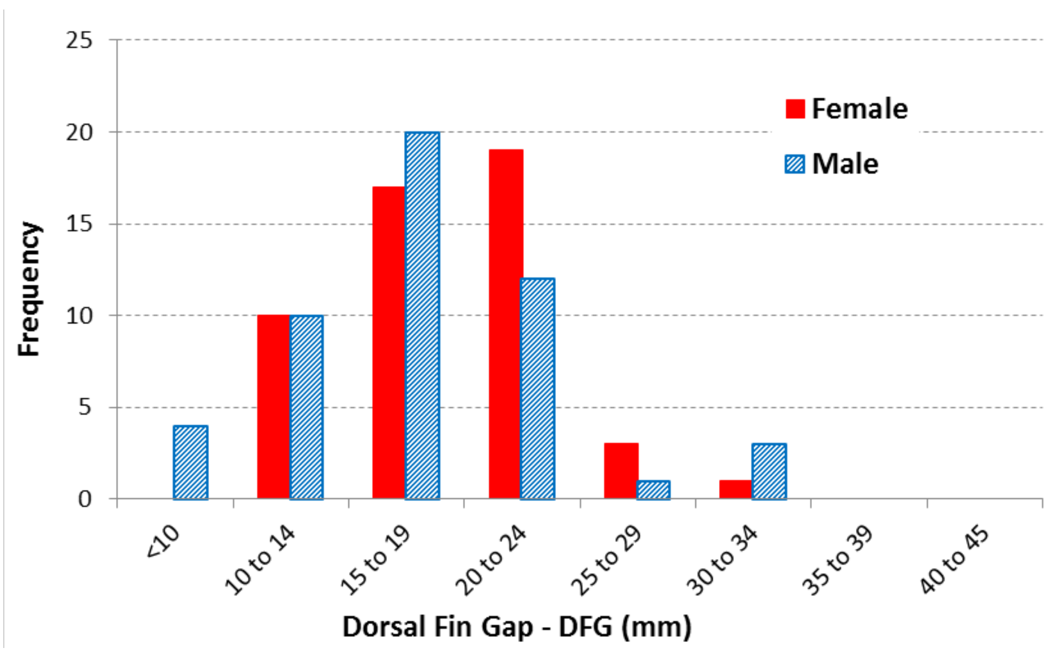
Appendix 22. Relationship of Weight (g) to Length (mm) for female and male Pacific lamprey captured at Willamette Falls on August 9, 2016.



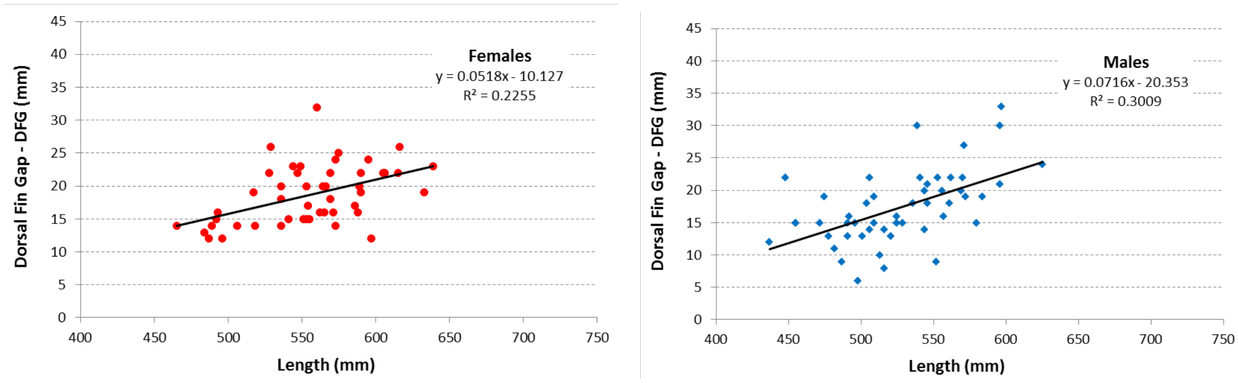
Appendix 23. Gonadosomatic Index - GSI (%) frequency distribution for female and male Pacific lamprey captured at Willamette Falls on August 9, 2016.



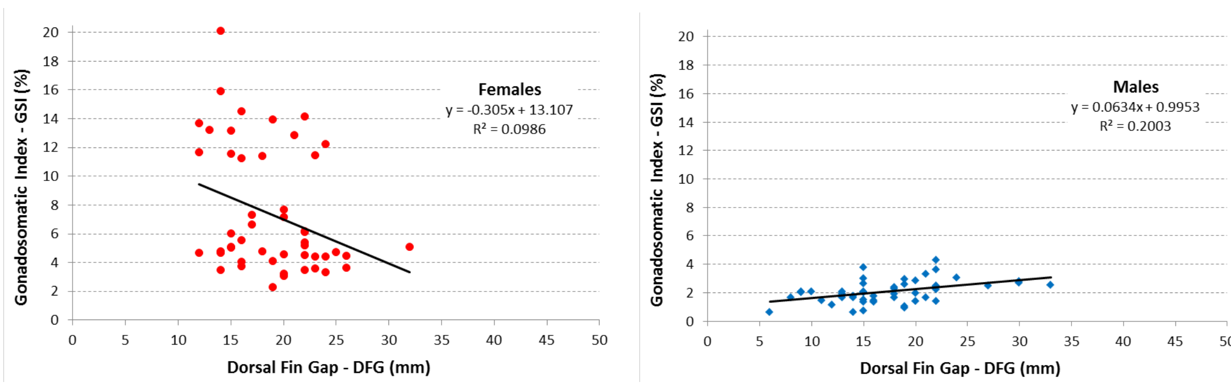
Appendix 24. Dorsal fin gap – DFG (mm) frequency distribution for female and male Pacific lamprey captured at Willamette Falls on August 9, 2016.



Appendix 25. Relationship of Dorsal Fin Gap - DFG (mm) to Length (mm) for female and male Pacific lamprey captured at Willamette Falls on August 9, 2016.



Appendix 26. Relationship of Gonadosomatic Index - GSI (%) to Dorsal Fin Gap – DFG (mm) for female and male Pacific lamprey captured at Willamette Falls on August 9, 2016.



Appendix 27. Relationship of Gonadosomatic Index - GSI (%) to Dorsal Fin Gap/Length (%) for female and male Pacific lamprey captured at Willamette Falls on August 9, 2016.