Physiological indices of seawater readiness in postspawning steelhead kelts

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Abstract – Management goals to improve the recovery of steelhead (*Oncorhynchus mykiss*) stocks at risk of extinction include increasing the proportion of postspawning fish that survive and spawn again. To be successful, postspawning steelhead (kelts) migrating downstream to the ocean must prepare physiologically and physically for a seawater transition. We sampled blood, gill filaments, and evaluated the external condition of migrating kelts from an ESA-listed population in the Snake/Columbia River system over two consecutive years to evaluate their physiological readiness for transition to seawater. We chose attributes often considered as measures of preparation for seawater in juveniles, including gill Na^+,K^+ ATPase activity, plasma electrolytes and hormones to consider factors related to external condition, size and sex. We found kelts in good external condition had plasma profiles similar to downstream-migrating smolts. In addition, we found more than 80% of kelts ranked in good external condition had smolt-like body silvering. We compared measures from migrating kelts with samples obtained from hatchery fish at the time of spawning to confirm that Na^+, K^+ ATPase activity in kelts was significantly elevated over spawning fish. We found significant differences in gill Na^+, K^+ ATPase activity in migrating kelts between the years of sampling, but little indication of influence of fish condition. We conclude that the postspawning steelhead sampled exhibited a suite of behaviours, condition and physiology characteristic of fish prepared for successful transition to a seawater environment.

Key words: steelhead trout; physiology; smolt; kelt; iteroparity

Introduction

Unlike most Pacific salmon, steelhead trout (*Oncorhynchus mykiss*) are iteroparous and after spawning are capable of migrating back to the ocean to mature and spawn again. The proportion of steelhead populations that successfully repeat spawn can range from none to more than 70% in some stocks and varies over years (Withler 1966; Burgner et al. 1992; Busby et al. 1996; Lohr & Bryant 1999; Crespi & Teo 2002; Quinn & Myers 2004; Null et al. 2013). The frequency of iteroparity has often been correlated with the length of the freshwater migration and time spent fasting in freshwater before spawning (Burgner et al. 1992).

In many rivers such as the Columbia, hydropower development and fish passage facilities and flow modifications have likely altered the historical proportion of steelhead successfully returning to the ocean, but predevelopment rates for many populations are not known (Wertheimer & Evans 2005; Wertheimer 2007; Keefer et al. 2008). Recent management efforts to protect Endangered Species Act listed steelhead trout in the Pacific coast have implemented measures to increase the proportion of the population that survives to repeat spawn, including improved downstream passage conditions (Wertheimer 2007; Evans et al. 2008; Hatch et al. 2013; Penney & Moffitt 2013). Although steelhead have complex life histories that can combine anadromous and resident life histories (e.g., Courter et al. 2013; Teo et al. 2013; Van Doornik et al. 2013), steelhead that return to the ocean to recover to spawn again must be able to survive the osmoregulatory transition between the freshwater and marine environments.

Little is known about the effects of prolonged fasting and energy loss that occurs during migrating, maturing and postspawning steelhead (Penney & Moffitt 2014) on the physiological capacity of kelts for return to a hyperosmotic environment. Studies of Atlantic salmon *Salmo salar* provide some insight into the physiological capacity of postspawning salmonids. Talbot et al. (1992) reported that ionic regulation in Atlantic salmon kelts exposed to seawater was rapid. However, Atlantic salmon have somewhat different metabolic challenges as their spawning occurs in the fall when aquatic productivity is low, and often kelts are known to overwinter in freshwater. Jonsson et al. (1991a,b, 1997) evaluated the metabolic costs of reproduction and migration in Atlantic salmon, and recently, Halttunen et al. (2013) speculated on factors affecting the diversity of life-history strategies in Atlantic salmon to consider selective pressures of sex, size and energy allocations.

In contrast to the limited information on kelt physiology, numerous studies describe the condition and physiological metrics of downstream-migrating juvenile salmonids (e.g., Smith 1993; McCormick et al. 1998; Wagner & Congleton 2004; Hayes et al. 2012). In juvenile salmon, smoltification is a well-described process whereby internal and external changes prepare fish for ocean entry (Boeuf 1994; Bjornsson & Bradley 2007). Environmental cues that stimulate smoltification include photoperiod, temperature, lunar phases and river discharge (Zaugg & Wagner 1973; Hoar 1988; Bjornsson et al. 2011). In juvenile salmonids, behavioural changes also occur during the parr–smolt transformation to transition them from solitary or territorial behaviour to schooling behaviour and orientation near the surface of the water column. Parr marks on stream resident fish that become migratory are reduced and fish develop silver colouration (Smith 1993; Bjornsson & Bradley 2007; Holecek et al. 2012; Zydlewski & Wilkie 2013). Elevation of thyroxine hormone, T4, is associated with smolt body silvering as well affecting migration behaviour (Eales et al. 1991; Boeuf 1994; McCormick 2013). In smolts, gill Na^+ K^+-ATPase activity (hereafter NKA) is often used as an index of saltwater readiness (Zaugg et al. 1985; Boeuf 1994; Bjornsson & Bradley 2007; Zydlewski & Wilkie 2013).

If physiological and behavioural processes in steelhead kelts are parallel to those in smolts, preparation for seawater entry should include decreased territorial behaviour, downstream migration accompanied by elevations of NKA, regulation of plasma Na^+ and Cl^-, body silvering and detectable thyroxine. Moreover, these changes may be accompanied by increases in mobilised energy such as plasma glucose, even from severely energy-depleted kelts (Penney & Moffitt 2014).

The objectives of our study were to evaluate seawater readiness in steelhead kelts using similar measures used for smolts. Metrics included evaluation of external silvering, gill NKA and plasma sodium, chloride, glucose and thyroxine (T4). Furthermore, we evaluated changes in these metrics during freshwater residence by comparing steelhead sampled at sexual maturity with samples from migrating kelts. We hypothesised that kelts would differ from steelhead at maturity and show characteristics similar to juvenile smolts and other salmonid kelts preparing for seawater entry.

Methods

Sampling procedures

Migrating kelts – We collected postspawning downstream-migrating kelts that had been diverted from the juvenile fish bypass at Lower Granite Dam on the Snake River, Washington between 11 May–28 June 2009 and 1 April–2 July 2010 (Fig. 1). Lower Granite Dam is the most upstream dam on the Snake River and is located 695 river km upstream from the mouth of the Columbia River. Hatchery origin kelts (without adipose fins) were sampled in 2009, and both hatchery and natural origin kelts (with adipose fins) were sampled (48% natural) in 2010.

All fish were sampled lethally and euthanised with 250 $g \cdot l^{-1}$ tricaine methanesulfonate (Argent Laboratories, Redmond, WA), buffered with $NaHCO_3$. We recorded the sex, fork length (cm) and ranked the external condition of each fish as good, fair or poor based on several criteria including activity, injury and the presence of fungus (as per Penney & Moffitt 2013). Briefly, classification fish with no or minor injuries or fungal infections were classified in good condition; fish with moderate injury or fungal infection over 1–10% of body were considered as fair condition, and fish with severe injury or fungal infection >10% of body were considered as poor condition. In 2010, we further classified the body colour of kelts as silver or dark.

We removed blood from the caudal vessel of each fish with a heparinised 3-ml syringe, fitted with a 21-gauge 3-cm needle. Blood samples were stored on ice <1 h until they were centrifuged to separate red blood cells. The plasma samples were placed immediately in dry ice for transport to a -80 °C freezer until processing. We analysed the plasma for a suite of biochemical parameters including sodium, chloride, glucose and thyroxine (T4). Plasma metrics were determined by autoanalysers (dimension AR-IMT, Dade Behring Inc. Newark, Delaware; Gritman Medical Center, Moscow, Idaho; or Beckman Coulter CX5 and Olympus Au400e, Beckman
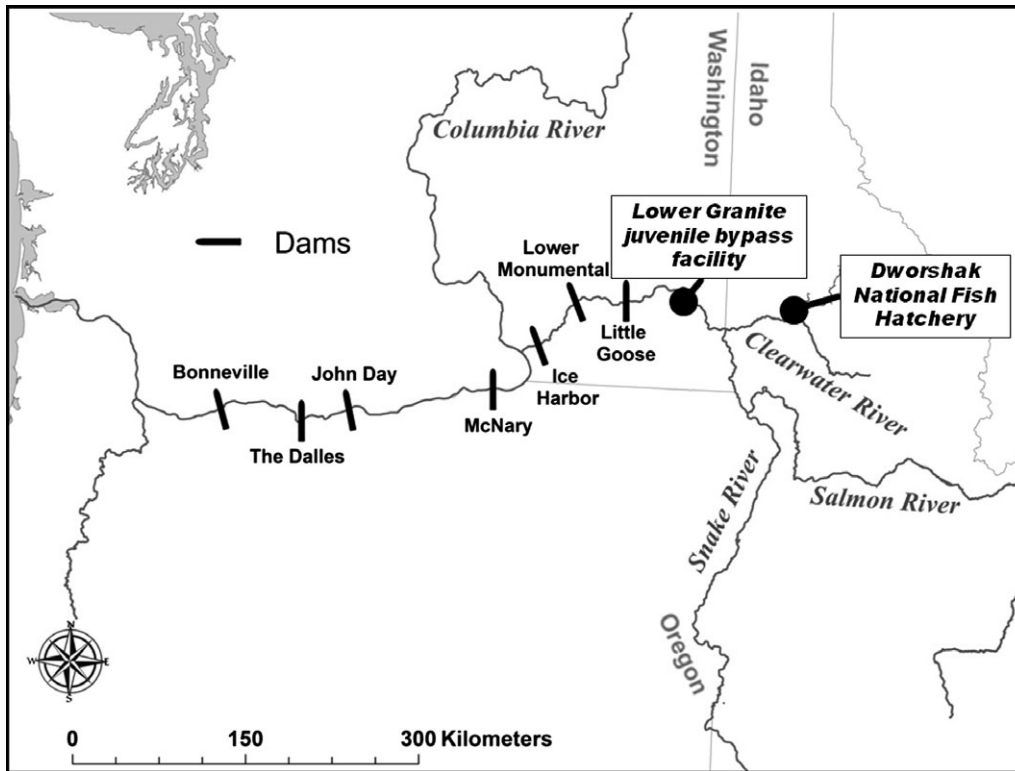
Fig. 1. Map of the Columbia/Snake River and location of sampling sites in Washington and Idaho.

Coulter Inc. Brea, California at Panhandle Animal Lab, Coeur d' Alene, Idaho). Quality assurance followed guidelines established by the Joint Commission for Accreditation of Health Care Organizations or by the College of American Pathologists, Veterinary Laboratory Association, respectively.

Gill filaments from each fish were removed from the first gill arch and placed into a 4-ml snap cap culture tube with 1-ml SEI buffer (0.3 mol·l^{-1} sucrose, 0.02 mol·l^{-1} disodium EDTA and 0.1 mol·l^{-1} imidazole) at pH 7.4. Each tube was placed on dry ice until transfer to −80 °C freezer. Samples were analysed for gill NKA as μmol Pi h^{-1} mg protein^{-1} (Biotech, Inc, Corvallis, Oregon) using methods outlined in Zaugg (1982).

Sexually mature steelhead – To serve as comparison with migrating kelts, we obtained samples of gill tissues, and plasma from hatchery origin steelhead that had migrated to the Clearwater River, entered the ponds at Dworshak National Fish Hatchery in October, and were lethally spawned in two separate weeks in late January 2010. Samples and processing of samples were identical to those used in migrating kelts.

Data analyses

Sampling constraints in spawning year 2009 limited our analyses to female kelts in good condition. Com-

parisons between 2009 and 2010 were made with dependent variables measured in good females only. Samples of kelts from spawning year 2010 were evaluated as dependent variables in general linear models with fish condition (good, fair or poor), sex (male, female), origin (natural, hatchery) and all pairwise interactions as explanatory variables. When interactions were not significant, we reduced the models to resolve significant main effects. We evaluated significant differences between significant least-squared means with Tukey's multiple comparisons. In all models, fork length was included as a covariate. Comparisons between mature steelhead and kelts were modelled to compare factors of sex (male, female) and phase (mature, kelt), and because all mature fish were in good condition, comparisons were restricted to good condition fish. We used SAS, version 9.2 for all statistical and data analysis (SAS Institute, Carey, North Carolina), and report significant values <0.05.

Results

The external condition of migrating kelts was a significant influence on plasma electrolytes, glucose and thyroxine (Figs 2 and 3). Because most kelts in spawning year 2009 were sampled from females in good condition, we made no statistical comparisons among condition or between sexes. In 2010, we
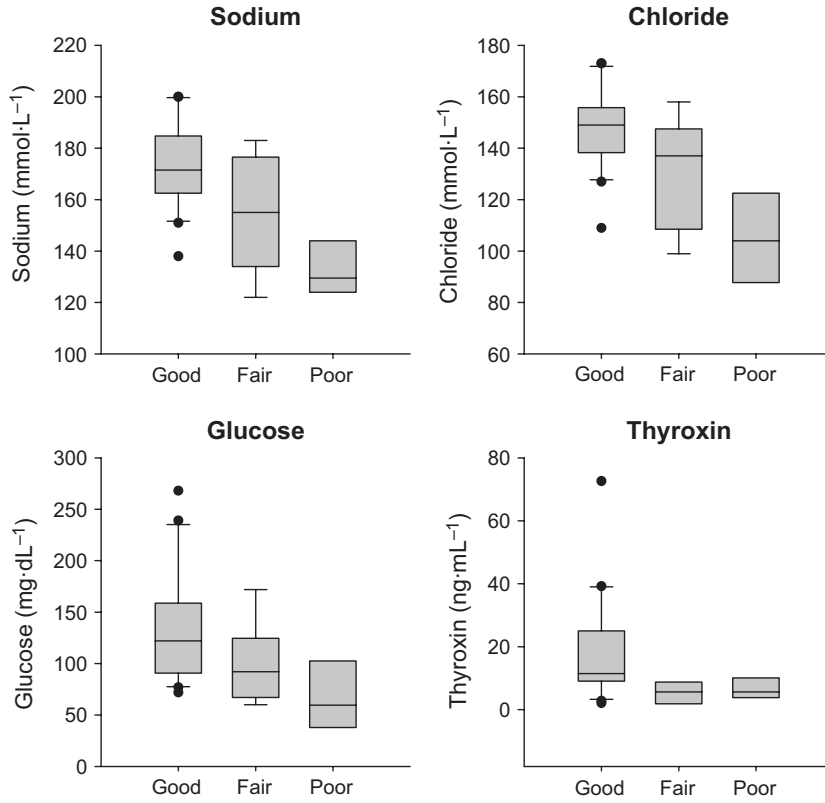
Fig. 2. Box plots of plasma metrics of kelts sampled in 2009, separated by fish condition. Sample sizes and number of males by condition: Good $N = 20$, three males; Fair $N = 9$, one male; Poor $N = 8$, one male. No tests of significance were conducted.
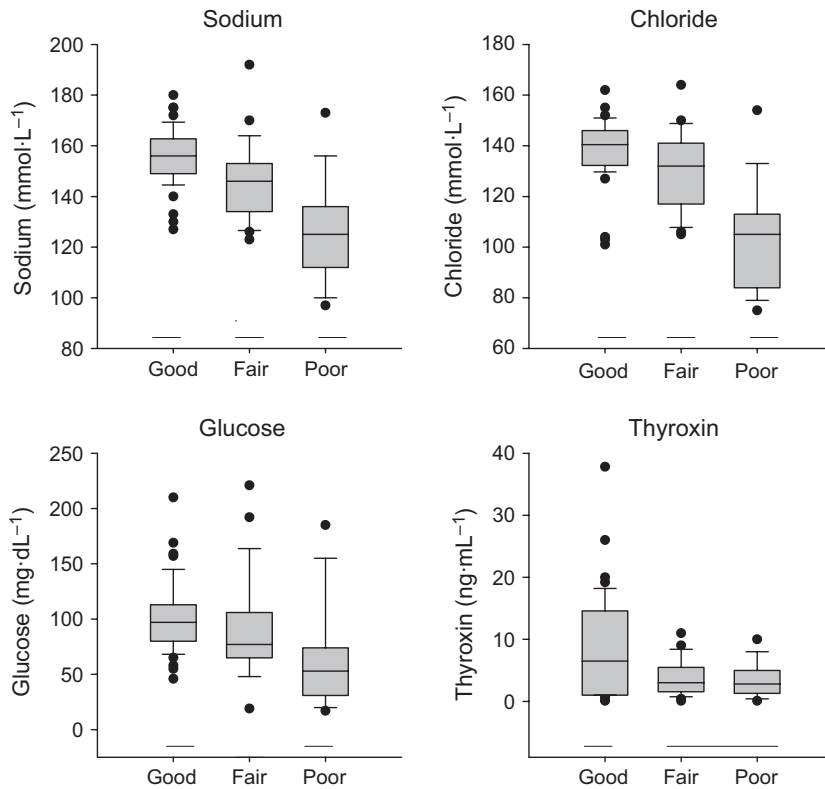

Fig. 3. Box plots of plasma metrics in kelts sampled in 2010, separated by fish condition. Sample sizes by condition: Good $N = 48$, 10 males; Fair $N = 25$, nine males; Poor $N = 19$, four males. Lines at the bottom of each plot indicate significant differences ($P < 0.05$) between individual least-squared means by fish condition.

Table 1. Summary of metrics from steelhead kelts sampled at Lower Granite Dam over two spawning years, 2009 and 2010. Samples are separated by fish condition. In 2010, samples were from 48 adipose clipped and 44 nonclipped fish.

|	Good		Fair		Poor	
	Males	Females	Males	Females	Males	Females
2009 Samples						
ATPase (μmol per ADP)						
Mean	1.25	1.57	1.49	1.99	1.68	1.79
Median	1.23	1.64		2.035		1.87
Range	0.68–1.83	0.27–3.34		0.13–3.73		0.83–2.84
N	3	17	1	8	1	7
Sodium (mmol·l^{-1})						
Mean	190.67	170.41	183	151.62	146	130.42
Median	193	168		152		126
Range	179–200	138–200		122–182		107–161
N	3	17	1	8	1	7
Chloride (mmol·l^{-1})						
Mean	159	145.59	158	125.87	118	103.42
Median	154	147		129.5		101
Range	150–173	109–173		99–149		71–142
N	3	17	1	8	1	7
Glucose (mg·dl^{-1})						
Mean	165.666	129.53	120	94.75	108	60.71
Median	152	104		81.5		47
Range	145–200	72–268		60–172		27–112
N	3	17	1	8	1	7
T4 (ng·ml^{-1})						
Mean	17.6	17.97	1.6	6.54	6.2	7.61
Median	15.2	11.4		6.8		5.1
Range	9.3–28.3	2.1–72.6		1.4–13.4		1.4–20.
N	3	17	1	7	1	7
Fork ln (cm)						
Mean	55.12	59.35	56	60.1	58	67.71
Median	54.25	57		57.25		64
Range	53–59	52–82		55–78.5		54–88
N	4	17	1	10	1	7
2010 samples						
ATPase (μmol·mg^{-1})						
Mean	0.48	0.82	0.72	0.66	0.42	0.65
Median	0.56	0.64	0.67	0.64	0.39	0.53
Range	0.09–0.86	0.07–2.51	0.32–1.08	0.14–2.39	0.19–0.73	0.11–2.76
N	10	38	9	16	4	15
Sodium (mmol·l^{-1})						
Mean	156.7	155.2	145.44	145.31	114.5	130.0
Median	158.5	155.5	146	139	112.5	126
Range	148–165	127–180	127–156	123–192	97–136	104–173
N	10	38	9	16	4	15
Chloride (mmol·l^{-1})						
Mean	142	137.74	131.111	127.9	95.25	105.93
Median	142.5	140	132	124.5	96.5	105
Range	131–149	101–162	106–145	105–164	75–113	79–154
N	10	38	9	16	4	15
Glucose (mg·dl^{-1})						
Mean	110.5	98.38	106.44	79.94	108.75	51.4
Median	98	97	102	69	112	46
Range	72–210	46–169	48–221	19–192	26–185	17–91
N	10	37	9	16	4	15
T4 (ng·ml^{-1})						
Mean	11.5	8.14	5.22	2.85	4.75	3.05
Median	10.5	6.	5.	3.0	4.	2.1
Range	1.–26.	0.1–37.8	1.–11.0	0.1–9.0	1.–10.	0.1–8.
N	10	38	9	16	4	15
Fork ln (cm)						
Mean	58.5	62.16	61.56	61.31	63.25	60.0
Median	59	60.0	59	57.5	60	59.0
Range	54–62	52–78	56–72	55–80	57–76	48–76
N	10	38	9	16	4	15
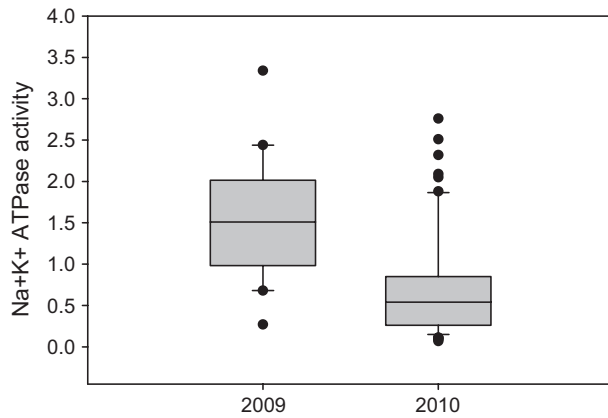
Fig. 4. Gill Na$^+$K$^+$-ATPase activity for good condition female kelts collected at Lower Granite Dam by spawning year 2009 ($N = 20$) and 2010 ($N = 38$).

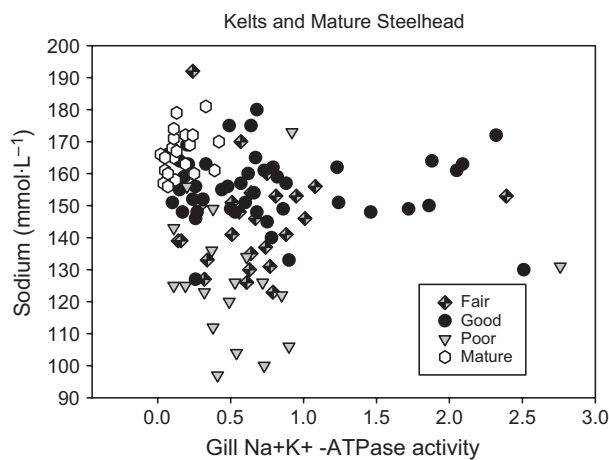Fig. 5. Scatter plot comparison of plasma sodium and gill Na$^+$K$^+$-ATPase in steelhead sampled at spawning and migrating as kelts, separated by fish condition, spawning year 2010. All mature spawning fish were good condition.

sampled representatively throughout from the migration from males and females of all conditions and considered these factors in analyses. We found kelts in good condition had significantly higher plasma sodium and chloride and higher plasma glucose (Fig. 3; all $P < 0.001$). Multiple comparisons of variables compared between conditions showed in all cases poor fish were significantly different from good condition fish (Fig. 3). We found no significant differences between male and female kelts for any metric except for plasma glucose. Male kelts had significantly higher plasma glucose concentrations over females ($F_{1,86} = 8.92$, $P < 0.004$; Table 1). We detected no significant differences between natural or hatchery origin kelts sampled in 2010.

In comparisons of good condition female kelts between the two spawning years, we found kelts had significantly higher plasma sodium and thyroxine in 2009 (Na $F_{1,38} = 18.32$; $P = 0.001$; T4 $F_{1,38} =$

11.67; $P < 0.01$). The same trend held in gill NKA (Fig. 4). Because samples collected in 2009 were from mid-May through June, and to control for any variation in gill NKA elevation over time, we repeated our analysis using only samples from females collected mid-May through June with similar results ($F_{1,38} = 11.91$; $P = 0.014$). We found a significant influence of fish length in comparisons of NKA between years ($F_{1,38} = 4.09$, $P = 0.05$). The samples from 2009 had fewer fish >70-cm fork length (Table 1). Fork length was not a significant factor affecting the variance of any other parameters between the years, although few large fish were sampled in our study.

In comparisons made between mature and kelt phases, we found migrating good condition kelts had significantly elevated gill NKA over levels measured in mature fish at spawning ($F_{1,67} = 14.87$; $P < 0.01$; Fig. 5), and no significant differences were detected between males and females. Plasma electrolytes in both sexes of mature steelhead and good condition steelhead kelts were similar and within ranges considered normal. However, we found plasma thyroxine levels in mature steelhead were significantly higher than levels in good condition kelts ($F_{1,67} = 4.96$, $P = 0.03$) with no significant differences attributed to sex. We observed 39 of 47 good condition kelts in 2010 were bright silver (Fig. 6), but even silvered kelts had significantly lower thyroxine levels over mature steelhead (Fig. 7).

Discussion

Our study provides documentation of physiological preparation for seawater entry in steelhead trout kelts. Although repeat spawning is considered an important component in population stability, genetic diversity, studies of kelts comprised only 5% of all reports of salmonid marine migration and survival in a recent review of iteroparous migrating species by Drenner et al. (2012). Most studies of kelt physiology have focused on Atlantic salmon (Jonsson et al. 1991b, 1997; Talbot et al. 1992; Halttunen et al. 2013). Talbot et al. (1992) studied ionic regulation and responses in canulated Atlantic salmon kelts exposed to seawater and reported kelts were capable of rapid adaptation to saltwater. Within 48 h experimental salmon showed reduced urine flow and elevated intestinal Mg^{++} concentrations expected for osmoregulatory homeostasis in seawater. Bendall et al. (2005) reported migratory sea brown trout (*Salmo trutta*) migrated into the ocean rapidly after spawning and speculated that their physiological adaptation was more rapid than in juveniles.

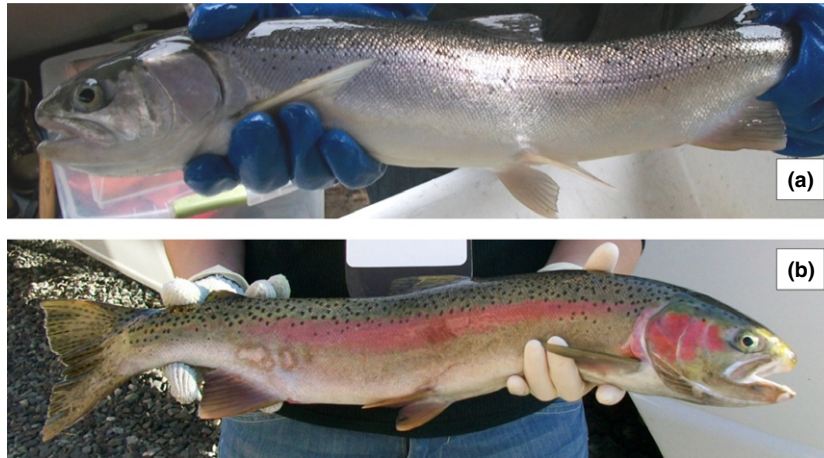We found parallels between smolts and migrating kelts in measure of plasma factors and external body

Fig. 6. Example of colouration of steelhead kelts. (a) Silver; (b) Dark colouration. Both were photographed and sampled at Lower Granite Dam WA.
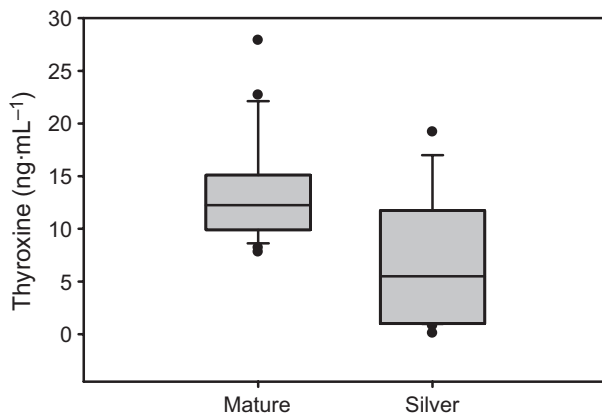

Fig. 7. Box plots of plasma thyroxine for mature fish at spawning ($N = 22$, 13 males) and silver coloured kelts ($N = 60$, 12 males).

colouration and condition. Plasma sodium and chloride were within the ranges reported for migrating smolts (McCormick & Bjornsson 1994; Wagner & Congleton 2004; Kennedy et al. 2007; Hanson et al. 2011; Hayes et al. 2012). However, poor condition kelts likely were not ready for seawater (Table 1), as measures were below median values reported by Manera & Britti (2006) for *O. mykiss* of 155 and 130 mm·l^{-1} for sodium and chloride, respectively, and outside of the normal Gaussian range provided by Manera & Britti (2006).

We found plasma glucose was significantly higher in good condition kelts. Manera & Britti (2006) reported normal median glucose of 98 mg·dl^{-1} for rainbow trout and our median glucose values for good condition female kelts were 104 and 97 mg·dl^{-1} for 2009 and 2010, respectively. As kelts are largely fasting in freshwater, glucose was likely indicative of energy reserves (Penney & Moffitt 2014), rather than a stress factor often measured in smolts (Congleton et al. 2000). The elevated glucose

of male steelhead over females regardless of condition poses an area for additional research. This finding, combined with the fact that fewer males were observed migrating as kelts in our study, leads us to speculate about sex differences in life-history strategies. Seamons & Quinn (2010) studied steelhead in a small coastal system in Washington State and speculated that smaller males may not actively participate in spawning, migrate back downstream earlier to grow to a larger size the following year. However, this reproductive strategy is not likely viable for populations that make long spawning migrations, such as in the Snake/Columbia River system. Male kelts in large river systems are reported to have lower rates of iteroparity (Busby et al. 1996; Keefer et al. 2008; Null et al. 2013). Recent studies using genetic and complex tagging systems reveal the diversity of life-history strategies displayed in *O. mykiss* populations including the ability to residualise, and males appear to use that strategy most often (Van Doornik et al. 2013).

Gill NKA is often used as an index of juvenile smoltification where levels elevate during downstream seaward migration (Hart et al. 1981; Zaugg et al. 1985; Wagner & Congleton 2004; Bjornsson & Bradley 2007) and increase substantially in seawater (McCormick 2013). We reported total gill NKA activity and did not distinguish between the two isoforms that have somewhat different functions in *O. mykiss* (Richards et al. 2003).We found significant elevation of gill NKA in migrating kelts over measures in mature steelhead at spawning. Shrimpton et al. (2005) reported a decline in gill NKA during upstream breeding migrations of sockeye salmon as they approached spawning sites. Although gill NKA was somewhat lower than values often reported for smolts, we believe the significant elevation of kelts over mature steelhead sampled indicates

physiological preparation for seawater. We have no explanation for the significantly higher gill NKA in kelts in 2009 compared with samples in 2010, but the survival of migrants varies over the years and likely is influenced by a number of environmental factors. Moreover, our samples were from mixed stocks of kelts that had spawned at locations throughout the river basin.

The rate of downstream migration in smolts is often linked to gill NKA (Kennedy et al. 2007), and faster migrants have less likelihood of mortality from predation. Likely, many mammals prey on migrating kelts, but American white pelican (*Pelecanus erythrorhynchos*) predation of kelts was documented through recovery of PIT-tags on colonies in the Columbia River (D. D. Roby, Oregon State University, personal communication). As all fish in our study were sampled lethally, we have no data regarding migration timing, but good condition kelts are reported more likely to survive downstream migration through the Columbia/Snake River hydropower system than poor condition kelts (Keefer et al. 2008; Jones 2012; Colotelo et al. 2013).

Plasma thyroxine hormone (T4) is considered an important factor associated with smoltification in juvenile salmonids and affects the silvering of smolts and behavioural changes such as schooling and migrating downriver (Bjornsson et al. 2011). In smolts, T4 elevates early and may decrease, but can also fluctuate due to water temperature, nutrient intake and fluctuations in flow or water quality (Eales et al. 1991; Bjornsson & Bradley 2007; Ojima & Iwata 2007).

We have no baseline T4 in early migrating prespawn steelhead, but T4 at sexual maturity was significantly higher over measures in kelts. A link between circulating T4 and stage of upstream migration has been suggested for adult Atlantic salmon. Youngson & Webb (1993) reported levels of T4 were highest in mature adults captured at tributaries near the time of spawning. Our measures of T4 were significantly different between sampling years (Figs 2 and 3), perhaps due to environmental factors such as river flow, but the concentrations were elevated in good condition kelts relative to those in fair or poor condition. Eales et al. (1991) reported values in prereproductive Atlantic salmon ranged between 6.4 and 9.8 ng·ml^{-1}, and T4 levels in kelts were low in nonfeeding kelts, regardless of gender or eventual reproductive state. Our plasma T4 levels in mature steelhead were somewhat higher.

Silvering is observed in early upstream migrants and then re-appears at the time of downstream kelt migration, indicative of preparation for life in the ocean (Shrimpton 2013). A proportion of kelts collected at Lower Granite Dam had silver colouration (Fig. 5), and we found silver colour and elevated T4 were more frequently associated with good condition kelts. In large river systems such as the Columbia River, however, T4 and NKA may start lower and increase as the fish approach the ocean (Smith 1993).

Increasing the proportion of steelhead iteroparity is a goal to aid in recovery of stocks of management concern to improve genetic fitness and increase reproductive contributions (Keefer et al. 2008; Narum et al. 2008; Seamons & Quinn 2010; NOAA 2011; Null et al. 2013). In rivers with hydropower systems, downstream-migrating kelts have many of the same challenges as smolts, but energy resources in kelts are considerably lower (Penney & Moffitt 2014). Smolts may have higher risks to predation over larger steelhead kelts, but the larger fish size poses additional challenges navigating through turbines and the juvenile fish bypass systems at the lower Snake and Columbia River Dam. Mortality through the Snake and Columbia River hydropower system was estimated to range from 84% to 96% for kelts tagged at Lower Granite Dam, rkm 695 and recovered at Bonneville Dam (Wertheimer & Evans 2005). Experimental collection and transportation around dams in trucks and barges have been tested with mixed results (Evans et al. 2008; Moffitt et al. unpublished data). However, in more recent years, hydromanagement has moved towards more voluntary surface spill at the dams to benefit both kelts and smolts (Johnson et al. 2005; Wertheimer 2007; Snake River Kelt Management Plan 2012). Tagging studies conducted during the increased spill have been directed to determine more precise routes of passage and measure survival (Colotelo et al. 2013). These recent studies support that steelhead kelts are more likely to move downstream via surface spill routes than through juvenile bypass systems, and there is a positive relationship with flow. Similarly, Atlantic salmon kelts are also reported to migrate downstream near the surface, and into the estuary maintain their surface swimming with some diving for feeding, and in general displaying behaviours similar to smolts (Hedger et al. 2009).

For steelhead and Atlantic salmon, many factors affect salmonid survival after arrival in the estuary (Muir et al. 2006; McCormick et al. 2009; Scheuerell et al. 2009; Muir & Williams 2012; Halttunen et al. 2013). The proportion of kelts surviving to spawn again in the following year as sequential or skip-spawners after a additional year at sea can be compared with rates expected for the smolt-to-adult survival of releases of anadromous steelhead or salmon. For example, in the Columbia/Snake River Basin, regional management goals for smolt-to-adult return rates of steelhead range from 2% to 6% (Underwood et al. 2003; NPCC 2009; CSS 2010),

and the goal for Snake River steelhead iteroparity is 6% (Snake River Kelt Management Plan (KMP) 2012). However, smolt-to-adult return rates for river migrants in the Snake River system have not exceeded 2% for wild or hatchery steelhead consistently (Sanford & Smith 2002; CSS 2010). Keefer et al. (2008) reported kelt iteroparity rates to Lower Granite Dam were 1.2% with variations between years similar to smolts. We pose that smolt-to-adult return rates and steelhead iteroparity rates show similarities throughout the Columbia River system and may be higher for kelts from tributaries closer to the ocean. The Kalama River, a lower Columbia River tributary, reports rates from 1.5% to 15% for smolts (Myers et al. 2006), and 15% for steelhead adults (Leider et al. 1986). In the Hood River, which flows into the Columbia River upstream of Bonneville dam, SAR Rates average 1.4% where summer run steelhead kelt iteroparity rates are 6–10%.

In conclusion, our study identified and measured several metrics in steelhead that relate to their physiological preparation to return to an ocean environment after spawning. Steelhead kelts in good external condition appeared physiologically capable of adjustment to the ocean environment and showed physiological, physical and behavioural parallels to salmonid smolts during their seaward migration.

Acknowledgements

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