Environ Biol Fish
DOI 10.1007/s10641-009-9569-1

Seasonal variation in diel behaviour and habitat use by age 1+ Steelhead (*Oncorhynchus mykiss*) in Coast and Cascade Range streams in Oregon, U.S.A.

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Received: 24 April 2009 / Accepted: 20 October 2009

Abstract The seasonal diel behaviour of age 1+ steelhead from Coast and Cascade Range streams in Oregon was examined in the field and in laboratory streams. During the summer, fish from both areas were active during the day in natural streams: they held position in the water column in moderate velocities and depths. At night, fish were in slower water, closer to the bottom above smaller substrates. In winter, diel behaviour differed between the two groups. Coastal fish exhibited behaviour similar to that observed in the summer. Cascade Range fish were not observed during the day, but were found at night, holding positions close to the bottom in slower water. In laboratory streams, fish from both regions were subjected to a decreasing temperature regime from 16°C to 2°C. Use of cover for concealment during the day was negatively correlated with water temperatures for both groups. However, the shelter-seeking response to declining water temperatures was significantly greater for Cascade fish than it was for coastal fish. Field and laboratory observations of diel behaviour support the hypothesis that steelhead from the two geographic regions have different adaptive strategies for winter conditions and that these differences, because they persisted even in laboratory conditions, are probably genetically based.

Keywords Steelhead trout · Seasonal diel behavior

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Introduction

Daily and seasonal activity patterns of temperate freshwater fish are, in general, plastic (Ali 1992), meaning that the behaviour of an individual or population can change with varying environmental conditions. Such flexibility in behaviour may allow fish to improve their chances of survival in areas with seasonally-changing environments. Seasonal changes in diel habitat use and behaviour have been observed in numerous species of stream-dwelling juvenile salmonids (Whalen et al. 1999; Armstrong and Griffith 2001) and other fishes (Greenwood and Metcalfe 1998; Metcalfe and Steele 2001). Behavioural changes occur in response to water temperature, ice formation (Heggenes et al. 1993; Whalen et al. 1999), current velocity (McMahon and Hartman 1989; Heggenes et al. 1993), water clarity (Valdimarsson and Metcalfe 1998), and light levels (Greenberg et al. 1996), or some combination of these. The extent and type of behavioural change balances the trade-off between increased

Published online: 11 November 2009

susceptibility to predators and meeting metabolic demands (Fraser et al. 1995; Valdimarsson and Metcalfe 1998; Reebs 2002).

Seasonal changes in diel behaviour and habitat use should vary among populations of the same species that experience different environmental regimes if there is local adaptation and associated survival benefit. However, few studies have actually examined the behavioural differences between fish populations from different regions. Valdimarsson et al. (2000) found that Atlantic salmon (*Salmo salar*) and Arctic char (*Salvelinus alpinus*) from streams with different thermal regimes exhibited different responses to declining water temperatures. Responses were not as the authors predicted: fish from cooler temperature regimes exhibited shifts in diel behaviour at higher temperatures than fish from warmer regimes. Fraser et al. (1995) observed that diel behaviour of Atlantic salmon in populations that experience ice formation changed from being active during the day in summer to being active at night as temperatures declined below 10°C. The authors speculated that fish from warmer temperature regimes, where ice may not form in the winter, should respond similarly to those from colder temperature regimes.

Pacific salmon and trout (*Oncorhynchus* spp.), and other salmonids, are distributed across areas with widely varying environmental conditions. As a result, populations are highly adapted to local conditions in behavioural, morphological, and physiological characters (Taylor 1991; Quinn 2005). Many of these traits are believed to be genetically controlled and contribute to the long-term persistence of these populations.

The distribution of steelhead trout (anadromous *O. mykiss*) in western North America encompasses areas with vastly different seasonal thermal regimes. Streams in interior and northern areas generally experience lower flows and turbidity, and colder water temperatures than those in warmer coastal and southern areas. As a result, 1+ steelhead from colder regimes may be more vulnerable to predation because of increased visibility (Gregory and Levings 1998) and reduced metabolism (Metcalfe et al. 1986) during winter. This higher predation risk should favor a seasonal change in diel shelter-seeking behaviour in the winter to maximize survival among fish in colder streams. Fish from warmer and seasonally less variable coastal areas, in contrast, should exhibit less seasonal variation in diel behaviour because temperatures are within a range favorable to metabolic performance. If the response of fish from these different areas is genetically related, each group should exhibit different patterns of diel behaviour seasonally, and respond differently to a common temperature regime. To test these hypotheses we: (1) quantified changes in summer and winter diel behaviour and habitat use by fish from streams in the Coast (warmer and less seasonal variation) and Cascade Ranges (cold in winter) in western Oregon; and (2) determined the response of each group to declining water temperatures in laboratory streams.

Materials and methods

Field

Study area

Juvenile steelhead populations in Coast Range and Cascade Range streams were selected for this study on the assumption that regional environmental and physiographical differences (elevation, climatic regime, etc.) would result in local adaptations in seasonal behaviour and habitat use. Four Coast streams (Cummins, Tenmile, Big and Cape Creeks) and four Cascade streams (Copeland, Calf, Steelhead, and Canton Creeks) of western Oregon (Fig. 1) were used to determine the day and night patterns of pool habitat use. Streams in both regions were relatively small 3rd- to 4th-order streams (Strahler 1957) with bankfull channel widths that ranged from 10 through 17 m. The geology of both areas is basalt.

The coastal streams were on the central Oregon coast and drained directly into the Pacific Ocean (Fig. 1). Coastal climate is relatively mild and stable, with less seasonal variability in temperatures compared to the Cascades. Water temperatures in the coastal streams ranged from 8°C to 16°C in the summer and 5°C to 12°C in the winter (Table 1). Most precipitation comes as rain in the winter, which results in frequent high flows.

The Cascade streams were tributaries of the North Umpqua River, on the west side of the Cascade Range (Fig. 1). The climate in this region can be more extreme and more seasonally variable than in the Coast Range. Water temperatures in these streams ranged from 12°C to 20°C in the summer and 0°C to 8°C in the winter. Most precipitation comes in the

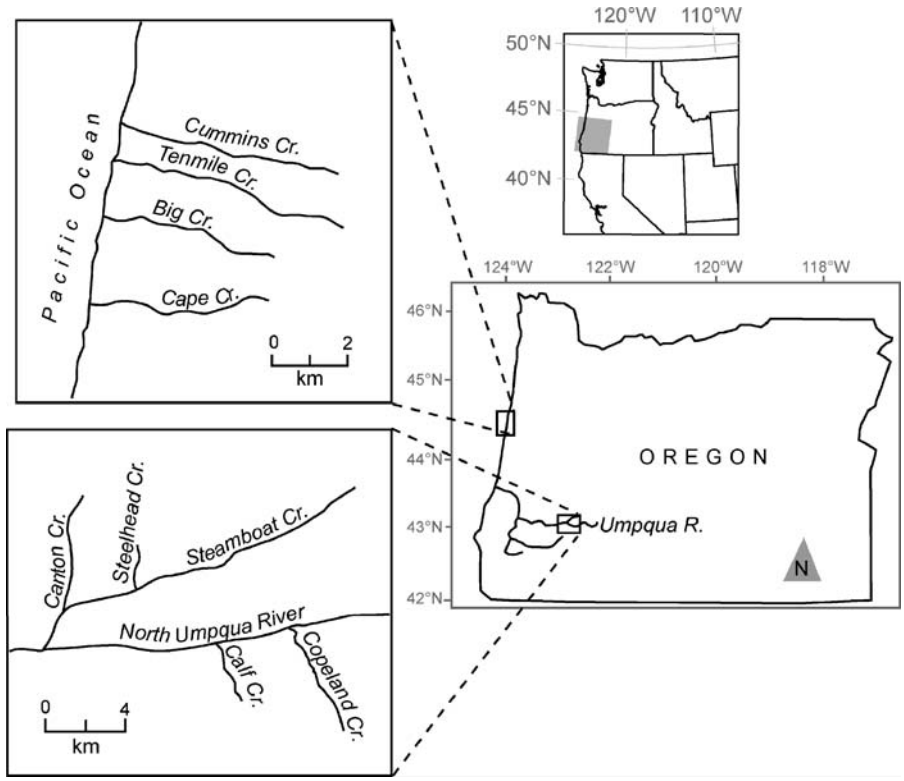

Fig. 1 Locations of Cascade and Coast Range study streams in Oregon, USA

winter, and can be in the form of rain or snow. Ice and anchor ice formation is common during the winter in the Cascade stream channels.

Steelhead populations in both regions are a part of the Oregon Coast Evolutionarily Significant Unit (ESU) (NOAA 1996). Generally, populations within an ESU are derived from a common lineage. However, there are some genetic differences between steelhead populations within this ESU. Hatch (1990) found that steelhead populations from coastal Oregon were genetically different along a gradient of basin size. The Umpqua River is one of the largest basins (>2,000 km^2) within this ESU, while the four coastal streams are small (<200 km^2). There are differences in run timing, which can be genetically determined (Quinn 2005), between the two areas. Most steelhead from this ESU exhibit winter run timing (i.e., enter freshwater in the late fall to winter to spawn), but the Umpqua River contains both summer (i.e., enter freshwater in the late spring and summer) and winter run steelhead (NOAA 1996).

Diel counts

We focused on pools in this study because they are the preferred habitat of 1+ steelhead (Hartman 1965; Reeves et al. 1998). Study sites in each stream were located starting at the first access point upstream from the confluence of a coastal stream with the Pacific Ocean or upstream from the confluence with a larger-order stream for the Cascade streams. Starting at these points and working upstream, the first eight pools were

Table 1 Mean and stand deviation of the dimensions of pools that were studied in the Coast and Cascade regions of Oregon

Parentheses indicate standard deviation

	Summer			Winter		
	Length (m)	Width (m)	Depth (cm)	Length (m)	Width (m)	Depth (cm)
Coast	21.0 (5.3)	4.2 (1.7)	50.8 (10.2)	18.4 (6.6)	6.5 (2.8)	61.0 (14.0)
Cascade	31.2 (13.1)	8.2 (3.7)	46.6 (12.7)	27.8 (14.7)	11.2 (3.0)	45.5 (13.7)

identified. Three of these pools were then randomly chosen to sample. Dimensions of the pools are shown in Table 1.

Paired day and night counts of juvenile steelhead (1+) were made by snorkeling in the three selected pools in each stream in each region and season. Fish counts were conducted by divers (GHR and JBG) between the hours of 10:00–15:00 (day) and 22:00–02:00 (night). One day and night survey was conducted in each stream during each sampling period. Summer and winter observations were made on the coast between 8–13 August 1990 and between 11–25 February 1991, respectively. In the Cascade streams, summer observations were made between 30 August and 5 September 1990 and winter observations between 20–26 January 1991.

Divers entered the water at the downstream end of each unit and slowly crawled or swam upstream while counting every observed 1+ steelhead, which were assumed to be any steelhead >90 mm in length. Fish size was estimated by comparing fish length with incremental marks on a Plexiglas data slate. Diurnal observations preceded nocturnal observations, and both dive sessions were completed in the same 24 h period. Waterproof dive lights were used to make night-time observations. Underwater visibility of ≥3 m was required for a dive. Water temperatures in the eight study streams were taken with hand-held thermometers immediately prior to observational dives (Table 2).

Table 2 Dates of snorkeling survey, water temperatures, and stream discharge in Coast and Cascade Range study streams

	Survey dates (day/night)	Temperature (°C)		Discharge (m^3s^{-1})
		day	night	
Summer survey, 1990				
Coastal streams				
Cummins Cr.	8–9 Aug.	16.0	14.5	0.174
Tenmile Cr.	9–10 Aug.	16.0	14.0	0.452
Big Creek Cr.	10–11 Aug.	14.5	11.5	
Cape Cr.	8–9 Aug.	15.0	12.0	
Cascade streams				
Copeland Cr.	30–31 Aug.	16.5	14.0	0.222
Calf Cr.	30–31 Aug.	17.0	14.0	0.049
Steelhead Cr.	30–31 Aug.	16.0	14.0	
Canton Cr.	30–31 Aug.	17.0	15.0	
Winter survey, 1991				
Coastal streams				
Cummins Cr.	24–25 Feb.	8.5	8.0	1.43
Tenmile Cr.	23–24 Feb.	9.0	8.0	2.76
Big Creek Cr.	25–26 Feb.	8.5	8.5	
Cape Cr.	11–12 Feb.	8.5	7.5	
Cascade streams				
Copeland Cr.	20–21 Jan.	4.5	4.0	2.34
Calf Cr.	21–22 Jan.	2.0	1.0	1.27
Steelhead Cr.	24–25 Jan.	2.5	2.5	
Canton Cr.	24–25 Jan.	2.0	2.0	

Stream discharge was measured only in streams where microhabitat utilization was observed and quantified

Microhabitat use

A detailed survey of diel microhabitat use was then made in the selected pools of Cummins and Tenmile Creeks (Coast) and Copeland and Calf Creeks (Cascade) on the day following completion of the diel counts. Divers entered the water at the downstream end of the pool and moved slowly upstream. Each sighted juvenile steelhead (1+) was observed for 1 min to 2 min. If the individual appeared to be holding a focal position (Kalleberg 1958), or otherwise occupying a particular station (Edmundson et al. 1968), and did not appear alarmed or displaced, the diver estimated its length and measured the focal elevation of the fish (the vertical distance of the fish above the substrate to the nearest centimeter) with a meter stick. The diver marked the focal position of the fish by placing a brightly-coloured numbered stone on the substrate. This procedure was repeated for all undisturbed 1+ steelhead within each pool. We assumed that fish on or close to the bottom of the pool or on the margin of the stream were inactive, similar to Whalen and Parrish (1999).

Divers returned to the stream the following day to measure seven additional microhabitat characteristics at the focal position of each observed fish. These were: 1) focal water velocity—current velocity measured at the position of each fish; 2) surface velocity—current velocity measured 5 cm below the water surface directly above each fish's position; 3) bottom velocity—current velocity measured 5 cm above the substrate directly below each fish's position; 4) total depth to the nearest cm of the water column in which the fish was observed; 5) distance to nearest cover object—any physical object or broken water surface that could provide a hiding place large enough to conceal a fish when viewed from

above; 6) stream width at focal position; and 7) bank distance—lateral distance from each fish's location to the nearest stream bank. These variables were used to examine diel and seasonal patterns of microhabitat use by steelhead in the coastal and Cascade regions. Velocities and discharge (Table 2) were measured with a Marsh-McBirney Model 201 current meter according to Platts et al. (1987).

Data analysis

Observational pairs of day and night count data in pools during the summer and winter in each stream were compared using paired-sample *t* tests. Group means for Cascade and coastal streams were also compared for significant differences ($P \leq 0.05$) using paired-sample *t* tests.

The frequency distribution of habitats for streams from the same region and between streams from the different regions did not differ (Kolmogorov-Smirnoff test $P > 0.05$). We, therefore, combined the diel microhabitat use data according to season and region into groups: coastal summer day, coastal summer night, coastal winter day, coastal winter night, Cascade summer day, Cascade summer night, and Cascade winter night. There was no Cascade winter day group because no fish were observed at this time. Discriminant function analysis was used to evaluate diel and seasonal segregation between these groups based on seven of the measured variables. A quadratic analysis was used because of significant heterogeneity in the covariance matrices ($P < 0.0001$; χ^2 test). Bottom velocity was not used because it was highly correlated with focal velocity (Pearson's Correlation Coefficient= 0.83, $P < 0.0001$). The seven variables included in the analysis were focal elevation, focal velocity, surface velocity, distance to cover, total depth, bank distance, and stream width. The first five of these variables were log transformed to normalize the data. Statistical analyses were performed with SAS/STAT statistical software (V. 9.1.3, 2004, SAS Institute Inc., Cary, NC).

Laboratory

Study design

Age 1+ steelhead from a coastal stream (Tenmile Creek) and a Cascade stream (Canton Creek) were observed in two circular stream aquaria (Reeves et al. 1987) to examine the effect of water temperature on diel behaviour. Each aquarium was 76 cm wide, 61 cm deep, and 18.4 m in circumference. Each was divided into two equal sections by a screened partition placed across the midpoint so that each section had two pool and two riffle areas with surface substrate consisting entirely of gravel <1 cm in diameter. Five tubular terra-cotta drainage tiles, 311 mm long by 136 mm in diameter, provided the only cover for fish in each section. They were almost completely buried within the substrate and had wood caps fastened by epoxy to both ends to prevent filling by substrate, but which also allowed entry by fish through semicircular openings. The sides of the tiles were cut away longitudinally and these cut surfaces were placed flush against the Plexiglas viewing walls of the channels to allow easy verification of cover use.

Artificial daylight was provided by nine 60-W incandescent bulbs suspended at equal intervals over each aquarium. Winter photoperiod was simulated by use of a timer and camera that controlled light intensity (Everest and Rodgers 1982), providing cycles of 12 h of light followed by 12 h of darkness. The light phase consisted of a 1.5 h "dawn" where light intensity gradually increased from zero to full and a 1.5 h "dusk" where full light intensity gradually dimmed to zero.

Steelhead used in the experiments were captured by electrofishing from Canton Creek in the Cascades on 8 December 1990 and from Tenmile Creek in the Coast Range on 15 January 1991. Prior to their introduction into the experimental channels, fish were held for 4 weeks in a 122 cm diameter circular fiberglass tanks fed by well water on a flow-through design. Water temperature in the holding tanks fluctuated between 12°C and 14°C. Fish were fed to satiation once daily with thawed frozen brine shrimp (*Artemia* spp.), and bi-weekly with meal worms (*Tenebrio* spp).

Before placement in the stream aquaria, fish were weighed to the nearest 0.1 g and measured to the nearest 1.0 mm fork length, then given fin-clips to facilitate individual identification. The mean (SD) length and weight of fish from the coastal stream used were 149.2 mm (39.7) and 37.1 g (13.4), respectively. The mean (SD) size of fish from the Cascade stream was 130.2 mm (14.2) and 24.1 g (7.9). Four fish from each stream were placed in each section of the aquaria.

A total of 16 fish from each region were used for the experiment in four replicate trials. Fish density in both experiments was slightly less than one fish·m^{-2}.

Fish were allowed 1 week to habituate to the stream aquaria. During this period water temperature in the stream aquaria was slowly raised to 16°C starting from the temperature of the water in the circular holding tank from which the fish had been retrieved. Fish adjustment to the aquaria and 16°C water was confirmed by ensuring that variation in tail beat rate and breathing rate became constant over time. All fish appeared acclimated to the stream channel well before the end of 1 week.

During observations in the laboratory channels, fish were fed thawed frozen brine shrimp via a food delivery system described by Reeves et al. (1987). Daily rations were equal to 10% of the total wet weight of fish in each aquarium as measured at the start of the experiment and were provided in two equal rations: once in the morning after 1 h of full light intensity and again 1 h before initiation of dusk.

Day and night observations of fish use of the cover structures were made as water temperature was decreased from 16°C to 2°C, and then increased again to 16°C, at a rate of 1°C each day. Fish from coastal and Cascade populations were tested separately in trials that each lasted 28 days. Temperature changes were made at night after the last observation session. Diel use of cover structures was recorded five times each day: three times during full daylight, and twice during the hours of darkness. Daylight observations were made just prior to morning feedings, at midday, and just prior to the pre-dusk feeding. Times for the midday and night-time observations were randomly chosen each day. The criterion for the midday observation was that it be made at least 1 h after the morning feeding and at least 1 h before the dusk feeding; the night-time observations were made at least 1 h after the onset of total darkness and at least 1 h before the initiation of dawn.

Data analysis

Logistic regression was used to examine the effect of water temperature on cover use by coastal and Cascade 1+ steelhead. The multiple observations made during the day and night were averaged for each partition or aquarium. The lowest and highest cover use proportions observed in each replicate were standardized to values approaching zero and 100%, respectively, then linearly transformed by natural logarithm for use in the logistic regressions. A regression was performed for each of the four trials for fish from each stream and for all of the partitions combined. Trials for coastal and Cascade fishes were paired by aquarium partition and compared. Slopes of the logistic equations that described the use of cover versus water temperature by coastal and Cascade fish in each of the four partitions were used as response indicators in the paired *t* tests.

Results

Field

Diel counts

The count of 1+ steelhead in streams in the two regions varied seasonally. In the summer, day and night counts of fish in pools of coastal and Cascade streams and the means of all streams in each region did not differ ($P>0.05$; *t* test) (Table 3). However, the pattern between the two regions differed in winter. Counts of 1+ steelhead in the coastal streams were generally similar to summer results, except in Big Creek, where numbers counted at night were significantly higher ($P<0.05$; *t* test) (Table 3). The mean count for all sampled streams did not differ ($P>0.05$; *t* test). In the Cascade streams, counts were significantly greater at night than during the day ($P<0.05$; *t* test) in all streams except for Steelhead Creek. The overall mean for the difference between day and night counts in the Cascade streams was significant, however ($P<0.05$; *t* test).

No fish were seen during the daytime winter dives in the Cascade streams. Ancillary dives performed during dusk discounted the possibility that juvenile steelhead were making diel migrations out of observed units or other movements that could result in patchy distribution not detected in the sampled pools. As daylight diminished, fish density increased slowly and no fish were observed to enter or exit a specific habitat unit. Therefore, we believe that any differences between day and night fish numbers were due to fish using nearby cover more during the day than at night. An intensive search during the day found only two steelhead in a pool-riffle sequence, where over 100 were observed the previous night. Every stone

Table 3 Number of 1+ steelhead counted in pools of the eight study streams at different times of day and night in the summer and winter

Stream	Summer count				Winter count			
	Total no. fish observed	Mean no./pool		Difference (day–night)	Total no. fish observed	Mean no./pool		Difference (day–night)
		day	night			day	night	
Coastal								
Cummins Cr.	60	8.7	11.3	−2.6	39	7.0	6.0	1.0
Tenmile Cr.	47	6.3	9.3	−3.0	57	9.3	9.0	−0.4
Big Cr.	88	15.3	14.0	1.3	137	6.0	39.7	−33.7*
Cape Cr.	101	17.0	17.0	0.0	80	11.0	15.0	−4.0
Coastal mean	*74.0*	*11.8*	*12.9*	*−1.1*	*78.3*	*8.3*	*17.6*	*−9.2*
Cascades								
Canton Cr.	64	7.7	13.7	−6.0	27	0.0	9.0	−9.0*
Steamboat Cr.	25	4.0[a]	7.0	−3.0	26	0.0	8.7	−8.7
Calf Cr.	52	10.0	7.3	2.7	18	0.0	6.0	−6.0*
Copeland Cr.	69	5.3	17.7	−12.4	62	0.0	20.7	−20.7*
Cascade mean	*52.5*	*7.7*	*11.4*	*−4.7*	*33.3*	*0.0*	*11.1*	*−11.1**

[a] Only one pool was counted due to the presence of mergansers (*Mergus merganser*) in the other two pools

*Differences significant at $P<0.05$

large enough to conceal a fish but small enough to be moved was overturned in the search, suggesting that the steelhead must have been concealed in the interstitial spaces of very large substrates or cracks in bedrock.

Microhabitat use

Quadratic discriminant analysis of the measured microhabitat variables resulted in a strong separation among the seven groups of location, season, and time of day. The discriminant function derived in the analysis had a high level of discriminatory power ($P<0.0001$; Wilks' λ). *Cohen's Kappa*, a measure of the classification rate against that of chance assignment, was 0.73 (95% CI=0.60−0.85), which suggested that the classification based on the variables was 73% better than random assignment.

The first two discriminant axes of the analysis were significant ($P<0.0001$) and represented 90% of the variance. Axis 1 (Fig. 2a) indicated that in summer, fish in both regions used similar habitats at each time of day and that there were strong diel differences in microhabitat use by 1+ steelhead. Fish generally used areas with lower focal (<3 cm s^{-1}) and surface (<15 cm s^{-1}) velocities and were at lower focal elevations (<3 cm) at night than during the day (focal velocity >8 cm s^{-1}, surface velocity >25 cm s^{-1}, and focal elevations >20 cm) (Fig. 2a). In winter, coastal fish were in different habitats during the day and at night, similar to the summer pattern (Fig. 2a). They were higher off the substrate (>30 cm) and in faster water (surface velocity >30 cm s^{-1}, focal velocity <15 cm s^{-1}) during the day than at night (surface velocity <20 cm s^{-1}, focal velocity <10 cm s^{-1}, focal elevations <5 cm). Cascade fish were in similar velocities and holding positions at night in the winter as they were in the day during the summer (Fig. 2a).

Stream width was the main variable associated with the second axis (Fig. 2b). This axis suggested that during the summer, coastal and Cascade steelhead used wider stream areas at night than during the day, and that this pattern was more pronounced for Cascade fish (Fig. 2b). In the winter, coastal fish were found in microhabitats of similar width between the night and day dives and the habitats they were found in were wider in winter than in the summer. Cascade steelhead used wider stream habitats on winter nights relative to summer days or nights, and they were not seen at all during winter days (Fig. 2b).

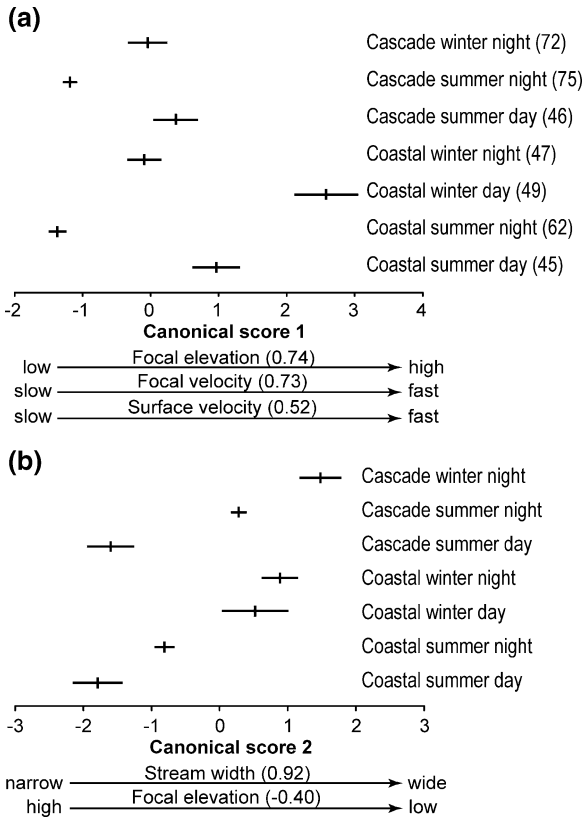

Fig. 2 Mean canonical discriminant scores (*vertical line*) and 95% confidence interval (*horizontal line*) for first two axes of discriminant analysis for 1+ steelhead from coast and Cascade streams. Axis 1 is "a". Axis 2 is "b". Factor loadings from the analysis are given in paranthesis after variables. Only loadings above 0.40 are shown. Sample sizes are shown in *parentheses*

Laboratory

In the laboratory streams, use of cover by juvenile steelhead from coastal and Cascade streams varied with water temperature and time of day (Fig. 3). During simulated daylight, the number of fish using the cover structures in each partition was negatively correlated with water temperature in the experiments. The slopes of the regressions from the individual aquaria ranged from 0.373 to 0.546 (R^2=0.55−0.88) for coastal fish and from 0.660 to 0.675 (R^2=0.93 −0.95) for Cascade fish (Table 4). The slope values were always less for coastal steelhead, and the differences increased as the water temperature decreased toward 2°C (Fig. 3). At any given water temperature between 16°C and 2°C, a significantly higher proportion of Cascade fish versus coastal fish used cover (P<0.05; paired t tests), and the differences were most apparent at temperatures below 12°C (Fig. 3). Fish from each location were never observed in the cover structures at night, regardless of temperature.

Discussion

Differences in the seasonal diel behaviours observed in this study suggest that there was adaptation to local conditions by the two groups. These results are similar to those of Valdimarsson et al. (2000), but are contrary to the predictions of Fraser et al. (1995), who examined the response of Atlantic salmon to declining water temperatures. They suggested that the response to declining temperatures should be similar for any population.

Our work suggests that there were likely inherent controls on the behavioural responses of the populations that we studied. However, we can not make the statement with absolute certainty because of limitations in the study design. We only used fish from one stream in each region in the laboratory experiments, thus we cannot easily extrapolate results to the whole region. Nonetheless, the strength of the pattern of response to declining temperatures by fish from the different regions, and the consistent patterns observed in the field, clearly support the inference that there is likely a genetic component to the observed responses by the fish from the two regions. Valdimarsson et al. (2000) also concluded that differences in responses between fish populations from areas with different environmental regimes were genetically derived.

Recent research suggests that there can be great individual variability in diel activity patterns within salmonid populations (Railsback et al. 2005; Breau et al. 2007). In this view, individuals select a combination of habitats and activities that maximize their future potential for growth and survival, and there is no inherent tendency in behaviour. Thus, there should be a range of behavioural responses to given environmental conditions. However, we observed little variation in behaviour among individuals within a given population whether in the field or the laboratory. Other laboratory studies have also shown that there are differences in the daytime shelter-seeking tendencies of salmonid populations in winter (Valdimarsson and Metcalfe 1998).

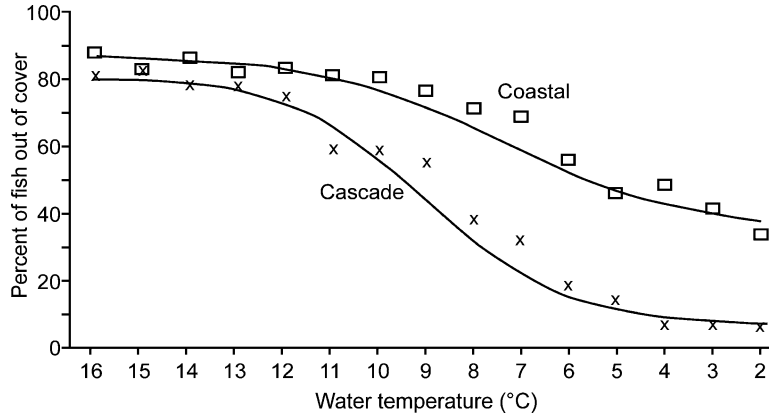

Fig. 3 Relationship between water temperature and diel use of cover structures for concealment by Coast and Cascade Range 1+ juvenile steelhead in laboratory streams. Regressions shown are from all aquaria combined, with logistic curves fitted to the data points for daytime cover use. All fish were out of cover structures at night

Differences in seasonal behaviours between the two groups are likely an adaptation to a complex interaction of the physical environment, physiological limitations, and variability in risk of predation associated with water temperature. The Cascade streams were colder during the winter than were coastal streams. Selection of microhabitats depends on a balance between energy gain and the cost of obtaining it (Cunjak 1996; Railsback et al. 2005), which is directly influenced by water temperature (Smith and Li 1983). Swimming performance and the ability to capture prey (Webb 1978) and escape predators (Álvarez and Nicieza 2003) are significantly reduced at cooler temperatures, especially in high velocity currents (Metcalfe et al. 1986). Metcalfe et al. (1999) argued that as the energetic cost of obtaining food increases, stream fish conserve energy by being concealed rather than expending energy defending feeding positions. Flow regimes in these systems also differ, which may influence turbidity and the susceptibility of salmon to predators (Gregory and Levings 1998). Flows are generally lower in the winter in the Cascade streams and higher in the coastal streams. The main predators in these streams during the winter are birds and mammals, and we believe that water clarity would likely affect their success in the same manner. Mergansers (*Mergus merganser*) were observed foraging in pools during the winter at one of the Cascade streams. The potential increased susceptibility to predation because of colder and clearer water, along with reduced metabolic performance, is a plausible explanation for the winter behaviour of Cascade steelhead.

Table 4 Parameter values of logistic equations describing day cover use versus water temperature by coastal and Cascade 1+ juvenile steelhead trout in partitions of laboratory streams and for each population overall

Partition	Coastal trout			Cascade trout		
	Intercept	Slope	R2	Intercept	Slope	R2
I	−1.95	0.452	60%	−6.20	0.668	93%
II	−4.72	0.546	88%	−6.63	0.675	93%
III	−4.36	0.466	69%	−5.91	0.660	95%
IV	−2.84	0.373	55%	−5.90	0.658	93%
Overall	−3.62	0.499	89%	−6.12	0.682	97%

Lack of a major change in the pattern of diel behaviour for coastal fish is probably attributable to warmer water temperatures in the winter. Water temperatures in the coastal streams generally remained above 5°C, a critical level for metabolic performance in various salmonids (Elliott 1972; Windell et al. 1976). As a consequence, the difference in potential ability to escape predators and to capture prey items between summer and winter may be minimal in coastal streams. Also, warmer water temperatures may require longer foraging times for coastal fish to meet metabolic needs. Researchers who found a pattern of seasonal change in diel behaviour in other salmonids similar to the Cascade fish (Heggenes et al. 1993; Whalen and Parrish 1999) argued that with low temperatures and reduced metabolism, fish are able to remain completely sheltered during the day.

These differences in summer day and night microhabitats for the fish from both regions were consistent with other studies of diel changes in habitat use by juvenile steelhead (Edmundson et al. 1968; Riehle and Griffith 1993; Bradford and Higgins 2001) and other salmonids (Valdimarsson and Metcalfe 1998;

Whalen and Parrish 1999; Jakober et al. 2000). These researchers also reported that fish moved to shallower water closer to the stream margin at night, but this was not observed in our study. Instead, we found that coastal and Cascade fish used moderate to deep areas of the pools and remained at the same distance from the stream margin during day and night. One potential reason for this difference is that our observed fish were only in pool habitats, which are moderate to deep by definition, whereas other studies may have included riffles and other shallow water habitats.

Seasonal diel activity patterns are important when considering the ecology of salmonid populations for research or management purposes (Heggenes and Dokk 2001). Hogan and Church (1989) concluded that habitat models for salmonids were at best only regionally valid because of variation in the behaviours of populations in other areas. Variations in seasonal diel behaviour among areas with differing climate and hydrologic regimes, like those documented in this study, support this. Understanding seasonal diel behaviour provides insights into habitat requirements for other times and seasons than summer days, which is generally the only period considered in many habitat models. Taking these differences into account is particularly critical for the development of management actions. Models that do not consider local adaptations in seasonal behaviour and habitat requirements may not achieve desired results and may waste valuable financial resources. At worst, management based on such models may have unintended negative consequences to the populations of interest.

Acknowledgements A. Atkins, B. Campbell, C. Dewberry, D. Moore, F. Vasser, D. Price, and J. Ziedler helped with field work. D. Olsen, H. Li, and R. Beschta reviewed the first versions of this manuscript. Comments by J. Rosenfield and three anonymous reviewers contributed to improvements in the manuscript. K. Burnett provided guidance with statistical analyses. K. Ronnenberg produced the graphics and provided editorial support. Financial support for this study was provided by the USDA Forest Service, Aquatic and Land Interaction Program, Pacific Northwest Research Station, Corvallis, Oregon.

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