

Seasonal changes in spatial patterns of *Oncorhynchus mykiss* growth require year-round monitoring

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Abstract – Growth and movement of juvenile salmonids influence the expression of individual life history traits and production of adults at the population scale. We individually marked and recaptured juvenile *Oncorhynchus mykiss* over the course of a year in Murderers Creek, a semi-arid tributary to the South Fork John Day River in Northeast Oregon. We tagged *O. mykiss* in three reaches with differing stream gradient, stream temperature and fish density. Mean growth rates differed significantly among reaches and seasons with a significant interaction between reach and season. Reaches with high growth rates shifted across Murderers Creek among seasons. Stream reaches with high growth during the winter had low growth during summer and vice-versa. The proportion of individuals moving at the reach scale during summer was low ($\leq 2.6\%$), suggesting that individuals did not track resources at the reach scale. The spatio-temporal variation in growth indicates that monitoring stream salmonids across multiple seasons is necessary to accurately characterise the production of different stream reaches.

Key words: salmonid ecology; endangered species; fish growth; monitoring

Introduction

Many factors influence freshwater growth rate, including food availability (Filbert & Hawkins 1995; Metcalfe et al. 1999; Imre et al. 2004), physical cover (Thorpe 1987), stream temperature (Myrick & Cech 2000; Marine & Cech 2004; Murphy et al. 2006), behavioural patterns (Metcalfe et al. 1988, 1999), and intraspecific (Keeley 2001) or interspecific (Reeves et al. 1987) competition. Growth rate therefore integrates the environmental experience of an individual fish and is an important indicator of fish development (Van den Avyle & Hayward 1999). For anadromous fish, increased freshwater growth rate decreases the time needed to attain minimum size thresholds for migration to saltwater (Peven et al. 1994; Cucherousset et al. 2005), potentially decreasing the risk of freshwater mortality. Size at

smoltification, which is the product of freshwater growth rate and residency time, can also influence marine survival (Ward et al. 1989; Lundqvist et al. 1994; Tipping 1997).

For Atlantic salmon *Salmo salar* and steelhead trout *Oncorhynchus mykiss*, a life history trade-off exists between anadromy and residency (Thorpe 1987; Zimmerman & Reeves 2000). Resident maturation can occur in less time and with less mortality risk than anadromous maturation, but at the cost of reduced fecundity (Kendall et al. 2015). Changes in growth rate influence this anadromy-residency trade-off (Metcalfe 1998; Morinville & Rasmussen 2003; McMillan et al. 2011). For instance, individuals with faster growth and higher lipid levels may be more likely to adopt resident maturation (Sloat & Reeves 2014). Environmental conditions controlling fish growth change spatially within catchments (Wright

2000; Reeves et al. 2011; McMillan et al. 2013), potentially creating reach- and season-specific growth responses by juvenile salmonids. Therefore, interactions between reach-scale growth and inter-reach movement may contribute to shaping the life history of individual *O. mykiss*.

Given the importance of freshwater growth rate to fish life history (Juanes et al. 2000; Cucherousset et al. 2005) and subsequent survival (Juanes et al. 2000; Letcher et al. 2002), growth is often monitored as an indicator of habitat quality. However, the mobility of stream fish (Gowan & Fausch 1996; Armstrong et al. 1997) can make growth rate monitoring challenging. Individual marking and detection techniques, such as Passive Integrated Transponder (PIT) tags, have increased our knowledge of growth patterns and movement (Juanes et al. 2000; Kahler et al. 2001; Bacon et al. 2005). Historically, many individual-based studies focused on growth or survival patterns in short spatial and temporal (often during summer) periods (Juanes et al. 2000; Letcher et al. 2002; Bacon et al. 2005). However, understanding growth and movement, and the resulting implications for life history patterns at the stream scale across multiple seasons better reflects watershed management needs (Fausch et al. 2002). Managers need to know the appropriate scale to implement cost-effective conservation and restoration actions, whereas researchers need to know the appropriate spatial scale to monitor the effectiveness of these actions.

Factors limiting fish growth and abundance may change among seasons. As a result, research is increasingly accounting for larger spatial and temporal grains (Ebersole et al. 2006, 2009; Reeves et al. 2011; Roni et al. 2012). For instance, temperatures in portions of desert streams may limit both salmonid growth and spatial distribution during summer (Li et al. 1994; Feldhaus et al. 2010), but not winter. In response to high summer stream temperatures, salmonids may behaviourally thermoregulate or migrate to find more optimal thermal and growth habitat (Ebersole et al. 2003), potentially causing reach-specific changes in density, growth and survival among seasons (Ebersole et al. 2006).

The goal of our study was to evaluate spatio-temporal variation in growth during all four seasons, as this is a key driver of life history patterns and population productivity. To accomplish this, we studied growth and movement of individually marked *O. mykiss* in Murderers Creek, a tributary of the South Fork John Day River, Oregon. We theorised that: (i) individual growth rates would vary among reaches and seasons, and (ii) individual *O. mykiss* would actively migrate seasonally among multiple reaches to maximise growth rate. The specific

research hypotheses that we tested were as follows: density of *O. mykiss* would not differ among seasons and reaches (H_1); growth rate of individually tagged *O. mykiss* would not differ among seasons and reaches (H_2); and *O. mykiss* from reach 1 (the warmest reach monitored) would immigrate into or through reach 2 (where stream temperatures were cooler) during summer (H_3).

Methods

Study location description

The South Fork John Day River basin (SFJD) supports native, naturally reproducing summer-run steelhead (anadromous) and rainbow trout (resident). Most of the *O. mykiss* in the SFJD are <200 mm fork length (FL), and although the population we sampled is composed of both mature resident and immature anadromous individuals (McMillan et al. 2011), none were externally identifiable as being either resident (trout) or anadromous (juvenile summer steelhead). Thus, we use *O. mykiss* to describe all individuals captured and tagged. *O. mykiss* are distributed throughout the SFJD, including four principal tributaries downstream of Izee Falls (Fig. 1), which is a barrier to upstream migration by all *O. mykiss*. Adult steelhead and resident rainbow trout spawn March–June. Anadromous *O. mykiss* emigrate from the SFJD during October to May and migrate through the Columbia River to the Pacific Ocean during April–June (Tattam et al. 2013). We selected Murderers Creek as a location of intensive study from December 2004 to February 2006 (Fig. 1). Murderers Creek is a fourth-order stream basin that encompasses 14,632 ha in Northeast Oregon (Fig. 1) and ranges in elevation from 914 to 2133 m.

Our sampling frame for Murderers Creek included its lowermost 18 km (Fig. 1). Within this section, we identified three distinct geomorphic reaches (Frissell et al. 1986). These reaches, previously described by Weber et al. (2014), have similar channel widths, but differing gradients. We randomly selected a monitoring site within each of the three stream reaches. Following the nomenclature of Weber et al. (2014), sites were labelled ‘one’, ‘two’ and ‘three’ in ascending order proceeding upstream from the SFJD (Fig. 1). Sites encompassed at least five pools, ranged in thalweg length from 99 to 391 m and were sampled five times between December 2004 and February 2006 to encompass four intervals that approximated each season.

Murderers Creek discharge (recorded by an Oregon Water Resources Department pressure gauge 0.3 km upstream from the SFJD) varied by more than two orders of magnitude during our study period.

Fig. 1. Map of the South Fork John Day River (SFJD) and Murderers Creek. Dashed arrow denotes stream flow direction. Inset shows the location of the SFJD (grey shaded area) within the state of Oregon and the United States. Coloured stream areas denote three reaches, and numbered arrows mark the sampling site within each reach of Murderers Creek. Stream temperature loggers were operated at each sampling site.



Minimum discharge ($0.07 \text{ m}^3 \cdot \text{s}^{-1}$) occurred on 28 August 2005 and maximum discharge ($9.14 \text{ m}^3 \cdot \text{s}^{-1}$) occurred on 31 December 2005. Stream temperatures were recorded continuously (i-Button thermochron and Onset Optic Stowaway temperature loggers) with temperature loggers in reach two for the duration of the study period, and in reaches 1 and 3 from June 2005 to January 2006 (Fig. 1). We used one-way analysis of variance (ANOVA) and multiple comparisons (using a Bonferroni adjustment to minimise type 1 error rate) to evaluate differences in mean daily stream temperature among reaches during summer and fall.

Fish capture, tagging and density estimation

We used three different fish capture techniques to minimise the effect of capture-induced bias in the size of fish PIT tagged. When stream temperatures were $>8^\circ\text{C}$, we captured *O. mykiss* using either a snorkeler or a backpack electrofisher (Smith-Root 12-B, Vancouver, WA) to 'herd' fish from pools downstream into a bag seine ($3.7 \times 1.2 \text{ m}$, with 6.4 mm mesh). This method was also used in riffles $>40 \text{ cm}$ deep, whereas in riffles $<40 \text{ cm}$ deep we electrofished and dipnetted fish. When stream

temperatures were $<8^\circ\text{C}$, we night snorkelled with a dive light (C-8 UK Sunlight, with LED bulb) and captured *O. mykiss* with a handheld dipnet.

We captured and PIT-tagged ($12 \times 2 \text{ mm}$, 134.2 kHz ; Digital Angel Corp.) *O. mykiss* at each site during five sampling periods (December 2004, March 2005, June 2005, September 2005 and January 2006, Table 1), to measure fish growth during four intervals which approximated (but did not exactly match) each season. Each individual was anaesthetised (MS-222 , $45 \text{ mg} \cdot \text{l}^{-1}$ stock solution) and PIT tagged in the peritoneal cavity (Prentice et al. 1990), or recorded as a recapture if previously tagged. Location of capture (to the channel unit scale) and FL (nearest mm) was recorded on each capture occasion. Fish were allowed to recover in a dark, well-oxygenated container and released into their channel unit of capture. Sites were sampled on 2 days each during June and September, and 3 days each during January to estimate linear density of *O. mykiss* via mark-recapture. We used Program Capture (M_t Chao model, White et al. 1982), to estimate abundance, and hence density per linear m, in each site. We tested H_1 by comparing density among reaches (all seasons pooled) using one-way ANOVA. Sample size was insufficient to use ANOVA for comparison of reaches

Table 1. Summary of newly PIT-tagged (New) and previously PIT-tagged (Recaptured) *Oncorhynchus mykiss* ($>75 \text{ mm}$ fork length) captured in Murderers Creek. Number of individuals captured and mean fork length (FL) is summarised by fish growth period measured (Season), date of sampling (Sampling) and reach. NT = no new PIT-tagged *O. mykiss*, but all nontagged captures were measured. Recaptures which occurred during December 2004 were tagged in summer 2004, during a companion study (Tattam et al. 2013).

Season	Sampling	New <i>O. mykiss</i>						Recaptured <i>O. mykiss</i>					
		Reach 1		Reach 2		Reach 3		Reach 1		Reach 2		Reach 3	
		<i>n</i>	FL	<i>n</i>	FL	<i>n</i>	FL	<i>n</i>	FL	<i>n</i>	FL	<i>n</i>	FL
Winter	Dec 2004	50	135	33	129	17	121	9	154	6	151	3	110
Spring	Mar 2005	21	130	40	101	16	116	8	134	12	100	5	144
Summer	Jun 2005	69	123	66	120	28	102	4	144	9	153	7	134
Fall	Sep 2005	38	125	80	130	25	134	31	136	28	148	20	135
	Jan 2006	NT	141	NT	107	NT	122	15	156	19	128	8	149
	PIT Total	178		219		86		67		74		43	

within a single season. Therefore, 95% confidence intervals were used to visually compare density estimates among reaches within seasons.

Statistical analysis of growth rate

We used relative growth rate (Van den Avyle & Hayward 1999), or change in length from initial length per unit time, as our metric to test H_2 . We used two-way ANOVA with multiple comparisons (with a Bonferroni adjustment to minimise type 1 error rate) among reaches and seasons. Eleven per cent of individual *O. mykiss* used for growth rate estimates were measured during multiple seasons. We conducted the two-way ANOVA both with and without the repeatedly measured individuals and found the same reach-season rank outcomes. Thus, we report the analysis including repeatedly measured individuals to maximise sample size.

Detection of movement

We used two methods to detect summer movement of PIT-tagged *O. mykiss* and test H_3 : (i) operation of an instream PIT-tag array, (ii) reach-level fish capture events that were spatially and temporally interspersed between the site-level sampling events. We theorised that PIT-tagged individuals from reach 1 (the warmest reach monitored) would migrate into or through reach 2 during summer to occupy cooler stream temperatures. Thus, we PIT-tagged 306 *O. mykiss* in reach 1 during June 2005 and deployed stationary PIT tag arrays in reach 2 (from May 1 to September 27, 2005) to detect upstream movement by these (and other) PIT-tagged *O. mykiss*. We used detection weirs composed of a submersible rectangular antenna (31×80 cm, Biomark Inc., Boise, ID, USA) anchored upright and perpendicular to the thalweg with v-shaped weirs of 1.27 cm plastic mesh screening placed against the banks and onto the stream bottom to direct fish through the antenna. Antennas were operated by a Destron Fearing 2001F transceiver which recorded tag code, detection date and time, and were separated by 237 m thalweg length to allow determination of fish movement direction. We estimated the efficiency of the lower antenna at detecting upstream-moving migrants as the count of fish detected at both antennas divided by the sum of fish detected at both antennas and fish detected at only the upstream antenna (Zydlewski et al. 2006). Monitoring of downstream migration during fall and winter was conducted and reported by Tattam et al. (2013).

Mobile fish capture events used to detect summer fish movement among reaches were described in detail by Tattam et al. (2013). In short, capture effort

was equally distributed among each reach in Murderers Creek on a weekly basis from June to September. The starting channel unit for each day's capture effort was randomly assigned without replacement (each starting channel unit was drawn from a contiguous habitat inventory of all channel units in each reach), to sample the maximum possible linear extent. Linear stream distance sampled each day ranged from approximately 80 to 200 m. Over 1500 *O. mykiss* were captured throughout Murderers Creek (Tattam et al. 2013; Table 1), interrogated for PIT tag presence (and tagged if not a recapture), and their location recorded at the channel unit scale. We organised capture–recapture data into a 3×3 matrix comparing the reach of recapture during summer 2005 (for each capture occasion if fish were recaptured more than once) with the most recent prior reach of capture.

Results

Seasonal mean daily mean temperatures in Murderers Creek varied significantly among reaches ($F_{2,225} = 51.3$, $P < 0.0001$; Fig. 2) with a longitudinal cline during summer. Summer daily mean temperature in reach 1 was significantly higher ($P < 0.0001$) than reach 2. Summer daily mean temperature in reach 3 was significantly lower ($P < 0.0001$) than both reaches 1 and 2. Daily mean stream temperatures during fall were not statistically different ($F_{2,294} = 0.1$, $P = 0.88$) among reaches (Fig. 2).

From December 2004 to February 2006, we PIT-tagged 483 *O. mykiss* at three sites on Murderers Creek (Table 1). We captured 100 *O. mykiss* at both the beginning and end of a single season and used these individuals to estimate seasonal growth. There was evidence of a difference in *O. mykiss* density among reaches ($F_{2,6} = 4.98$, $P = 0.05$). Comparison of 95% confidence intervals (Fig. 3) suggests there were no significant differences in mean density of *O. mykiss* among reaches in June 2005. During September 2005, reach 1 had a significantly lower density than reach 2, and reach 2 in turn had a significantly lower density compared to reach 3 (Fig. 3). During January 2006, there was no significant difference in density between reach 1 and reach 2. Conversely, estimated density in reach 3 was significantly higher than density in either reach 1 or reach 2 (Fig. 3).

Relative growth rate (Fig. 4) had significant seasonal ($F_{3,88} = 62.6$, $P < 0.0001$) variation with a significant first-order interaction between season and reach ($F_{6,88} = 4.5$, $P < 0.001$). Winter growth rates varied significantly among reaches ($F_{2,88} = 3.0$, $P = 0.05$, Fig. 4) with suggestive evidence of a

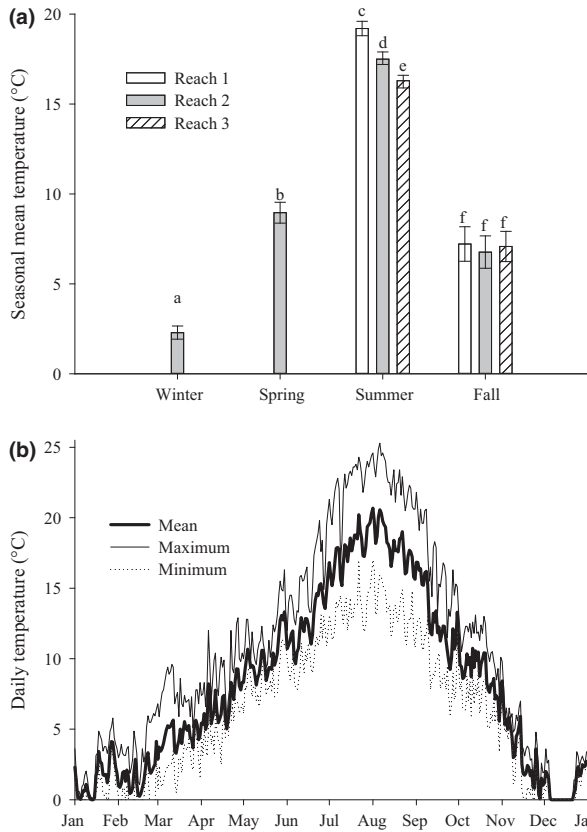


Fig. 2. Seasonal means of daily mean stream temperatures at sampling sites on Murderers Creek (panel a). Error bars are 95% confidence intervals. Letters commonly shared among bars indicate sites that were not significantly different ($P > 0.05$). Daily stream temperature in reach 2 of Murderers Creek from 1 January to 31 December 2005 is presented in panel b.

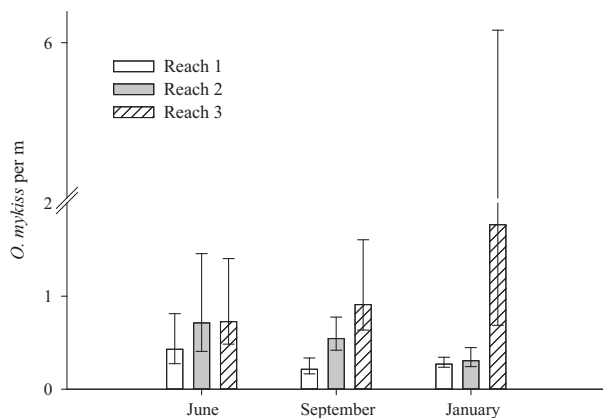


Fig. 3. Estimated linear density of *Oncorhynchus mykiss* at three sampling sites in Murderers Creek during June 2005, September 2005 and January 2006. Error bars are 95% confidence intervals.

difference between reaches 1 and 3 ($t = 1.9$, d.f. = 88, $P = 0.06$), and significant evidence that growth rate in reach 3 was lower than reach 2 ($t = 2.3$, d.f. = 88, $P = 0.02$). Spring growth rates were significantly higher than any other season

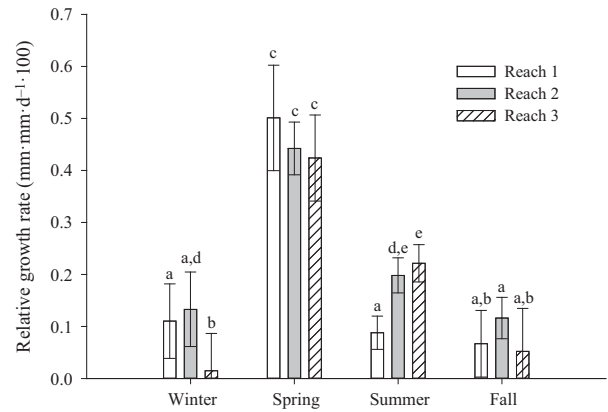


Fig. 4. Seasonal pattern in relative growth rates of 100 PIT-tagged *Oncorhynchus mykiss* in Murderers Creek from December 2004 through January 2006. Error bars are 95% confidence intervals. Letters commonly shared among bars indicate reach-season combinations that were not significantly different ($P > 0.05$).

($P < 0.0001$ for all pairwise comparisons, Fig. 4) and were not significantly different among reaches ($F_{2,88} = 0.7$, $P = 0.48$). Summer growth rates differed significantly between reach 1 and reaches 2 and 3 ($F_{2,88} = 18.2$, $P < 0.0001$, Fig. 4). In contrast to winter, relative growth in reach 1 was significantly lower than reach 2 ($t = -4.7$, d.f. = 88, $P < 0.0001$) and reach 3 ($t = -5.5$, d.f. = 88, $P < 0.0001$), with no significant difference between reaches 2 and 3 ($t = -0.9$, d.f. = 88, $P = 0.35$). Fall growth rates were not significantly different among reaches ($F_{2,88} = 1.5$, $P = 0.23$, Fig. 4).

Six PIT-tagged *O. mykiss*, four of which originated from our June 2005 tagging in reach 1, were detected migrating upstream past the PIT array between June 17 and July 20 (Figs 1 and 5). We estimated that our PIT array was 50% efficient at detecting upstream migrant *O. mykiss*. Given our efficiency estimate, we estimated that 2.6% of the 306 PIT-tagged *O. mykiss* released in reach 1 during June 2005 moved upstream past the PIT array in reach 2. Movement occurred coincident with rising stream temperatures, but prior to the summer maximum temperature (Fig. 5). Mobile recaptures corroborated the PIT array data. We made 241 recapture events (some individuals were recaptured more than once) from June to September 2005, and in only 2 of those events (0.8%) was the reach of prior capture different than the reach of recapture (Table 2). In one of the two movement events, a fish moved two reaches upstream, and in the other, a fish moved two reaches downstream (Table 2).

Discussion

Reaches of high fish growth shifted across Murderers Creek among seasons. Areas with high *O. mykiss*

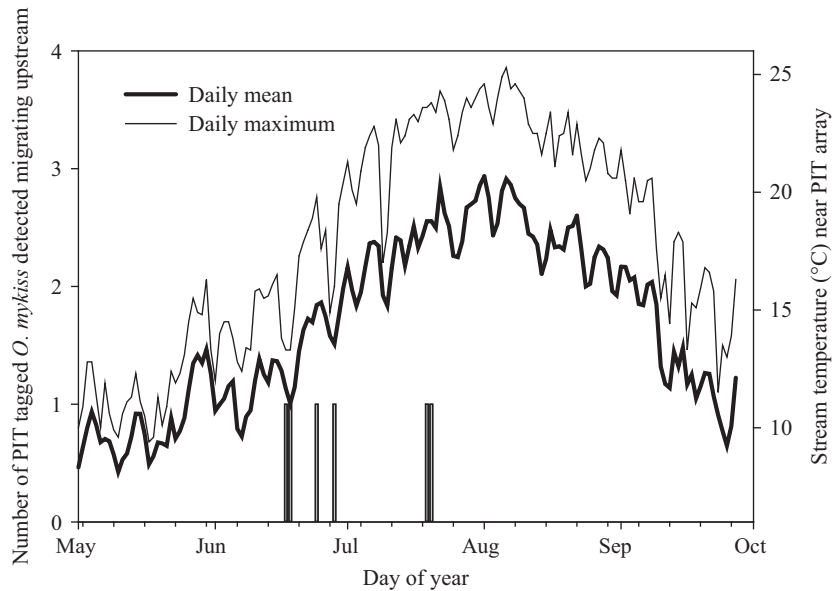


Fig. 5. Relationship between detection of upstream migrating PIT-tagged *Oncorhynchus mykiss* (bars, left vertical axis) and daily stream temperature (line, right vertical axis) in Murderers Creek from 1 May 2005 to 27 September 2005. The PIT array was located in reach 2 of Murderers Creek.

Table 2. Matrix of PIT-tagged *Oncorhynchus mykiss* recaptured in three reaches of Murderers Creek. Recaptures occurred from June 2005 through September 2005. Each recapture event (some individuals were recaptured multiple times) is paired with its most recent prior capture event.

Reach of prior capture	Reach of recapture			Totals
	1	2	3	
1	76	0	1	77
2	0	86	0	86
3	1	0	77	78
Totals	77	86	78	241

growth during winter (reach 1) had low growth during summer, and hence, their contribution to production would be underestimated with summer-only sampling. Ebersole et al. (2006) sampled at a similar spatial scale and also observed high growth rates shift among reaches across different seasons. In their study, an intermittent stream with medium-sized juvenile coho salmon *Oncorhynchus kisutch* at the end of summer became the reach of highest growth during winter. These studies in tandem indicate that reaches of lower summer productivity (Moore Creek in the study by Ebersole et al. 2006, and reach 1 of Murderers Creek in our study) should be evaluated over the course of an entire year to accurately depict their importance to salmonid production.

In addition to among-site and among-season variation, relative growth rate also varied among individuals within each site and season. Although our recapture sample size was low during some seasons, we were still able to document a broad range of individual growth rates. For instance, we observed individual growth rates during summer in reach 1

which ranged from 0.00 (0% of the mean) to 0.17 mm·day⁻¹ (189% of the mean). This was similar to the variation observed by Juanes et al. (2000), but differed from Bacon et al. (2005), who observed little individual variation in growth rates of Atlantic salmon parr. Different spatial scales of sampling, rather than recapture sample size, likely contributed to these contrasting results. Bacon et al. (2005) sampled solely within a 140 m stream section; conversely, Juanes et al. (2000) sampled a 1 km section of stream. In comparison, we sampled 853 m distributed across 18 km. These studies in combination indicate that, to encompass individual growth variability and accurately measure production at a stream scale, individual monitoring should be nested within seasonal monitoring of different stream reaches.

Oncorhynchus mykiss in Murderers Creek achieved the majority of their annual FL growth during spring. This occurred at mean temperatures (9.0 °C in reach 2) below the reported optimal growth temperature (15–19 °C; Richter & Kolmes 2005). Bacon et al. (2005) and Juanes et al. (2000) both observed a similar discrepancy, with the fastest annual growth of Atlantic salmon parr occurring during spring in colder than ‘optimal’ temperatures. Positive change in photoperiod during spring likely contributed to the highest growth rates of the year through neuroendocrine stimulation (Higgins 1985; Saunders & Harmon 1990). Our results corroborate the theory that change in photoperiod has a larger influence on growth than temperature (Higgins 1985). However, it is also important to consider seasonal changes in optimal growth temperature. For instance, Averett (1969) found that optimal growth temperatures for coho salmon were lower during winter and spring

than summer. Optimal spring growth temperatures for coho were one-third of optimal summer temperature (Averett 1969). Although spring temperatures in Murderers Creek were below 15 °C (the optimum range presented by Richter & Kolmes 2005), they met or exceeded 5 °C on most spring days (Fig. 2). Macroinvertebrate drift biomass, which was an important component of summer fish growth in this stream (Weber et al. 2014), likely mediated the relationship between stream temperature and fish growth during spring as well. Monitoring changes in stream temperatures, food availability and the associated physiological response of salmonids (e.g. Feldhaus et al. 2010; Weber et al. 2014) has been focused on summer periods. However, given the importance of spring to the overall growth of the *O. mykiss* we studied, understanding how future changes in spring stream temperature affect fish growth should also be a component of salmonid monitoring.

Annual patterns in growth rate were not driven solely by temperature, which is consistent with prior studies (Nicola & Almodovar 2004; Larsson et al. 2005). Winter growth rates differed among reaches during a season when stream temperatures are typically homogenous. During summer, there was a significant difference in temperature between reaches 2 and 3, but no difference in growth rate. Density of benthic and drift macroinvertebrates was higher in reaches 1 and 2 compared to reach 3 during summer 2006 (Weber et al. 2014). We theorise that increased prey availability in reach 2 was sufficient to offset temperature-driven metabolic increases (Hughes & Grand 2000). Expanding the prey availability monitoring conducted by Weber et al. (2014) to the winter and spring seasons would improve our understanding of the mechanisms influencing the temperature–growth relationship in these seasons where growth varied among reaches and then reached its annual maximum respectively. Irrespective of mechanism, the reach-scale differences in growth we observed were superimposed on a photoperiod-correlated annual pattern, yet remained substantial enough to potentially alter life history trajectories (McMillan et al. 2011).

The paucity of summer movement we found is in contrast to some observations of high movement rates for stream salmonids (Gowan & Fausch 1996, 2002; Kahler et al. 2001). Although we technically accepted H_3 , as we were able to document summer migration by a few individual *O. mykiss* from reach 1 into reach 2, two independent methods indicated that >95% of *O. mykiss* in Murderers Creek remained in their reach of tagging during summer. For *O. mykiss* in reach 1, this meant that they remained in reach 1 despite peak temperatures (27 °C) exceeding reported thresholds where growth ceases (Richter & Kolmes 2005). Although nearby populations of

O. mykiss have adaptive tolerance of high water temperatures (Gamperl et al. 2002; Rodnick et al. 2004), an upstream migration of 6 km would have decreased ambient temperature and in turn increased growth (presuming no density-dependent reduction in growth rates). Perhaps stream temperatures near the upper incipient lethal temperature (Richter & Kolmes 2005) are necessary to stimulate upstream migration of a substantial portion of the population. Future testing of this hypothesis would assist management, as a temperature trigger for upstream migration could be matched with discharge on a stream-specific basis to ensure that man-made fish passage structures (e.g. fish ladders at irrigation diversion dams and culverts at road crossings) effectively pass fish upstream during critical periods. However, factors in addition to stream temperature appear to influence movement. For example, the distribution of juvenile salmonids in experimental stream channels with cover habitat under-matched food abundance (Giannico & Healey 1999) indicating that food was not the sole driver of fish distribution. Rather fish distribution can be mediated by cover habitat availability and not respond linearly to food abundance (Giannico 2000). Research in Murderers Creek similarly suggests that response to high summer stream temperatures was mediated by a combination of increased prey abundance in warmer reaches (Weber et al. 2014), higher winter growth rates in warmer reaches (Fig. 4) and lower summer density in warmer reaches (Fig. 3).

Management implications

Sampling only during summer would have provided an inaccurate assessment of the spatial distribution of fish growth in Murderers Creek. Low summer growth rates in reach 1, if considered in isolation, implied that this is an unproductive reach that *O. mykiss* would emigrate from during summer. However, in contrast to our hypothesised upstream migration, most tagged *O. mykiss* remained in reach 1 of Murderers Creek during summer despite experiencing lower growth and higher temperatures relative to upstream reaches. Our growth rate monitoring during prior seasons revealed that *O. mykiss* in reach 1 had experienced higher winter growth relative to upstream areas (reach 3) which provided a ‘jump start’ on annual growth. At the beginning of summer, newly tagged individuals were, on average, 3 mm longer in reach 1 than reach 2, and 21 mm longer in reach 1 than reach 3. Salmonids monitor and allocate their lipid levels (Bull et al. 1996) depending on whether they are on a trajectory to smolt the following spring (Metcalf et al. 1988). Thus, as a result of beginning summer at a larger size, *O. mykiss* in reach 1 may have projected that their size or energy levels

were sufficient to stay on a desired growth trajectory, obviating the need for resource tracking at the reach scale.

In sum, we demonstrated that localised differences in the environment affected growth within a stream, and these differences were sparsely tracked by individual fish at the reach scale during summer. While longitudinal changes in the riverscape (Fausch et al. 2002) certainly influence phenotypic expression (e.g. residency in cool headwater streams vs. anadromy in warmer high-order streams, McMillan et al. 2011), our results also indicate the existence of a temporal component to the riverscape. Fish size distributions observed within a reach during a single season are influenced by growth during prior seasons. Furthermore, phenotypic expression in partially migratory species like *O. mykiss* is influenced by growth during key seasonal 'windows' (Silverstein et al. 1998; McMillan et al. 2011). Monitoring growth at a longer time scale (e.g. annual rather than seasonal estimates of growth rate) would average across these key growth windows and miss important biological data. Monitoring growth and movement during as many seasons as possible is hence important for accurately characterising the biota present along the riverscape and advancing our knowledge of partial migration.

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