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Growth of juvenile steelhead *Oncorhynchus mykiss* under size-selective pressure limited by seasonal bioenergetic and environmental constraints

J. N. THOMPSON*† AND D. A. BEAUCHAMP‡

**Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington, 98195, U.S.A. and ‡U.S. Geological Survey, Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington, 98195, U.S.A.*

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Increased freshwater growth of juvenile steelhead *Oncorhynchus mykiss* improved survival to smolt and adult stages, thus prompting an examination of factors affecting growth during critical periods that influenced survival through subsequent life stages. For three tributaries with contrasting thermal regimes, a bioenergetics model was used to evaluate how feeding rate and energy density of prey influenced seasonal growth and stage-specific survival of juvenile *O. mykiss*. Sensitivity analysis examined target levels for feeding rate and energy density of prey during the growing season that improved survival to the smolt and adult stages in each tributary. Simulated daily growth was greatest during warmer months (1 July to 30 September), whereas substantial body mass was lost during cooler months (1 December to 31 March). Incremental increases in annual feeding rate or energy density of prey during summer broadened the temperature range at which faster growth occurred and increased the growth of the average juvenile to match those that survived to smolt and adult stages. Survival to later life stages could be improved by increasing feeding rate or energy density of the diet during summer months, when warmer water temperatures accommodated increased growth potential. Higher growth during the summer period in each tributary could improve resiliency during subsequent colder periods that lead to metabolic stress and weight loss. As growth and corresponding survival rates in fresh water are altered by shifting abiotic regimes, it will be increasingly important for fisheries managers to better understand the mechanisms affecting growth limitations in rearing habitats and what measures might maintain or improve growth conditions and survival.

Key words: feeding; growth; prey energy; size-selective mortality; water temperature.

INTRODUCTION

Survival in fishes is often influenced by growth rate, as faster-growing individuals are less likely to succumb to size-selective mortality (SSM) (Sogard, 1997). In anadromous salmonids, mortality is high during freshwater rearing (Quinn, 2005; Kennedy *et al.*, 2008) and mortality in marine habitats may be related to size achieved during critical early growth periods (Ward *et al.*, 1989; Nislow *et al.*, 2000; Beamish & Mahnken, 2001; Melnychuck *et al.*, 2007; Duffy & Beauchamp, 2011).

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†Author to whom correspondence should be addressed. Tel.: +1 206 795 4214; email: jamie.thompson@noaa.gov

Metabolism and growth of juvenile salmonids is primarily affected by water temperature (McCullough *et al.*, 2009; Mantua *et al.*, 2010; Wenger *et al.*, 2011), food quality and quantity (Filbert & Hawkins, 1995; Jenkins & Keeley, 2010; Jonsson *et al.*, 2013) and feeding rate (Hughes & Dill, 1990; Hill & Grossman, 1993; Bradford & Higgins, 2001; Hayes *et al.*, 2007). Larger-bodied salmonids are more sensitive to these factors than smaller ones (Hanson *et al.*, 1997; Forseth *et al.*, 2001; Connolly & Petersen, 2003; Beauchamp, 2009); increasing the feeding rate or energy density of prey, however, can dramatically counteract temperature and size-mediated constraints on growth. Beauchamp (2009) used bioenergetics simulations for different sized salmonids to demonstrate how increased feeding rate or energy density of prey improved growth potential, expanded the temperature ranges supporting positive growth or reduced thermally induced mass loss. This analysis highlighted the need to increase understanding of how feeding rates, prey energies and water temperatures interact to affect growth across the mosaic of habitats that support different life stages of stream-rearing salmonids (Rosenfeld & Hatfield, 2006; Bellmore *et al.*, 2013; Weber *et al.*, 2014), and how such data could be used to potentially improve or maintain growth and survival of juvenile salmonids (Rosenfeld, 2003).

Steelhead *Oncorhynchus mykiss* (Walbaum 1792) commonly rear in riverine habitats for 2 or 3 years (Hard *et al.*, 2007), where feeding rate (Hill & Grossman, 1993; Kennedy *et al.*, 2008), water temperature and food sources fluctuate (Wipfli & Baxter, 2010; Benjamin *et al.*, 2013), influencing growth rates and survival over time and space (Schlosser, 1991; Rosenfeld *et al.*, 2005; McCarthy *et al.*, 2009). Juvenile salmonids that utilize habitats with more optimal growing conditions often show increased survival (Nislow *et al.*, 2000; Bond *et al.*, 2008; Kennedy *et al.*, 2008). Different habitats, however, could have unique consequences for growth and survival among different life stages (Rosenfeld & Hatfield, 2006). Furthermore, climate change is expected to alter hydrological, geomorphological and thermal regimes of river habitats, potentially affecting growth and survival of stream-rearing salmonids (Beechie *et al.*, 2006*a*).

In recent decades, *O. mykiss* in Puget Sound, Washington, U.S.A., have declined and were listed as threatened under the U.S. Endangered Species Act in 2007 (Rausch, 2007). Increased freshwater growth of juvenile *O. mykiss* improved survival to smolt and adult stages (Thompson & Beauchamp, 2014), thus prompting an examination of factors affecting growth during critical periods that influenced survival through subsequent life stages. For three tributaries with contrasting thermal regimes, a bioenergetics model was used to evaluate how feeding rate and energy density of prey influenced seasonal growth and stage-specific survival of juvenile *O. mykiss*. Sensitivity analysis examined target levels for feeding rate or energy density of prey during the growing season that improved survival to the smolt and adult stages in each tributary.

MATERIALS AND METHODS

STUDY AREA

The Skagit River basin (8544 km^2; Fig. 1) is the largest river basin in Puget Sound and supports regionally abundant populations of anadromous salmonids [Chinook *Oncorhynchus tshawytscha* (Walbaum 1792), coho *Oncorhynchus kisutch* (Walbaum 1792), chum *Oncorhynchus keta* (Walbaum 1792) and pink salmon *Oncorhynchus gorbuscha* (Walbaum 1792), *O. mykiss* and bull trout *Salvelinus confluentus* (Suckley 1859)]. Elevation and dominant

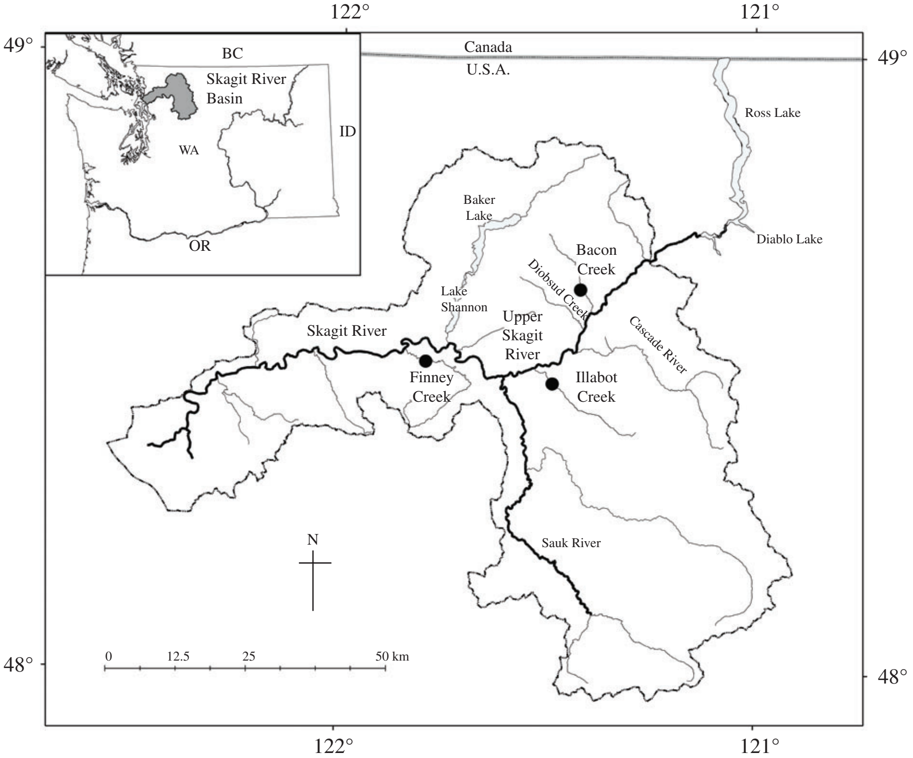

FIG. 1. Skagit River basin study area showing Bacon, Illabot and Finney Creeks where smolt trapping, temperature monitoring and seasonal electrofishing and macroinvertebrate drift sampling were conducted. Adult *Oncorhynchus mykiss* were captured in Finney Creek for direct comparisons with juvenile and smolt life-stage samples captured in Finney Creek. Adult *O. mykiss* could not be captured in Bacon and Illabot Creeks, so adults captured in the upper Skagit River main stem were used for comparisons with juvenile and smolt *O. mykiss* sampled in Bacon and Illabot Creeks. Water temperatures from Cascade River were used in place of Bacon Creek, and winter drift from Diobsud Creek was used in place of Bacon Creek for simulations. WA, Washington; ID, Idaho and OR, Oregon U.S.A.; BC, British Columbia, Canada.

precipitation type influence heterogeneity in habitat and hydrologic and water temperature regimes (Beechie, 1992), and could influence the importance of stream habitats for salmonids that rely on extended freshwater rearing, such as *O. mykiss* (Beechie *et al.*, 2006*a*; Lowery *et al.*, 2013). Timing and magnitude of peak annual stream discharge and associated thermal conditions differ among the snowmelt-dominated zone, the mixed rain and snow zone and the rain-dominated zone (hereafter referred to as rain, mixed or snow zones; Fig. 2). This study evaluated the relative influence of seasonal feeding behaviour, prey energy density and environmental factors on growth among two mixed zone tributaries with contrasting thermal regimes, Finney (elevation 61 m a.s.l.) and Illabot (103 m a.s.l.) Creeks and one snow zone tributary, Bacon Creek (160 m a.s.l.). These tributaries represented a diversity of habitats used by juvenile *O. mykiss* in the Skagit River basin (Kinsel *et al.*, 2013).

STUDY DESIGN

Annual bioenergetics model simulations were run for *O. mykiss* sampled as juveniles, smolts and adults (life-stage groups). Age 2 and 3 year juveniles and smolts, and adults that had smolted at age 2 or 3 years (Table I) were sampled in or adjacent to each tributary. Daily growth

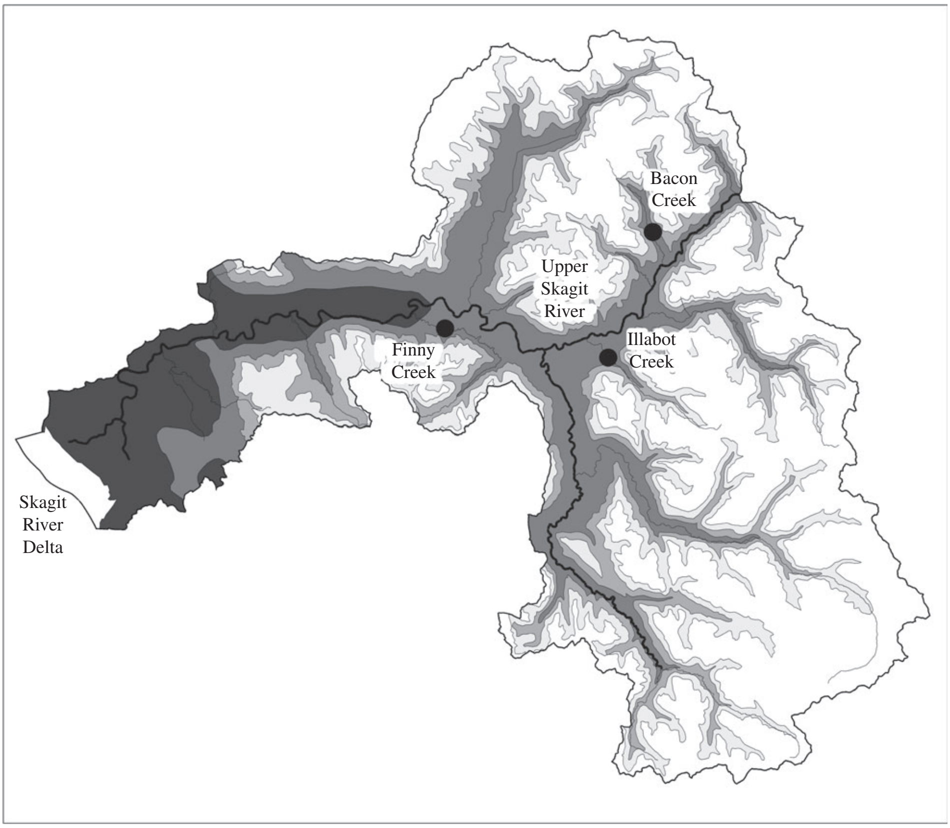

FIG. 2. The upper Skagit River main stem (〰) and (●) Bacon, Illabot and Finney Creeks shown relative to the distribution of precipitation zones (■ and ■, rain; ▨, rain–snow; □ and □, snow) in the Skagit River basin (Data source: Washington Department of Natural Resources; www.ecy.wa.gov/programs/wr/ws/wtrsuply.html).

($g\,g^{-1}\,day^{-1}$) during the second (annuli 1–2) and third (annuli 2–3) years of life was estimated for each life-stage group to quantify annual growth disparities among candidate smolt (juvenile group) and candidate adult (juvenile and smolt groups) *O. mykiss v.* those that actually survived to adulthood (adult group). Annual growth, daily temperature and seasonal energy density of prey in each tributary were used in a bioenergetics model to estimate the annual amount of prey consumed and annual feeding rates for each life-stage age group. These outputs were then compared among life-stage groups to determine how much additional prey would be required by the average juvenile to successfully reach the smolt or adult stages and by the average smolt to become an adult. Sensitivity analysis was then conducted on growth to determine to what degree increasing the feeding rate or energy density of prey during the growing season could improve growth and survival for a given thermal regime.

FISH SAMPLING

Juvenile *O. mykiss* were captured seasonally between August 2011 and May 2012 from stream margin transects up to 400 m long at each sample site using single-pass upstream backpack electrofishing (Smith Root; Model 12-B; 400–1000 V, standard pulse 80 Hz, 500 μs; www.smith-root.com) without block nets (Bateman *et al.*, 2005). Electrofishing practices

TABLE I. Sample size and mean ± S.E. fork length (L_F) of *Oncorhynchus mykiss* at time of capture by precipitation zone, sample site and age for the juvenile life-stage group sampled by electrofishing (summer 2011 to winter 2012), the smolt life-stage group sampled using smolt traps (January to June 2012, but primarily April to May 2012) and the adult life-stage group sampled by angling or in fishery nets as by-catch (2008 to 2012)

Precipitation zone	Sample site	Age (years)	Juvenile group		Smolt group		Adults*	
			n	L_F (mm)	*n*	L_F (mm)	*n*	L_F (mm)
Snow	Bacon Creek	2	4	147 ± 5	16	161 ± 3		
Snow	Bacon Creek	3			11	187 ± 3		
Mixed	Illabot Creek	2	5	138 ± 10	69	174 ± 2		
Mixed	Illabot Creek	3	3	176 ± 20	41	192 ± 2		
Mixed	Upper Skagit River†	2‡					12	773 ± 26
Mixed	Upper Skagit River†	3‡					17	726 ± 21
Mixed	Finney Creek	2	16	130 ± 3	15	162 ± 4	18	700 ± 23
Mixed	Finney Creek	3	10	168 ± 10	9	183 ± 5	8	630 ± 46

*Age at smolt and L_F at time of capture as adult.

†Adults captured in the upper Skagit River were used for bioenergetics simulations in Bacon and Illabot Creeks.

‡Age at smolting.

followed protocols prescribed by the Washington Department of Fish and Wildlife (WDFW; Temple & Pearsons, 2005) and all activities involving vertebrates conformed to the University of Washington Office of Animal Welfare IACUC protocol #3286-20. Captured salmonids were anaesthetized with buffered MS-222 and measured for fork length (L_F; to within 1 mm) and body mass (M; to within 0·1 g). Scale samples were removed from the preferred area above the lateral line between the dorsal and adipose fins (DeVries & Frie, 1996). *Oncorhynchus mykiss* are highly plastic with regard to their life-history trajectory and are capable of residing in fresh water (rainbow trout), or migrating to sea (steelhead; Kendall *et al.*, 2014). It is, therefore, possible that some juvenile *O. mykiss* sampled were not steelhead but were rainbow trout.

Oncorhynchus mykiss smolts were sampled at downstream migrant traps in Finney, Illabot and Bacon Creeks from February to June 2012, although most were sampled during peak seaward migration in April and May 2012. During trap operation, a sub-sample of smolts was measured (L_F) and scale samples were obtained from the preferred area.

Returning wild adult winter *O. mykiss* were sampled during 2008–2012 to provide a reference of juvenile growth trajectories that became adults (Pflug *et al.*, 2013). Adults sampled in the upper main stem Skagit River were used for growth analyses in Illabot and Bacon Creeks. The L_F for all adults was measured and scale samples were obtained from the preferred area.

BIOENERGETICS MODELLING

The Wisconsin bioenergetics model (Hanson *et al.*, 1997), with *O. mykiss* parameters from Rand *et al.* (1993), was used to fit consumption to annual growth of age 2 and 3 year *O. mykiss* for each life-stage group and tributary. Mean energy density of seasonal drift composition and daily water temperatures were used as model inputs to estimate total annual consumption (C, g) resulting from the net energy required to satisfy the estimated annual growth (G, g) and corresponding metabolism (Q) and waste (W) costs, $C = Q + W + G$. The equation estimated both C and feeding rate (% C_{max}, a proportion of the theoretical maximum C for a given body M and temperature) for each life-stage age group in each tributary. Additional simulations were run using initial body mass (M_i) from juvenile and smolt life stages with final year-end body mass (M_f) from smolt and adult life stages to determine the C or % C_{max} needed by the average juvenile or smolt to grow to the same size at annuli as was observed for individuals that survived

TABLE II. Prey energy densities by energy density category and taxa-life stage used in *Oncorhynchus mykiss* bioenergetics model simulations (energy density values from McCarthy *et al.*, 2009). Fifteen per cent of the blotted wet mass in each energy density group was considered indigestible for bioenergetics model simulations

Energy density category	Taxa life stage	Energy density ($J\,g^{-1}$)	Energy group	Mean energy density ($J\,g^{-1}$)
Low energy	Diptera larvae–nymph*	2911	Aquatic nymph and larvae	3072
Low energy	Trichoptera larvae†	3509	Aquatic nymph and larvae	3072
Low energy	Ephemeroptera nymph	3076	Aquatic nymph and larvae	3072
Low energy	Plecoptera nymph	3076	Aquatic nymph and larvae	3072
Low energy	Annelida	2789	Aquatic nymph and larvae	3072
Medium energy	Winged insect	4225	Aquatic adult and terrestrial larvae	4249
Medium energy	Terrestrial larvae	4272	Aquatic adult and terrestrial larvae	4249
High energy	Coleoptera adult	6387	Terrestrial adult	5761
High energy	Other terrestrial adult	5134	Terrestrial adult	5761

*Mean of larval and nymph stages.

†Mean of soft and rigid body forms.

to these later stages. Simulations spanned an annual growth period of 365 days between annuli 1 and 2, and 2 and 3. 1 April was selected as the starting date for model simulations because this represented the median date for annulus formation. Literature values for energy density ($J\,g^{-1}$) of consumer (Lowery & Beauchamp, 2015) and prey items (Table II; McCarthy *et al.*, 2009) were used. Seasonal prey energy densities for invertebrate drift in each tributary were used as the seasonal diet input under the assumption that drift samples represented the seasonal energy density of prey (Johnson, 2007; Johnson *et al.*, 2013). Macroinvertebrates were not sampled during spring, so winter drift energy density values were used as surrogates for spring energy density values in model simulations (Thompson *et al.*, 2011).

ANNUAL GROWTH

Annual freshwater growth was estimated using backcalculation of scale radius (R_S) to L_F (mm) at each freshwater annulus ($L_F = 144{\cdot}8\ R_S + 32$; $r^2 = 0{\cdot}89$; $P < 0{\cdot}001$; Thompson & Beauchamp, 2014). Because the bioenergetics model uses M instead of L_F to simulate growth, linear regression estimates of L_F at each annulus were converted to M using a regression between $\log_{10}$-transformed values for both L_F and M measured from *O. mykiss* sampled as juveniles in the Skagit River basin (range = 45–235 mm L_F; $n = 628$; $r^2 = 0{\cdot}99$; $P < 0{\cdot}001$): $M = L_F^{2{\cdot}94}\ 1{\cdot}52 \times 10^{-5}$. Mean M at annuli 1, 2 and 3 were used as M_i or M_f inputs for bioenergetics model simulations.

WATER TEMPERATURES

Mean daily water temperatures (° C) were estimated for each tributary and were used as the daily thermal input for bioenergetics models. Temperature data loggers (Onset Water Temperature Pro v2 Data Logger, U22-001; www.onsetcomp.com) were deployed in each tributary and water temperature was recorded continuously at 20 min intervals between 17 February and 31 July 2011 in Illabot Creek and between 1 July and 15 August 2011 in Finney Creek. Both of these loggers were lost during scour events prior to subsequent data downloads. Therefore, daily temperature for the remainder of the year at these sites was estimated using linear regression with complete annual daily water-temperature data collected from other tributaries in the

Skagit River basin that showed similar water-temperature regimes (Cassie, 2006). No data from the Bacon Creek logger were downloaded prior to losing the logger. Therefore, continuous water-temperature data were not available for Bacon Creek. Instead, mean daily water temperatures from the Cascade River (305 m a.s.l.), a nearby tributary within the snow zone of the upper Skagit River, were used as a surrogate for Bacon Creek.

DRIFT SAMPLING

Energy density of seasonal macroinvertebrate drift composition was used in model simulations as an approximation of seasonal energy content in 1 g of diet in each tributary (Weber *et al.*, 2014). A single drift net (150 μm mesh) was deployed along the stream margin at depths $\leq$0·50 m, upstream of an electrofishing sample transect in which juvenile life stages of *O. mykiss* were captured. The frame opening of the drift net was 50 cm wide, 25 cm high, 1 m long and the diameter of the codend was 10 cm. The lower 20 cm of cross-sectional area of the net opening was submerged to capture sub-surface prey while simultaneously sampling prey drifting on the surface. Deployment durations (min) were recorded and varied in proportion to the time required to process fish at each site (range = 76–167 min, mean ± S.D. = 103 ± 25 min.; Culp *et al.*, 1994). Captured macroinvertebrates were placed into vials and preserved in 95% ethanol diluted with water. Benthic macroinvertebrates were not sampled. Prohibitive access prevented drift sampling in Bacon Creek during winter, so drift from an adjacent, medium-sized tributary, Diobsud Creek (118 m a.s.l.), was used for winter *O. mykiss* diets in Bacon Creek.

Invertebrates smaller than 1 mm were removed from processing because juvenile salmonids feed on the larger size fractions (Filbert & Hawkins, 1995; Keeley & Grant, 2001). Remaining invertebrates were separated by order and life stage (larvae, pupae or adult) and taxa were grouped by energy density (Table II; McCarthy *et al.*, 2009). Seasonal prey composition was calculated as the proportional biomass of each energy density group by blotted wet mass (g) and was used as the seasonal diet input for bioenergetics model simulations. To estimate seasonal mean energy densities (J g^{-1}) in the macroinvertebrate drift sample for each site, blotted wet mass (g) of each energy density group was converted to total energy (J) and the summed amount of joules in each energy group was divided by the total wet mass (g) of the composite drift sample.

GROWTH SENSITIVITY ANALYSIS

Temperature-dependent growth curves (Beauchamp, 2009) were created for 10 g (age 2 years) and 30 g (age 3 years) *O. mykiss* feeding at the approximate rates observed during this study (20–30% C_{max}) to determine sensitivity of growth to energy density of prey and lower (20% C_{max}), average (25% C_{max}) and higher (30% C_{max}) feeding rates across a range of observed and potential temperatures in each tributary. A second sensitivity analysis was conducted to test how increasing summer prey energy density from the nominal values of 3276–4308 to 5000 J g^{-1} could improve growth potential while continuing to feed at observed rates (McCarthy *et al.*, 2009).

RESULTS

BIOENERGETICS MODEL SIMULATIONS

Based on simulated growth trajectories, mean monthly growth was greatest during July to October (for all life-stage groups and sites), accounting for 80% of the growth between annuli 1 and 2 and 82% of growth between annuli 2 and 3. Substantial body mass was lost during December to March, especially in Illabot and Finney Creeks (mean of all life-stage groups and sites: −11% of growth between annuli 1 and 2 and −17% of growth between annuli 2 and 3; Fig. 3). Growth trajectories in the adult group were consistently higher than in the smolt and juvenile groups.

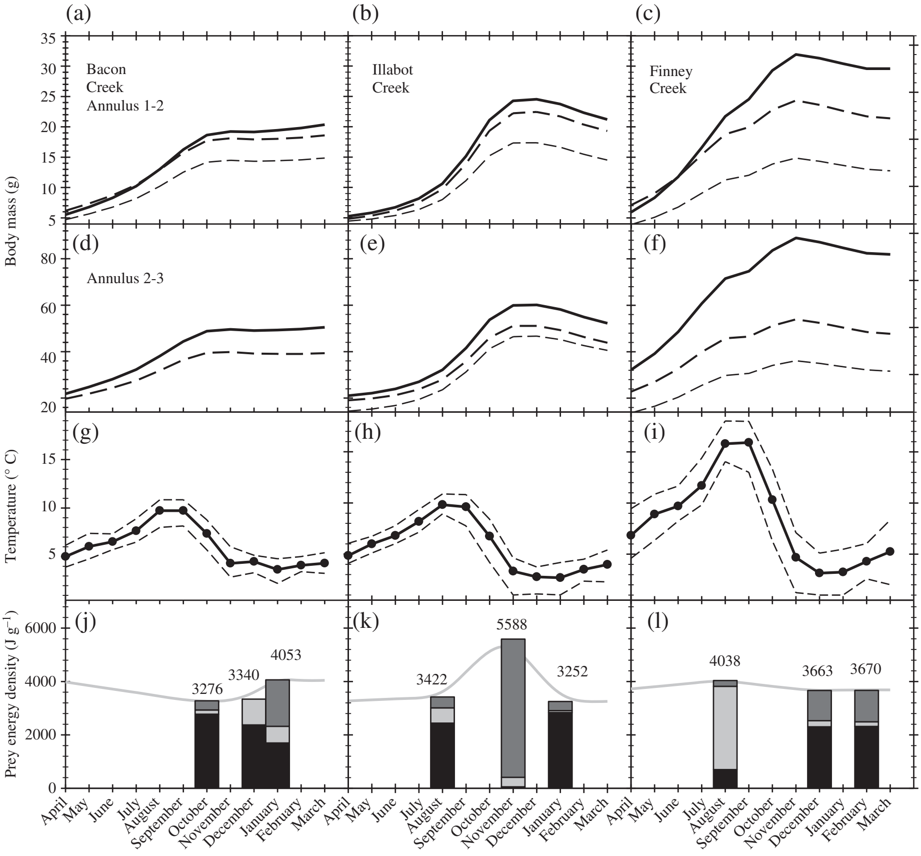

FIG. 3. Simulated growth trajectories for annuli (a–c) 1–2 and (d–f) 2–3 *Oncorhynchus mykiss* rearing in (a, d, g, j), Bacon, (b, e, h, k) Illabot and (c, f, i, l) Finney Creeks. Different lines demonstrate disparity in annual growth among (- - - -) juvenile, (— —) smolt and (——) adult life-stage groups. Feeding rate (see Table III), monthly water temperatures (g, h, i; ●, mean, ..., minimum and maximum), and seasonal energy density of drifting (■, low energy; ▨, high energy; □, medium energy) or simulated daily (——) macroinvertebrate prey influenced the shape and magnitude of growth trajectories.

Among tributaries and growth periods (annuli 1–2 and 2–3), annual C and % C_{max} by the juvenile and smolt groups were invariably less than or equal to the rates estimated for the same life stages from the adult group (Table III). In Illabot Creek, feeding rates for juveniles and adults were higher than in the smolt group between annuli 2 and 3. Annual growth (G) in the juvenile and smolt groups was generally lower than for the same life stages of the adult group; however, in Illabot Creek, G in juveniles and adults was higher than the smolt group between annuli 2 and 3 (Table III and Fig. 3).

Estimates of G and C varied among life-stage groups and tributaries, but seemingly small increases in annual feeding rates by juvenile and smolt groups led to substantial increases in C and G such that they attained the size at annulus 2 observed in smolt and adult groups (Table III). To reach the observed size of an average smolt, the juvenile

TABLE III. Bioenergetics simulation inputs [$G = M_f - M_i$, where G is growth (g) between annuli, M_f is final mass and M_i is initial mass] and outputs (feeding rate, % C_{max}, and consumption, C, between each annulus) for simulations conducted on *Oncorhynchus mykiss* captured at different life stages. Simulations estimated consumption during the freshwater period for each life-stage sample group based on growth observed between annuli 1 and 2, and annuli 2 and 3, seasonal energy density of the diet (based on macroinvertebrate drift composition) and daily thermal experience

Precipitation zone	Sample site	Growth period	Life-stage sample group	*n*	M_i (g)	M_f (g)	% C_{max}	*C* (g)	*G* (g)
Snow	Bacon Creek	Annuli 1–2	Juvenile	4	4·4	15·2	0·23	113·2	10·8
Snow	Bacon Creek	Annuli 1–2	Smolt	27	5·8	19·0	0·24	137·7	13·2
Mixed	Upper Skagit River	Annuli 1–2	Adult*	29	5·1	20·9	0·25	146·0	15·8
Snow	Bacon Creek	Annuli 2–3	Juvenile	0	–	–	–	–	–
Snow	Bacon Creek	Annuli 2–3	Smolt	11	19·0	39·9	0·25	272·1	20·9
Mixed	Upper Skagit River	Annuli 2–3	Adult*	17	20·9	51·4	0·27	333·3	30·5
Mixed	Illabot Creek	Annuli 1–2	Juvenile	8	4·4	14·2	0·22	96·6	9·8
Mixed	Illabot Creek	Annuli 1–2	Smolt	110	4·7	19·0	0·24	120·9	14·3
Mixed	Upper Skagit River	Annuli 1–2	Adult*	29	5·1	20·9	0·24	131·0	15·8
Mixed	Illabot Creek	Annuli 2–3	Juvenile	3	14·2	39·9	0·26	237·5	25·7
Mixed	Illabot Creek	Annuli 2–3	Smolt	41	19·0	43·0	0·25	258·8	24·0
Mixed	Upper Skagit River	Annuli 2–3	Adult*	17	20·9	51·4	0·26	299·4	30·5
Mixed	Finney Creek	Annuli 1–2	Juvenile	26	3·6	13·0	0·20	127·5	9·4
Mixed	Finney Creek	Annuli 1–2	Smolt	24	6·6	21·8	0·22	199·0	15·2
Mixed	Finney Creek	Annuli 1–2	Adult	26	5·3	30·4	0·24	247·3	25·1
Mixed	Finney Creek	Annuli 2–3	Juvenile	10	13·0	32·1	0·23	286·5	19·1
Mixed	Finney Creek	Annuli 2–3	Smolt	9	21·8	48·4	0·24	411·9	26·6
Mixed	Finney Creek	Annuli 2–3	Adult	8	30·4	83·5	0·28	641·0	53·1

n, Number of samples.

*Adults captured in the upper Skagit River main stem were used for bioenergetics simulations in Bacon and Illabot Creeks.

group required an additional 3·8–8·8 g of growth above their observed average between annuli 1 and 2, representing an increase of 1–3% C_{max} and 20·6–57·8 g of prey. To reach the adult life stage, the juvenile group required an additional 5·7–17·4 g of growth between annuli 1 and 2, an increase of 2–5% C_{max} and 30·6–110·3 g of prey. To reach the adult life stage, the smolt group required an additional 1·9–8·6 g of growth between annuli 1 and 2, an increase of 0–2% C_{max} and 9·0–54·4 g of prey.

Age 3 year juvenile *O. mykiss* were not captured in Bacon Creek; therefore, *G* and *C* estimates were not available between annuli 2 and 3 for this group (Table III). In Illabot Creek, *G* between annuli 2 and 3 in the juvenile group was 1·7 g greater than that of the smolt group. While overall *G* was greater in the juvenile group, the body mass attained at annulus 3 was still 3·1 g less than the smolt group. Although feeding rate was 1% point higher in the juvenile group than the smolt group, the juvenile group required an additional 14·0 g of prey to attain the size at annulus 3 observed in the smolt group. In Finney Creek, the juvenile group required an additional 16·3 g of growth between annuli 2 and 3 to reach the smolt stage, an increase of 3% C_{max} and 100·0 g of prey. In Illabot and Finney Creeks, the juvenile group required an additional 11·5–51·4 g of growth to reach the adult stage, an increase of 2–7% C_{max} and 51·3–298·2 g of prey. For all tributaries, to reach the adult stage, the smolt group

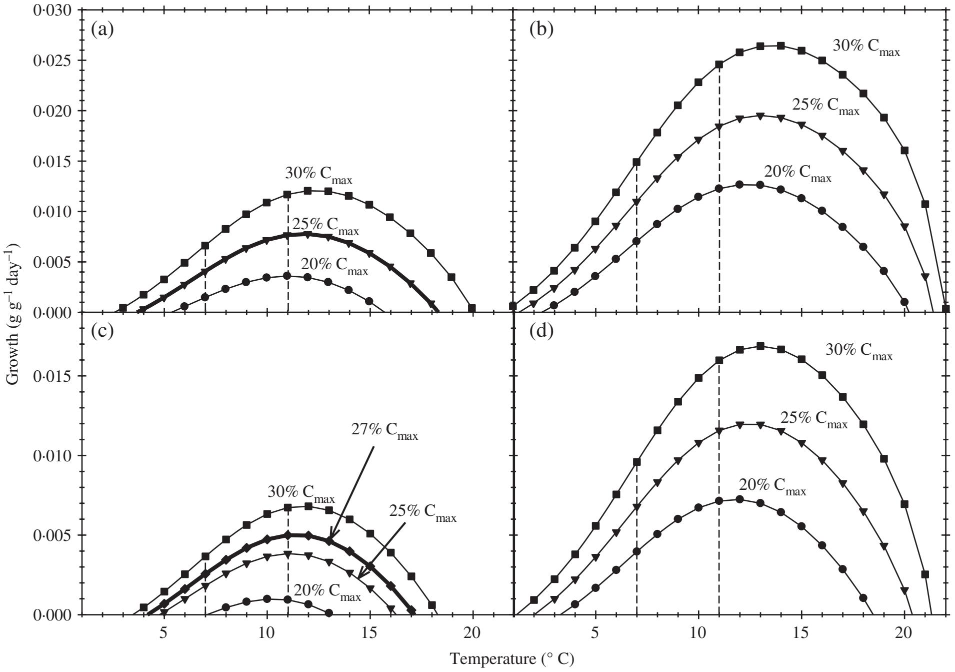

FIG. 4. Changes in daily growth rate in response to temperature and feeding rate for (a, b) 10 g (age 1 year) and (c, d) 30 g (age 2 years) *Oncorhynchus mykiss* in Bacon Creek feeding on a composite diet with (a, c) a mean energy density of 3276 J g^{-1} wet mass and (b, d) increased to 5000 J g^{-1}. —●—, 20% C_{max}; —▼—, 25% C_{max}; —■—, 30% C_{max}. The portion of each curve between ¦ indicates the thermal experience for *O. mykiss* during summer in Bacon Creek (7–11° C). —◆—, Scope for growth in the adult *O. mykiss* life-stage group over a range of temperatures given the observed summer prey energy density of 3276 J g^{-1}, and simulated annual feeding rates of (a) 25% (age 1 year) and (c) 27% (age 2 years) C_{max}.

required an additional 8·4–35·1 g of growth between annuli 2 and 3, an increase of 2–4% C_{max} and 37·9–205·2 g of prey.

GROWTH SENSITIVITY ANALYSIS

Growth potential (g g^{-1} day^{-1}) was greatest during summer temperatures (1 July to 30 September; range = 7–18° C) and varied among tributaries, but in all cases could have been improved by increasing the feeding rate or energy density of prey (Fig. 3). In Bacon Creek, increasing prey energy density during summer from 3276 to 5000 J g^{-1} more than doubled daily growth for both age 1 and 2 year *O. mykiss* among a range of feeding rates observed during this study (Fig. 4 and Table IV). In Illabot Creek, increasing prey energy density during summer from 3422 to 5000 J g^{-1} also more than doubled daily growth for both age 1 and 2 year *O. mykiss* among the range of observed feeding rates (Fig. 5 and Table IV). In Finney Creek, increasing prey energy density during summer from 4038 to 5000 J g^{-1} nearly doubled daily growth for age 1 and 2 year *O. mykiss* among the range of observed feeding rates (Fig. 6 and Table IV). In every case, increasing summer energy density of prey to 5000 J g^{-1} would have enabled

TABLE IV. Mean daily growth of juvenile *Oncorhynchus mykiss* during summer at different feeding rates (% C_{max}) and prey energy densities in three tributaries with contrasting water temperatures and prey sources. Energy density of prey was increased from observed drift sample values in Bacon (3276 J g^{-1}), Illabot (3422 J g^{-1}), and Finney (4308 J g^{-1}) Creeks to 5000 J g^{-1} (bold)

Creek sample site	Growth period	Summer energy density of prey (J g^{-1})	Mean daily growth (g g^{-1} day^{-1})		
			20% C_{max}	25% C_{max}	30% C_{max}
Bacon	Annuli 1–2	3276	0·003	0·006	0·009
Bacon	Annuli 1–2	**5000**	**0·010**	**0·015**	**0·020**
Bacon	Annuli 2–3	3276	0·001	0·003	0·005
Bacon	Annuli 2–3	**5000**	**0·006**	**0·009**	**0·013**
Illabot	Annuli 1–2	3422	0·003	0·007	0·010
Illabot	Annuli 1–2	**5000**	**0·010**	**0·015**	**0·020**
Illabot	Annuli 2–3	3422	0·001	0·004	0·006
Illabot	Annuli 2–3	**5000**	**0·006**	**0·009**	**0·013**
Finney	Annuli 1–2	4308	0·005	0·011	0·017
Finney	Annuli 1–2	**5000**	**0·011**	**0·018**	**0·025**
Finney	Annuli 2–3	4308	0·002	0·006	0·010
Finney	Annuli 2–3	**5000**	**0·005**	**0·010**	**0·015**

the average age 1 or 2 year juvenile *O. mykiss* to meet or exceed daily summer growth observed in the adult life-stage group, even while feeding at rates of 20% C_{max} or lower.

DISCUSSION

Feeding behaviour and environmental conditions uniquely affected growth across a range of stream habitats used by juvenile *O. mykiss* experiencing SSM in the Skagit River basin, but some basic patterns in growth potential among tributaries were evident from bioenergetics simulations. Water temperature regimes set the ultimate limits on growth potential in each tributary. Relatively warm temperatures during summer months accommodated faster growth, even when energy density of prey was low. Colder water temperatures limited growth during autumn and winter months, even when energy density of prey was high. However, elevated seasonal prey energy density appeared to buffer growth during prolonged, extremely cold fall and winter periods. Thus, while the present results indicated that general patterns in growth responses existed among the different tributaries, it is also apparent that the seasonality, timing and magnitude of available energy, within the constraints of the thermal regime, could cause significant variability in growth and survival of rearing salmonids over time and space.

Survival of *O. mykiss* to later life stages could be improved by increasing feeding rate or energy density of the diet during summer months, when warmer water temperatures accommodated increased growth potential. Fast growth during such periods could improve resiliency during subsequent periods of metabolic stress and mass loss (Biro

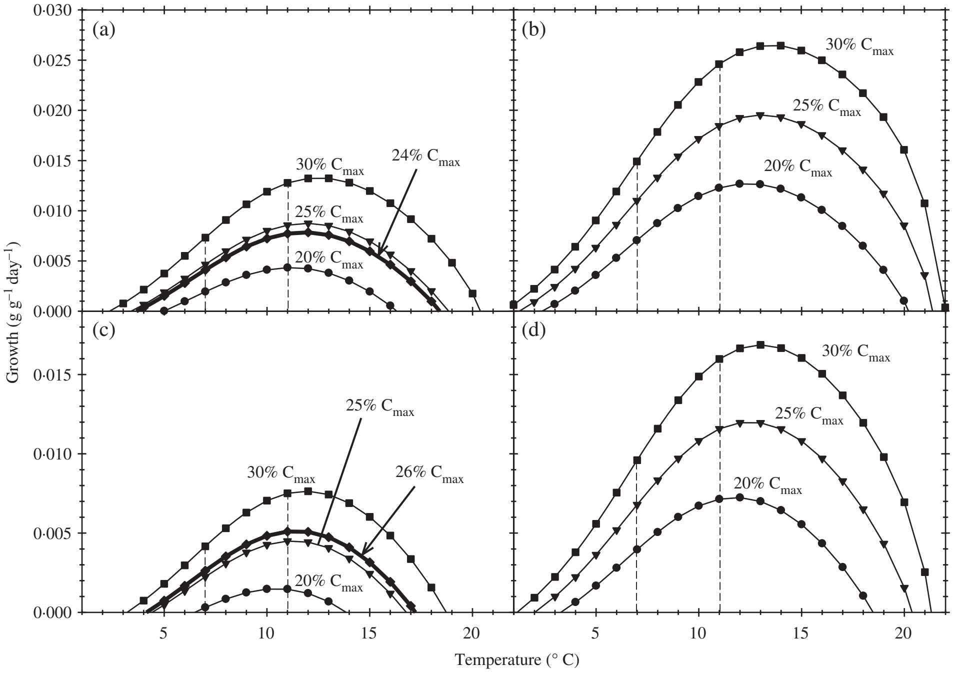

FIG. 5. Changes in daily growth rate in response to temperature and feeding rate for (a, b) 10 g (age 1 year) and (c, d) 30 g (age 2 years) *Oncorhynchus mykiss* in Illabot Creek feeding on a composite diet with (a, c) a mean energy density of 3422 J g^{-1} wet mass, and (b, d) increased to 5000 J g^{-1}. —●—, 20% C_{max}; —▼—, 25% C_{max}; —■—, 30% C_{max}. The portion of each curve between ¦ indicates the thermal experience for *O. mykiss* during summer in Illabot Creek (7–11° C). —◆—, Scope for growth in the adult *O. mykiss* life-stage group over a range of temperatures given the observed summer prey energy density of 3422 J g^{-1}, and simulated annual feeding rates of (a) 24% (age 1 year) and (c) 26% (age 2 years) C_{max}.

et al., 2004). Results of this study link the effects of freshwater environmental conditions on growth to survival in both freshwater and marine environments (Thompson & Beauchamp, 2014). This diagnostic approach could be useful in broader applications for identifying limiting factors for salmonids or other anadromous fishes where SSM at one or more stages in the life cycle are affected by growth rates established during early stages.

This study improved the understanding of how incremental changes in feeding behaviour and energy density of prey can fundamentally shift *in situ* growth responses and thermal tolerances of juvenile salmonids across different stream habitats. Such information could be useful in identifying goals for enhancement of feeding conditions (Imre *et al.*, 2004) and prey energy density (Allan *et al.*, 2003). For example, increases in terrestrial prey inputs could improve growth (Leung *et al.*, 2009), especially if coincident with temperatures that accommodate faster growth. Availability of terrestrial prey to salmonids is related to habitat location, interconnectivity (Polis *et al.*, 1997; Kawaguchi *et al.*, 2002) and selection (Giller & Greenberg, 2015). It is important to consider that potential benefits of increasing energy density of prey could be compromised if foraging habitat is impaired (Bradford & Higgins, 2001; Keeley, 2001), density or competition are increased (Millidine *et al.*, 2009), or predator

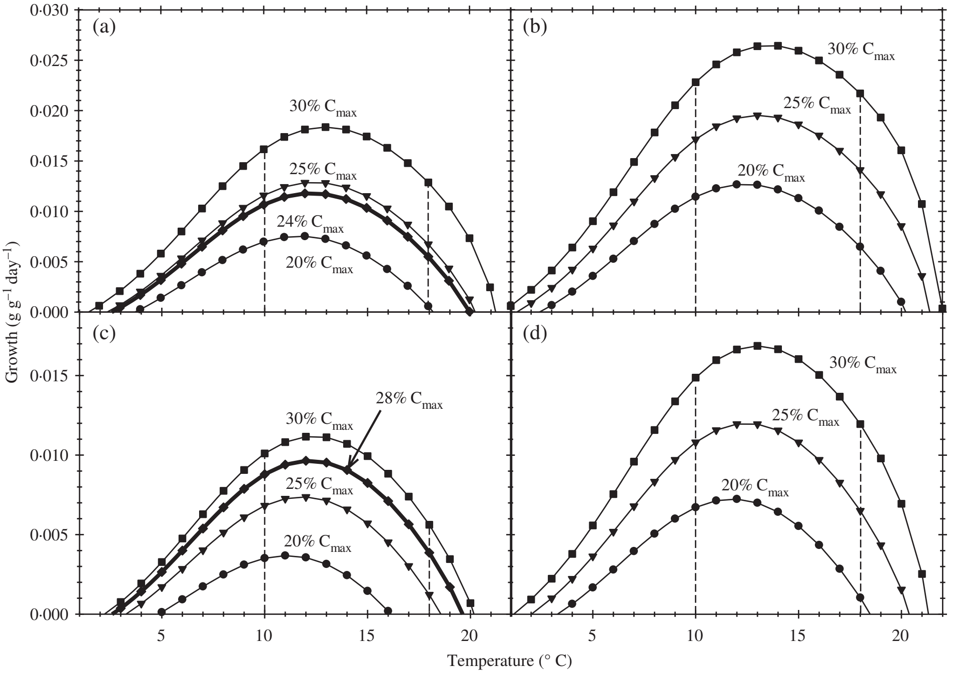

Fig. 6. Changes in daily growth rate in response to temperature and feeding rate for (a, b) 10 g (age 1 year) and (c, d) 30 g (age 2 years) *Oncorhynchus mykiss* in Finney Creek feeding on a composite diet with (a, c) a mean energy density of 4038 J g^{-1} wet mass, and (b, d) increased to 5000 J g^{-1}. —●—, 20% C_{max}; —▼—, 25% C_{max}; —■—, 30% C_{max}. The portion of each curve between ¦ indicates the thermal experience for *O. mykiss* during summer in Finney Creek (10–18° C). —◆—, Scope for growth in the adult *O. mykiss* life-stage group over a range of temperatures given the observed summer prey energy density of 4038 J g^{-1}, and simulated annual feeding rates of (a) 24% (age 1 year) and (c) 28% (age 2 years) C_{max}.

presence negatively affects feeding behavior or survival (Boss & Richardson, 2002; Biro *et al.*, 2004; Stamps, 2007; Lowery and Beauchamp, 2015). These scenarios emphasize the need to design catchment-process restoration programmes that account for whole-ecosystem habitat functionality (Beechie *et al.*, 2010), as solely improving growth potential for one habitat or one life stage will not necessarily lead to the recovery of populations.

Water temperature was identified as an important limiting factor on growth. Climate change will presumably alter upland hydrological processes that drive water-temperature regimes, thus increasing understanding of how water-temperature regimes affect aquatic ecosystems has become increasingly important (McCullough *et al.*, 2009; Olden & Naiman, 2010; Ruesch *et al.*, 2012). Changing water-temperature regimes will presumably have deleterious effects on some species or life stages of stream-rearing anadromous salmonids (Battin *et al.*, 2007), a presumption that has in part driven efforts to restore historical temperature regimes and improve in-stream refuge (Nichols & Ketcheson, 2013). The present analytical approach confirmed that water-temperature monitoring will continue to be useful for diagnosing which factors limit growth of rearing salmonids and how those factors could be addressed (Beer & Anderson, 2011; Wenger *et al.*, 2011).

Variability in growth potential could be tangentially related to precipitation zone (Hershey & Lamberti, 1998; Beechie *et al.*, 2010), but factors such as resource subsidies (Wilson *et al.*, 2014), water chemistry, discharge regime, riparian vegetation, land use and lithology also influence growing conditions (Welch *et al.*, 1998; Nakano *et al.*, 1999; Nakano & Murakami, 2001). These factors can vary widely within precipitation zones or tributaries (Ebersole *et al.*, 2003; McCarthy *et al.*, 2009). An improved stratification scheme for further study might delineate sample locations by channel type (braided, meander and confined; Beechie *et al.*, 2006*b*), water-temperature regime, prey energy density and habitat condition. To test this presumption, additional life-stage specific growth, invertebrate drift and water-temperature data are needed among additional sites in each precipitation zone.

Implications of this study could change if apparent SSM of *O. mykiss* resulted from selection of an alternate life history by *O. mykiss* (resident form). A significant resident component of *O. mykiss* inhabits the anadromous zone in the Skagit River basin (Pflug *et al.*, 2013). Thus, it is not certain that all juvenile life-stage samples in this study represent only the steelhead *O. mykiss* form. Ancillary data, however, indicated slower growth in the resident form of Skagit River basin *O. mykiss* (Thompson & Beauchamp, 2014). Life-history strategy in *O. mykiss* can be highly plastic throughout the life cycle (Quinn & Myers, 2004) and could be related to growth rate, where faster-growing individuals may be more likely to emigrate to sea at an earlier age and slower-growing individuals emigrate later (Forseth *et al.*, 1999) or may not emigrate at all (Metcalfe *et al.*, 1988; McCarthy, 2000). Conversely, while Battin *et al.* (2007) predicted that climate change could increase water temperatures in higher elevation drainages of Puget Sound (improving growth conditions), Benjamin *et al.* (2013) found that improved freshwater growth reduced anadromy of *O. mykiss* in a Columbia River basin stream (an inland catchment). Additional growth samples are needed to conclude whether growth segregation occurs across life-history forms of *O. mykiss* in the Skagit River basin (*sensu* Morita *et al.*, 2014).

Several assumptions were made in regard to bioenergetics model inputs. First, annual growth of life-stage groups was pooled among brood years (adult group 2005–2009; smolt group 2008–2010; juvenile group 2006–2010), so it was assumed that growth conditions among years were similar in each tributary. Growth conditions could have varied markedly among these years; however, L_F at annuli 1 and 2 were normally distributed, indicating normal variability in growth among brood years (Thompson & Beauchamp, 2014).

Second, it was assumed that macro-invertebrate drift samples represented the energy density of *O. mykiss* diets. Johnson (2007), Bellmore *et al.* (2013) and Johnson *et al.* (2013) indicated that juvenile *O. mykiss* diets varied somewhat in proportion to prey availability and invertebrate productivity and feeding by salmonids varies by time of day (Metcalfe *et al.*, 1997) and stream discharge (Nakano *et al.*, 1999). Ideally, drift is collected using replicate drift nets per site, during different day–night crepuscular periods and diet is collected concurrently from a sub-set of individual fish for use as inputs for the bioenergetics model (McCarthy *et al.*, 2009). Furthermore, in the absence of winter drift data from Bacon Creek, drift data collected in Diobsud Creek were used as a surrogate during winter due to its proximity to Bacon Creek and similarity in basin area and headwater source. Similarity in energy density of drifting prey between Bacon and Diobsud Creeks was not verified, thus significant differences could shift the results and implications. For example, if mean seasonal energy density is actually different from the samples collected here, more or less size-selective pressure could be exerted during different seasons. Furthermore, marine-derived food items, such as salmonid eggs and carcasses, contain far greater energy densities than invertebrates and represent important food items that could be consumed by faster growing juvenile *O. mykiss* (Armstrong *et al.*, 2010; Bentley *et al.*, 2012). In this study, spawning salmon were avoided, so drifting eggs, carcass and juveniles that may have been feeding on them were not sampled.

Third, in the absence of continuous temperature data, surrogate, or regression-based data from nearby tributaries were used. Regression-based water-temperature models are routinely used to estimate water-temperature regimes in the absence of continuous site-specific data (Cassie, 2006). Improved spatio-temporal coverage of temperature data, however, would verify estimated temperature results. Finally, growth of each life-stage group was assumed to reflect growth within the sampled tributary. Fish could have moved among sub-basins, but it is reasonable to assume that fish originated in streams in which they were captured because size frequencies within each tributary indicated that fish from each life-stage group grew to each annulus at reasonably similar rates (Thompson & Beauchamp, 2014).

Quantity and functionality of habitat influences feeding behaviour, growth (Keeley, 2001, 2003) and survival of salmonids (Nislow *et al.*, 2000). Habitat-specific bioenergetics models (Rosenfeld & Boss, 2001) have been used to identify bottlenecks in juvenile salmonid populations (Kennedy *et al.*, 2008). This study verified that habitat- and life-stage-specific bioenergetics models could be useful tools to quantify how improvements in growth conditions could increase survival. As growth and corresponding survival rates in fresh water are altered by shifting abiotic regimes, it will be increasingly important for fisheries managers to better understand the mechanisms affecting growth limitations in rearing habitats and what measures might maintain or improve growth conditions and survival.

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