Juvenile coho salmon track a seasonally shifting thermal mosaic across a river floodplain

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SUMMARY

1. Seasonal variation in river water levels creates a shifting mosaic of habitat conditions associated with variables such as water temperature, chemistry and prey availability to consumers. Previous work has shown that fishes can exploit spatial variation in water temperature, but less is known about how they respond to shifts in the spatial arrangement of habitat conditions through time.
2. Juvenile coho salmon (*Oncorhynchus kisutch*) are the numerically dominant fish species in many southwest Alaskan streams, which exhibit seasonal variation in water level and temperature due to changes in precipitation and snowmelt. We assessed the degree to which juvenile coho salmon exploit the associated shifting mosaic of water temperature by monitoring the spatial distribution of water temperatures and juvenile coho salmon in the lake-influenced reaches of a southwest Alaskan stream. We also monitored the diets of juvenile coho salmon relative to the spatial distribution of prey taxa.
3. Juvenile coho salmon exhibited two scales of movement to track spatiotemporal variation in habitat conditions. First, over the course of 6 weeks, individuals moved among off-channel units, tracking shifts in the location of warm water habitat caused by receding water level. Second, individuals moved at diel time scales, foraging on benthic macroinvertebrates in the cold thalweg of the stream at night and then digesting prey in warmer off-channel habitats during the day.
4. Seasonally asynchronous variation in water temperature among off-channel habitat units produced portfolio effects in habitat conditions, such that coho salmon had continual access to warm habitat for digestion despite its ephemeral availability at discrete locations.
5. Our study demonstrates that behavioural thermoregulation by juvenile fishes can be important throughout the growing season and is not restricted to ephemeral events such as resource pulses or heat stress. Our results have implications for the conservation of highly connected, heterogeneous landscapes, and their ability to support economically and ecologically important species such as coho salmon.

Keywords: diel horizontal migration, shifting habitat mosaic, spatiotemporal variability, stream, thermal habitat, water temperature

Introduction

Freshwater ecosystems exhibit tremendous spatial variation in the abiotic and biotic conditions that support ecologically and economically valuable fish and wildlife. Processes such as weathering, erosion and water flows alter the spatial configuration of habitat conditions, generating a 'shifting habitat mosaic' across river floodplains (Stanford, Lorang & Hauer, 2005). Spatial and temporal scales of habitat distributions depend on the underlying physical mechanisms that generate physical heterogeneity in ecosystems. Glaciation alters the structure of entire stream networks and nested micohabitats as recently glaciated areas develop predictably along

centennial to millennial time scales (Sidle & Milner, 1989). High-magnitude floods occurring on annual to supra-annual time scales can completely reorganise the physical structure of floodplains (Tockner, Malard & Ward, 2000; Stanford *et al.*, 2005). However, on shorter time scales, seasonal fluctuations in water level interact with topography to expand and contract the main channel (i.e. thalweg), floodplain (i.e. off-channel) habitat and the physical connections between these habitat types (Mertes *et al.*, 1995; Malard, Tockner & Ward, 2000; Tockner *et al.*, 2000). How organisms exploit shifting habitat mosaics – especially on fine spatial and temporal scales – remain poorly understood and represents a key knowledge gap in developing habitat conservation strategies and habitat restoration goals for floodplain rivers.

Mobile organisms often exploit complementary habitats across river basins throughout their lives. At relatively long time scales, habitat shifts are associated with ontogenetic transitions: inundated floodplains serve as important spawning and nursery habitats for fish that spend most of their lives in the main stem of large rivers (Welcomme, 1985; Junk, Bayley & Sparks, 1989; King, 2004). On finer time scales, mobile organisms exploit spatial contrasts in environmental conditions through cyclic habitat use, such as diel horizontal migration (DHM). For example, sub-adult bull trout (*Salvelinus confluentus*) moved between deep pools and channel margins in response to changes in light intensity, presumably for feeding purposes (Muhlfeld *et al.*, 2003). Five fish species made spawning-related movements between the main stem of a river and its backwater in response to changes in water level, temperature and light (Hohausova, Copp & Jankovsky, 2003). While our ability to measure habitat variables across space and time is rapidly improving (Caissie, 2006; Bonar & Petre, 2015), our understanding of how interhabitat fish movements track changes in habitat conditions is limited.

Armstrong *et al.* (2013) showed that juvenile coho salmon (*Oncorhynchus kisutch*) exhibit DHM behaviour to exploit spatial heterogeneity in water temperature and trophic resource subsidies – gorging on eggs in cold water where sockeye salmon (*O. nerka*) spawn and then moving upstream to warmer areas to digest their unusually large meals. However, over a 5-year period during which mean stream flows varied more than 5-fold, the spatial patterning of water temperature shifted. Under low-flow conditions, juvenile coho salmon performed DHM along the longitudinal axis of streams by feeding on high-quality salmon eggs in cold water and then migrating upstream to digest in warm headwater

reaches. Under high-flow conditions when longitudinal variation in temperature was eliminated, coho salmon moved into off-channel habitats to access warm digestive habitat that was not available during low-water conditions. Thus, juvenile coho salmon adjusted their DHM behaviour to continually access warm patches of habitat in the face of interannual variation in the spatial patterning of water temperature (Armstrong & Schindler, 2013). One question that remains is whether fish can track mosaics of temperature that shift at finer time scales, such as within a single season. Stream water levels exhibit large fluctuations during the early portion of the growing season in Alaska, yet little is known about how fish track thermal heterogeneity across river floodplains during this energetically critical period.

The high-quality resource pulse provided by spawning sockeye salmon in streams is highly ephemeral compared to the length of the growing season for juvenile coho salmon. In the Wood River system of southwest Alaska, the period over which trophic subsidies are available to consumers may be less than 3 weeks within a single stream (Schindler *et al.*, 2010), <1/4 of the growing season (June–Sept.). The ability of juvenile coho salmon to exploit the short, high-latitude growing season is likely critical as juvenile body size is generally positively correlated with smolt-to-adult survival in coho (Holtby, Andersen & Kadowski, 1990) and other Pacific salmon species (e.g. Henderson & Cass, 1991; Koenings, Geiger & Hasbrouck, 1993). Feeding on stream invertebrates in the early summer before the arrival of marine-derived subsidies from spawning salmon likely provides the resources coho salmon the need to rebuild depleted energy stores and grow large enough to exceed the size threshold for consuming salmon eggs (~70 mm fork length; Armstrong *et al.*, 2010).

During the early growing season, stream water temperatures may be quite cold, as stream thermal regimes are dominated by snowmelt and backwash from downstream lakes. Whether juvenile coho salmon exploit spatiotemporal variation in water temperature and *in situ* trophic resources is not understood. We quantified how juvenile coho salmon interact with spatial and temporal heterogeneity in water temperature and *in situ* prey resources during the early portion of the high-latitude growing season of a small floodplain river. We (i) mapped the shifting mosaic of water temperatures available to juvenile coho salmon during June and July, (ii) characterised the benthic invertebrate prey community available across this mosaic, and (iii) monitored the spatial distribution and foraging behaviour of coho salmon in response to seasonal shifts in the patterning of

thermal and trophic resources across the flood plain as water levels changed.

Methods

Study system

This study was conducted on the delta of Bear Creek, a 4-km-long, third-order tributary stream that drains into Lake Aleknagik, one of five interconnected lakes in the Wood River watershed, southwest Alaska, U.S.A. (59°17′44.14″N 158°46′38.30″W, WGS84). In addition to the thalweg, Bear Creek exhibits extensive off-channel habitat, primarily as a para- and orthofluvial-ground-water-spring network across the floodplain. Stream width ranges from 4 to 12 m in the lower 1 km, with maximum pool depth from 30 to >100 cm throughout the system. Summer discharge ranges from approximately 0.2 m³ s⁻¹ at base flows to >3 m³ s⁻¹ following major rain events. The thalweg of Bear Creek exhibits thermal variability driven by two large groundwater springs located 1360 and 1670 m upstream of the stream mouth; thalweg water temperature downstream of these springs is relatively cold and spatially homogeneous (Armstrong *et al.*, 2013).

In the early summer when basin-wide runoff due to peak snowmelt is greatest, high lake conditions flood the lower ~300 m Bear Creek, significantly increasing off-channel habitat availability and connectivity to the thalweg. As lake level recedes, these off-channel units contract and become isolated from the main channel, or eventually desiccate. However, due to variation in the physical structure and topography of the floodplain, some habitats persist longer than others. Along both longitudinal (up and down the length thalweg) and lateral (between off-channel and thalweg habitats) gradients, stream flow, backwash from the lake, and groundwater input mix to varying degrees, generating spatial variation in water temperature among off-channel habitat units. As the relative contribution of these water sources changes due to receding lake level, changes in precipitation patterns and reduced magnitude of runoff from snowmelt, the spatial patterning of water temperature shifts. While warm microhabitat exists at the margins of many stagnant off-channel areas, three distinct habitat features within range of lake influence provide much larger areas (up to ~50 m²) of warm water habitat when inundated (Fig. 1). Unit A is a parafluvial-groundwater spring channel located 145 m upstream of the mouth. Units B and C are located 196 m and 51 m upstream, respectively, and exhibit soft sediment bottoms with

Fig. 1 Aerial view of the lake-influenced reaches (lower 300 m) of Bear Creek, Lake Aleknagik, Alaska, U.S.A. Off-channel units a, b and c labelled and shown in detail at right. Note that the connection between unit b and the thalweg is dewatered and unit c has formed into a distinct pool (lake level = 95 cm). All photos taken by Jason Ching on July 3, 2015.

negligible groundwater influence, but exchange substantially with thalweg water during high water levels (Fig. 1).

Seasonal variation in water temperature and lake level

The thermal characteristics of the stream–floodplain complex were monitored using a combination of calibrated iButton temperature loggers (Dallas Semiconductor, Dallas) and point measurements. Monitoring a shifting mosaic of water temperature with spatially fixed temperature loggers is challenging, so data from iButtons fixed in the thalweg were supplemented with point measurements of areas that were more difficult to monitor due to fluctuating water levels, damage to sensors from grizzly bear (*Ursus arctos*) activity, and fine-scale variation in water temperature. iButtons recorded a time series of temperature at 90 min (2008–2011) or 120 min (2014) intervals. During the years 2008–2011, some off-channel units lacked temperature data during the onset of the growing season. Field observations recorded during these early season periods confirmed that the lake and stream levels were high enough to flood these off-

channel units with flowing water and homogenise their temperatures with the thalweg. We have never observed measurable thermal heterogeneity across the wetted width of the flowing portion of the stream during flood stage (because it is well mixed), so we assumed that these off-channel habitats had water temperatures equal to that of the thalweg (where iButtons continuously monitored temperatures) during the early season period in which we lacked data. To characterise the thermal resources offered by off-channel habitats, we expressed our measurements as anomalies relative to the temperature of the lower thalweg (~200 m upstream of mouth). If iButtons were used, the measurement logged closest to the time of fish sampling was used. Otherwise, point measurements were taken at the time of sampling.

Between 2002 and 2015, summer lake level was monitored at the Aleknagik village dock (~8.7 km ESE of Bear Creek) every ~2 days as centimetres (cm) above a set benchmark. Only data from the study years (2008–2011, 2014–2015) were considered in the analysis.

Fish sampling

Juvenile coho salmon (age −0 to 2+) are the numerically dominant fish in Bear Creek (J. Armstrong & J. Baldock, unpubl. data). The spatial distribution and diets of coho salmon were intensively monitored during the early summer (early June–late July) in 2008–2011 and 2014–2015. Unlike many studies reporting the territoriality of juvenile coho salmon and their aversion to aggregate (see Dill, Ydenberg & Fraser, 1981), those residing in Bear Creek are patchily distributed; such that aggregations of 200+ individuals can occur in and around high-quality habitat, while most other areas remain unoccupied (Armstrong & Schindler, 2013). Pilot snorkel surveys identified off-channel units and areas of the thalweg that routinely held substantial numbers of juvenile coho salmon. Specifically, three lake-influenced off-channel units (as described above) were found to hold considerable numbers of juvenile coho salmon at various times throughout the early summer. Multiple thalweg areas with typical pool morphologies, large woody debris and undercut stream banks upstream of lake influence – at 427, 490 and 690 m upstream of the mouth – also often held large aggregations.

We conducted surveys of off-channel and thalweg habitats every ~3 days during daylight hours (1000–1800 hours). A targeted stick seining method was previously developed to sample the fish community (Armstrong & Schindler, 2013). Researchers surveyed each habitat for fish presence using both visual survey

with polarised glasses and snorkelling. If fish were detected, the downstream end of the unit was blocked with a 2.5 m × 4 m stick seine. A researcher on snorkel herded the fish into a school and flushed them into the net. This process was repeated until fish were no longer visible. This method proved to be effective at detecting and capturing fish in these confined habitat units.

Captured fish were anaesthetised in a 50 ppm solution of MS-222 (tricaine methanesulfonate; 2008–2011) or a 25 ppm solution of Aqui-S® 20E (active ingredient eugenol; 2014–2015), measured to the nearest 1 mm fork length, allowed to recover in pure stream water, and then released. The diets of some individuals (>75 mm fork length; 20–40 per unit) were sampled by gastric lavage; diet items were identified to order and enumerated.

Field observations of diet composition indicated that the spatial distribution of juvenile coho salmon during hours of darkness might differ substantially than what was observed during the day (see Results). To confirm this, we opportunistically conducted a single night survey (0100–0500 hours) of the lower 800 m of stream on June 26, 2014 using methods identical to daytime surveys. A large, waterproof flood lamp (50 W equivalent) was used to aid detection and capture efforts.

Benthic macroinvertebrate sampling

In 2014 and 2015, we used a Surber sampler (0.5 mm mesh, 0.0929 m^2 sampling area) to sample the benthic macroinvertebrate community and characterise the composition of prey taxa available to juvenile coho salmon throughout the stream–floodplain complex. Surber samples were taken from random locations within individual off-channel units as well as throughout the lower 800 m thalweg. We paid special attention when sampling in areas where water velocity was negligible (i.e. off-channel habitats) and watched for larger mobile taxa (e.g. Plecoptera larvae) that may have attempted escape as the community was swept into the net. Counts of taxa, identified to order, were aggregated across samples of a given date and location (e.g. thalweg or specific off-channel unit) to best represent the invertebrate community available in a specific habitat area, given that the spatial distribution of benthic macroinvertebrates is extremely patchy in lotic systems (Downes, Lake & Schreiber, 1993).

Data analysis

We quantified how the spatial patterning of water temperature shifted as a function of lake level and whether

or not juvenile coho salmon abundance shifted among off-channel habitats in parallel. Each sampling event (date and location specific) was assigned a corresponding lake level based on either the level observed on that date, or as the average of the day prior to and following the sampling date. For the 3 years with the most complete data (2010, 2011, 2014), mean coho salmon abundance and water temperature anomaly was calculated for each off-channel unit across a range of lake levels representing characteristically high, medium and low stages – median lake level of coho salmon habitat use (based on all 6 years of data; see Results) ± 9 cm (window size chosen to avoid overlap between medium and low stages). Local polynomial regressions (LOESS: Cleveland, 1979; R Core Team, 2015) with automatic smoothing parameter selection using bias-corrected Akaike information criterion (AIC$_C$: Hurvich, Simonoff & Tsai, 1998; Wang, 2010) were then fit by least squares to summarise patterns of absolute juvenile coho salmon abundance across a range of lake levels for each off-channel unit independently. LOESS smoothing curves were fit to log-transformed data and the output back calculated to the original plotting scale to avoid negative y-values that were produced when LOESS was fit to raw data, as negative values do not make sense for abundance data. The span parameter value calculated for unit B by the least-squares fitting procedure was slightly relaxed to better illustrate patterns of coho salmon abundance across a range of lake levels.

We analysed invertebrate community and fish diet samples to infer whether fish were feeding in different habitats than those in which they resided during the day. Two principal coordinates analyses (PCoA), based on separate Bray–Curtis distance similarity matrices, were used to characterise (i) thalweg and off-channel invertebrate communities, and (ii) diet composition of fish caught in either of those habitat types using ln-transformed counts of dominant taxa specified by order and life stage (Murdoch & Chow, 2013; Harrell, 2015; McGarigal, 2015; Oksanen *et al.*, 2015; R Core Team, 2015). Non-parametric multivariate analyses of variance (PERMANOVA: Anderson, 2001; Oksanen *et al.*, 2015) were used to test for significant differences in the invertebrate community available to fish in off-channel and thalweg habitats, as well as the feeding habits of fish caught in those two areas. Based on graphical assessments of ordination plots, we then focused the subsequent analysis on two prey taxa that appeared to drive a substantial proportion of the variation in both Surber and fish diet samples (Diptera and Plecoptera larvae). We coupled comparisons of the relative abundance of

these taxa – both within and among habitat types – with the proportion of fish diet samples that contained these taxa to infer primary foraging habitat of fish caught in lake-influenced off-channel habitat units. Fish diets containing salmonid fry (13% of all samples) were excluded from this analysis due to the inability of the Surber sampler to capture fry.

Results

Seasonal shifts in the thermal mosaic and habitat connectivity

The spatial patterning of water temperature across the stream–floodplain complex of lower Bear Creek shifted over the early summer feeding period as water levels receded. The observed patterns were consistent across multiple years; however, the exact date at which certain shifts occurred differed due to substantial interannual variation in lake level dynamics. Typically, lake level peaked in early June and then declined throughout the summer (Fig. 2). In some years, major precipitation events resulted in a rise in lake level during this overall period of decline, but never during the early portion of the growing season prior to the arrival of spawning sockeye salmon.
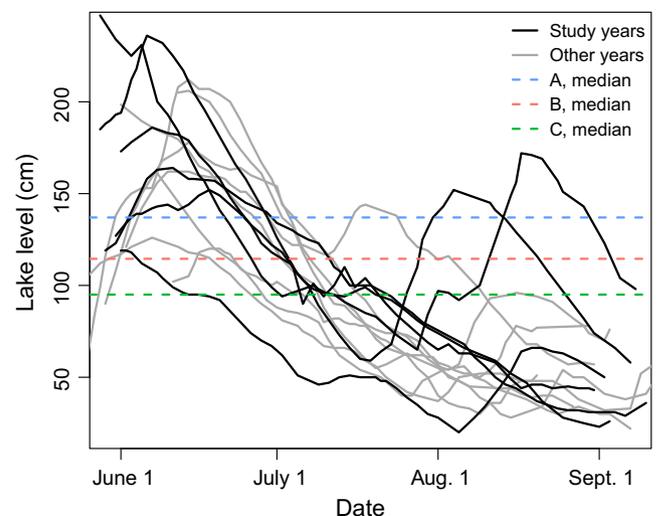

Fig. 2 Variation in water level in Lake Aleknagik (measured as cm above a standard benchmark) over the summer growth period (late May–early September). Solid black lines denote the 6 years during which the study took place (2008–2011, 2014–2015). Solid grey lines denote additional years in which lake level data are available, but surveys of Bear Creek were not conducted (2002–2007, 2012–2013). Dashed horizontal lines indicate the median lake level associated with juvenile coho salmon use of each lake-influenced off-channel unit: 137, 114 and 95 cm for units A, B and C respectively.
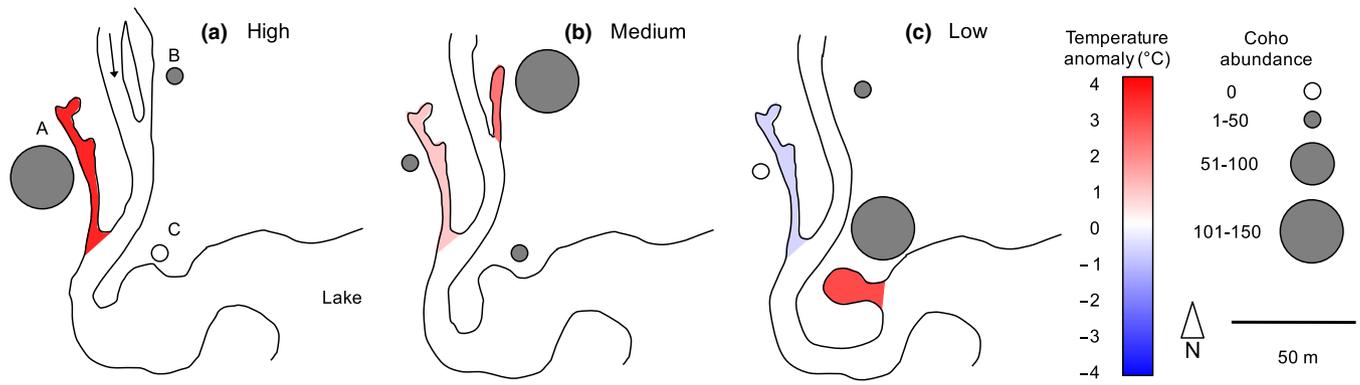
Fig. 3 Shifting mosaic of metabolically favourable temperatures and the associated response by juvenile coho salmon in the lower reaches of Bear Creek, Alaska, for the 3 years with the most complete data (2010, 2011, 2014). Snapshots are from ranges of lake levels representing three distinct spatial configurations of water temperature: (a) high (128–146 cm), (b) medium (105–123 cm) and (c) low (86–104 cm). The colour of each off-channel unit represents the mean temperature anomaly of that unit relative to the thalweg for all observations within the respective range of lake level; where warm colours (red) represent water that is warmer than the thalweg, and cold colours (blue) represent water that is colder than the thalweg. Grey circles mark units in which juvenile coho salmon are present, where the size of the circle represents mean fish abundance for all observations within the respective range of lake level. Open circles mark units devoid of fish. Flow direction and lake location are noted in panel (a). Note the physical changes in the wetted area of the stream (black line) as lake level recedes, particularly with respect to units B (which dewaters at low lake levels) and C. Fish were never observed in the lake-influenced reaches of stream thalweg during daylight surveys in these years.

High lake levels inundated the floodplain in the downstream portion of Bear Creek (up to 300 m upstream of mouth). While lake inundation greatly increased the area of off-channel habitat, the effect on water temperature was spatially variable (Fig. 3). The thalweg and lake were cold during the period of peak lake levels (24-h mean = 5–8 °C). Portions of the floodplain influenced by stream flow or wave action remained cold, whereas areas with stagnant water warmed substantially (mean of point measurements = 12.5 °C). The off-channel unit at the edge of lake inundation was warmest; as lake level receded, the location of warm, stagnant bodies of water shifted as units either became dominated by upwelling groundwater (~3 °C, unit A: ~107 cm) or dewatered (unit B: ~95 cm; unit C: ~67 cm). Notably, unit A warmed first, as much as 1–5 °C greater than the thalweg, followed by Unit B (+1–11 °C), and finally unit C (+1–11 °C; Fig. 3) as lake level receded over the course of the early summer. This progression of off-channel units sequentially characterised by relatively warm water conditions was consistent across 6 years of variable lake dynamics.

Shifting spatial distribution of juvenile coho salmon

Over the course of the early summer, the spatial distribution of juvenile coho salmon shifted among off-channel habitats as lake level receded (Fig. 4), and was coordinated with shifts in the thermal landscape (Fig. 3).
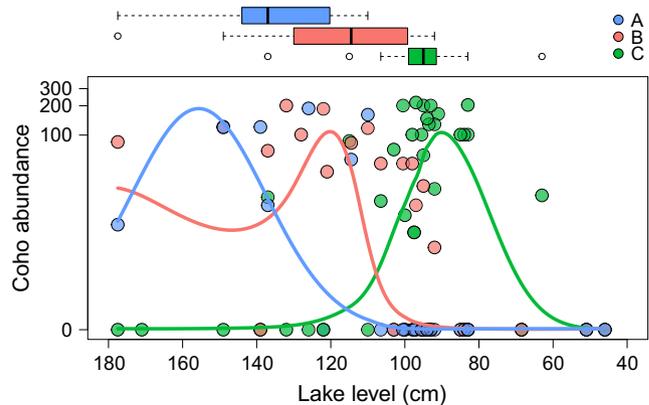

Fig. 4 Absolute abundance of juvenile coho salmon (plotted on a log scale) in off-channel units A (blue dots), B (red dots) and C (green dots) as a function of lake level (cm) during the years 2008–2011 and 2014–2015. Coloured lines represent 2-degree local polynomial regressions (LOESS) that illustrate patterns of habitat use across a range of lake levels for each of the lake-influenced off-channel units. Box plots summarise the range of lake levels over which coho salmon occupy each off-channel unit; thick black bars represent medians.

As water level receded, the distribution of juvenile coho salmon shifted to track the spatial patterning of warm water in the floodplain (i.e. from unit A to B, and B to C as each unit warmed and subsequently cooled or dewatered) although the exact lake level at which shifts occurred differed slightly among years due to interannual variability in other factors affecting the thermal mosaic and habitat connectivity (e.g. air temperature and precipitation). The

median lake levels associated with juvenile coho salmon use of each off-channel habitat were 137, 114 and 95 cm for units A, B and C respectively.

Juvenile coho salmon exhibited a strong affinity for warm water and were never observed in off-channel units with temperatures that were equivalent or colder than the thalweg. On average, off-channel habitat units occupied by juvenile coho salmon were 4.1 °C warmer than adjacent thalweg habitat (pooled mean of point measurements).

Benthic community and fish diet analyses

A comparison of the benthic macroinvertebrate community between off-channel and thalweg habitats, and fish diet contents demonstrated that juvenile coho salmon made high-frequency cyclic movements between these habitats, coupling areas of high digestive capacity

(warm-off channel) with areas of high foraging potential (cold thalweg). Analysis of the benthic macroinvertebrate community revealed distinct differences in the taxa associated with thalweg and off-channel habitat types. There was a significant difference in the invertebrate communities representative of off-channel versus thalweg habitats (PERMANOVA: $F = 4.76$, $R^2 = 0.241$, $P < 0.05$). Graphical assessment of PCoA ordination plots (PCo1 = 30%, PCo2 = 21%) supported PERMANOVA results and indicated that major differences in thalweg and off-channel benthic communities were driven by certain diagnostic taxa, specifically, Diptera were common in off-channel habitats and Plecoptera larvae were common in the thalweg (Fig. 5a).

A significant, 62-fold difference in the relative abundance of Diptera versus Plecoptera larvae was found in off-channel habitats (Welch's two sample t-test: $t = 5.06$, d.f. $= 7.02$, $P < 0.05$); while no such difference was
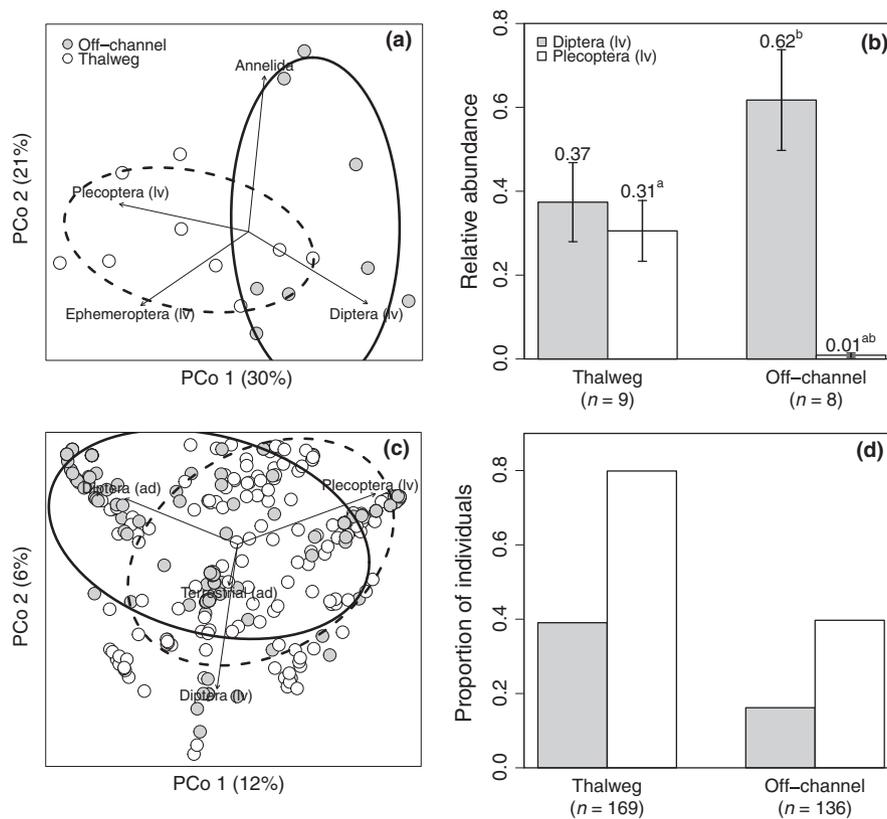

Fig. 5 (a) PCoA ordination of the benthic macroinvertebrate community (by dominant taxa, specified by order and life stage) associated with off-channel (grey dots) and thalweg (white dots) habitats. Solid (off-channel) and dashed (thalweg) ellipses depict one standard deviation of the pairwise dissimilarity scores per grouping. Statistically significant ($P < 0.05$) loading vectors (arrows) have been added to each plot to aid with interpretation. (b) Mean relative abundance of Diptera (grey bars) and Plecoptera (white bars) larvae in Surber samples taken from thalweg and off-channel habitats. Statistically significant ($P < 0.05$) pairwise comparisons are denoted by superscripts of bar labels. (c) PCoA ordinations of juvenile coho salmon diet composition (by dominant taxa, specified by order and life stage) for fish caught in off-channel (grey dots) and thalweg (white dots) habitats. (d) Proportion of juvenile coho salmon diet samples that contain either Diptera (grey bars) or Plecoptera (white bars) larvae for fish caught in either thalweg or off-channel habitats.

apparent in thalweg areas (two sample *t*-test: *t* = 0.58, d.f. = 16, *P* < 0.05; Fig. 5b). Further, a significant, 31-fold difference in the relative abundance of Plecoptera larvae was found for thalweg versus off-channel habitats (Welch's two sample *t*-test: t = 4.08, d.f. = 8.08, *P* < 0.05); while no such difference was found for Diptera larvae (Two sample *t*-test: *t* = −1.61, d.f. = 15, *P* < 0.05; Fig. 5b).

Despite differences in the invertebrate prey communities, the diets of fish caught in either habitat type were remarkably similar. There was a statistically significant difference in the diets of fish caught in alternate habitats (PERMANOVA: *F* = 18.74, R^2 = 0.0583, *P* < 0.05); however, due to a large sample size (*n* = 305), the power to detect subtle, but ecologically irrelevant differences was high. Graphical assessment of PCoA ordination plots (PCo1 = 12%, PCo2 = 6%) supported this conjecture and showed that although individual dietary composition varied considerably, there was substantial overlap in the diets of fish caught in alternate habitat types (Fig. 5c). Additionally, the same taxa that appeared to drive most of the variation in benthic community composition (Diptera and Plecoptera larvae) seemed to also drive variation in fish diet samples.

Further analysis of fish diet samples revealed that Plecoptera larvae were present in roughly twice the proportion of diets as compared to Diptera larvae, regardless of habitat type (Fig. 5d). Specifically, Plecoptera larvae were present in 80% and 40% of diet samples taken from fish captured in thalweg and off-channel habitats, respectively, while Dipteran larvae were present in just 39% and 16% of diet samples (Fig. 5c). Despite the scarcity of Plecoptera larvae in off-channel habitats, a substantial proportion of coho salmon caught in these habitats exhibited this taxon in their diet. These results suggest that juvenile coho salmon caught in off-channel habitats during the day forage primarily in the thalweg at night.

Comparison of the spatial distribution of juvenile coho salmon from a day/night survey support inferences made from benthic community and fish diet analyses. During daylight hours on June 23, 2014, 79% of juvenile coho salmon caught in the lower 800 m of stream habitat were caught in off-channel units (99% of which were caught in the three lake-influenced habitats); while only 21% were caught in thalweg areas. In contrast, during hours of darkness on June 26, 2014, only 16% were caught in off-channel habitats, while 84% were caught in thalweg areas (Fig. 6). These results support the inference that fish moved between off-channel and thalweg habitats on relatively short (diel) timescales.
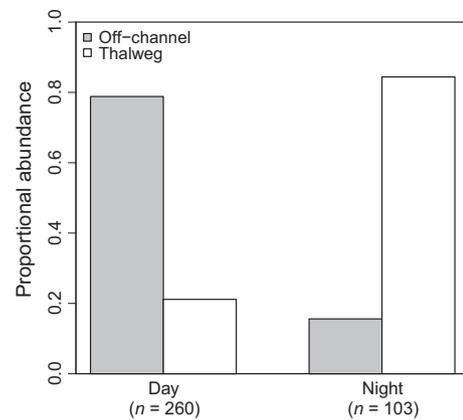

Fig. 6 Proportion of juvenile coho salmon caught in either off-channel (grey bars) or thalweg (white bars) habitats during a single day survey (June 23, 2014) and a single night survey (June 26, 2014) on Bear Creek, Alaska.

Discussion

Here, we show that juvenile coho salmon track intraseasonal shifts in the spatial patterning of temperature across the lower reaches of a river floodplain. Receding lake level mediated the inundation of the floodplain and the spatial patterning of water temperature such that the three off-channel units used by juvenile coho salmon as digestive habitat exhibited asynchronous dynamics in water temperature – each provided warm water conditions (12.5 ± 3.2 °C; pooled mean ± SD), relative to the thalweg (24-h mean = 5–8 °C) but at different lake levels, which occurred at different times. Our results reveal two scales of movement used by juvenile coho salmon that exploit spatiotemporal variability in habitat conditions. At weekly time scales, fish moved among off-channel habitats to track warm conditions that shifted across the floodplain due to receding water levels (Figs 3 & 4). In addition, at diel time scales, cyclic movements coupled warm digestion habitat in the floodplain with cooler foraging habitats in the main channel (Figs 5 & 6). Our results support previous work describing how scales of movement are driven by scales of change in resource availability (van Moorter *et al.*, 2013). The behaviour we document here complements earlier observations in this system where juvenile coho salmon were shown to track interannual variation in the spatial patterning of water temperature that arises due to variation in summer precipitation (Armstrong & Schindler, 2013).

Each off-channel habitat unit in our study provided ephemeral periods of warm water and thus enabled high digestive capacity in juvenile coho salmon. Depending on water level dynamics, the duration of warm conditions (8.3–19 °C) was approximately 15, 9

and 15 (mean of annual duration) days in habitats A, B and C, respectfully. However, because off-channel units exhibited asynchrony in their thermal response to receding water levels, coho salmon that moved among habitats could find warm conditions for digestion for as long as 40 days (2015). The striking shifts in the abundance of coho salmon among the three units provide strong evidence that fish were indeed tracking the shifting mosaic of water temperature. These results build on prior work illustrating how intact, heterogeneous landscapes produce portfolio effects in habitat quality that buffer mobile organisms from variation in environmental conditions (Kindvall, 1996; Oliver *et al.*, 2010; Schindler, Armstrong & Reed, 2015).

In high-latitude freshwater systems, it is well known that fish lose energy overwinter due to resource scarcity and reduced physiological performance and that positive energy balance may be restricted to as few as 1–4 months of the year (Conover, 1992; Biro *et al.*, 2004). During this brief growing season, juvenile fish must not only grow towards adult size but also recover from overwinter nutritional stress and acquire energy stores for the following winter. Previous work has revealed behavioural (e.g. Armstrong & Schindler, 2013; Armstrong *et al.*, 2013) and physiological (Armstrong & Bond, 2013) adaptations that allow salmonids at high latitudes to exploit episodic resource subsidies derived from spawning sockeye salmon, which generally occur late in the growing season. This study is novel in that it considers *in situ* trophic pathways during the onset of the growing season. While large-bodied fish with low mass-specific metabolic costs may persist on salmon subsidies alone (Armstrong & Bond, 2013), juvenile salmonids typically rely on *in situ* invertebrate prey for a substantial fraction of their annual energy budget (Reichert, Greene & Bilby, 2008; Armstrong *et al.*, 2010; Wipfli & Baxter, 2010). Our study showed that behavioural thermoregulation can be an important tactic for coho salmon not only during the high-magnitude pulsed subsidies of marine-derived resources during late summer and fall but also while fish are targeting invertebrates and *in situ* trophic pathways earlier in the growing season.

Our analysis suggests that juvenile coho salmon reside in warm off-channel habitat during the day to accelerate assimilation (i.e. the process that spans digestion and absorption) and perhaps to opportunistically feed, although any contribution to total dietary needs appears slight. At night, many of these individuals leave off-channel habitats, making feeding forays into the cold thalweg. Here, we use the spatial distribution of diagnostic prey taxa and their prevalence in fish diets to make

assumptions about the location and timing of foraging behaviour. This analysis likely underestimates the importance of thalweg-derived prey, such as Plecoptera larvae, in the diets of coho salmon as the energetic content per individual is higher than other abundant prey items, such as Diptera larvae (Cummins & Wuycheck, 1971; anecdotal evidence of body size, J. Baldock & J. Armstrong, unpubl. data). Additionally, our conclusions are strengthened by previous work, which shows that this population of fish makes nightly forays into the downstream 800 m of thalweg to feed (Armstrong *et al.*, 2013).

Growth potential for coho salmon (Corey, Leith & English, 1983; Ruggerone, 1989) and other salmonids (Brett, 1971; Sweka, Keith & Hartman, 1994) increases rapidly over the range of temperatures observed across the Bear Creek riverscape (i.e. from the colder stream thalweg to warmer off-channel habitats; daily means of ~5–13 °C). Temperature increases growth potential by accelerating the processing rates of multiple steps in the food-to-fuel pathway (Weiner, 1992; Piersma & van Gils, 2011), including assimilation. We argue that coho salmon residing in warm-off channel habitats experience increased growth rates by relieving thermal constraints on assimilation (as well as other physiological processes). Though we lack an appropriate gastric evacuation model to precisely quantify thermal constraints on assimilation (but see Ruggerone, 1989; which explores the effect of temperature on juvenile coho salmon gastric evacuation rate for relatively small meal sizes), we have shown experimentally that our study fish require multiple days to assimilate large meals and that the cold temperatures in the thalweg severely constrain assimilation (Armstrong *et al.*, 2013). Further, prior work on other fish species shows that multiple days may be required to process a single meal at low temperatures (Sweka *et al.*, 1994; Hop & Tonn, 1998), whereas the stomach can be filled and processed multiple times a day at higher temperatures (Juanes & Conover, 1994). In addition to this physiological evidence, juvenile coho salmon are known to defend territories (Mason & Chapman, 1965; Pucket & Dill, 1985) and would be very unlikely to form such dense aggregations unless they were digestively constrained and waiting for their guts to clear (Van Gils & Piersma, 2004).

Despite the obvious association between lotic and lentic systems, stream ecologists and limnologists have largely ignored patterns and processes that occur at the stream–lake interface. Existing work on unaltered stream--lake networks largely focuses on the downstream effects of lakes, while relatively little attention has been paid to lake effects on inlet streams (see review by Jones, 2010) such as Bear Creek. Stream and river

deltas are known to be hotspots of biodiversity (Willis & Magnuson, 2000) and production (Witthöft-Mühlmann, Traunspurger & Rothhaupt, 2005) within the stream–lake network. However, complex lake level dynamics due to variable patterns of precipitation and snowmelt can result in considerable changes to the physical habitat template and local environmental conditions of stream deltas; just as variability in flows modify the habitat mosaic upstream of lake influence (Stanford *et al.*, 2005; Whited *et al.*, 2007). This study is the first to describe how organisms interact with the shifting habitat mosaic of stream delta ecotones.

Ecological simplification (e.g. reduced niche diversity) due to loss of landscape complexity and ecological integrity is diagnostic of human-dominated landscapes worldwide (Peipoch *et al.*, 2015). Hydrologic alteration (Kingsford, 2000; Poff *et al.*, 2007) and shoreline armouring (McCartney *et al.*, 2012; Henning & Hentschel, 2013) directly suppress the mechanisms that generate and maintain active floodplains that provide growth opportunities to mobile organisms.

Most habitat restoration efforts focus on engineering 'desirable' habitat features (Roni, Hanson & Beechie, 2008) due to strict and narrowly defined aspects of river systems put forth by environmental legislation (e.g. US Clean Water Act, US Endangered Species Act). These engineered features are often static (i.e. secured in a concrete foundation) and not responsive to habitat-forming processes (Beechie & Bolton, 1999). Restoration efforts may have improved success if they instead address key landscape dynamics that are often overlooked, but ultimately responsible for nested biotic responses (process-based restoration: Beechie *et al.*, 2010). Restoring landscape complexity (including the processes responsible for spatially and temporally variable temperature regimes) would allow for the natural formation of habitats that are flexible to environmental variability and would foster the resilience and stability of animal populations that inhabit them.

This study highlights the biological importance of microhabitat features generated and maintained by multiple interacting landscape processes. We showed that juvenile coho salmon employ multiple scales of movement to exploit asynchrony in resources (temperature and food) within the context of the shifting habitat mosaic of a stream delta ecotone; this strategy should allow fish to increase energy acquisition during a critical life stage. Further, we demonstrate how intact floodplains generate portfolio effects in habitat conditions, in which asynchronous variation among habitats reduces the probability that conditions will become

unsuitable across the aggregate of habitats available to mobile organisms. In river ecosystems, allowing the processes of erosion, deposition and succession to play out across floodplains is likely critical for producing and maintaining the shifting habitat mosaic and the growth opportunities they provide for fishes and other mobile taxa.

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