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Complex temperature mosaics across space and time in estuaries: implications for current and future nursery function for Pacific salmon

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Water temperature is a key dimension of estuaries that can influence important biological processes including organismal growth, survival, and habitat use. For example, juvenile Pacific salmon rely on temperature-mediated growth opportunities in estuaries during seaward migration in the spring and summer. However, oncoming climate change is warming estuary temperatures and transforming growth potential. Yet, it is likely that estuary water temperatures are complex and dynamic across space and time. Here we investigated spatial and temporal patterns of water temperature across two contrasting estuaries on Vancouver Island, BC, and used these data to simulate juvenile Chinook salmon growth potential under both present conditions and a simplified scenario of climate warming. Summer temperatures were warmer and more spatially homogeneous across the Englishman River estuary relative to the Salmon River estuary. Within each system, temperature was variable across habitats and sites, appearing to be driven by a combination of local climate, river and ocean temperatures, tidal fluctuations, and habitat features. This shifting mosaic of temperatures generated a complex portfolio of growth opportunities for juvenile Chinook salmon. There were broad patterns of increasing growth potential across both systems as temperatures warmed in early summer. However, excessively hot late summer temperatures drove steep declines in growth potential across the Englishman River estuary, while positive trends continued through August in the Salmon River estuary. A simple climate change scenario revealed that estuaries and habitats may have differing vulnerabilities to increasing temperatures—with climate warming, favorable growth opportunities were even more constricted to early summer in the Englishman River estuary, but expanded across most habitats and times in the Salmon River estuary given lower baseline temperatures and higher habitat complexity. Collectively, this work underscores the importance of habitat complexity and local climate for maintaining diverse growth opportunities across estuaries, which may confer resilience to the nursery function of estuaries as temperature mosaics warm.

KEYWORDS

estuary, water temperature, nursery habitat, bioenergetics, oncorhynchus, climate change

1 Introduction

Estuaries are mosaics of interconnected habitats at the interface between watersheds and oceans. Therefore, they are shaped by complex interactions between terrestrial, marine, and atmospheric processes (Talley et al., 2003; Ray, 2005; Sheaves, 2009). These interacting processes generate spatio-temporal variability in key habitat conditions (Beck et al., 2001; Sheaves et al., 2015). Numerous habitat conditions, such as salinity, water temperature, vegetation, and geomorphology, vary across multiple spatial scales (Peterson, 2003; Fulford et al., 2011). For example, salinity profiles are often characterized estuary-wide (i.e. salt-wedge or well-mixed) given dominant river-tide interactions, but may also show significant local variability (i.e. between channels) due to differences in stratification and mixing processes throughout the estuary (Giddings et al., 2011). Many of these spatial patterns also change over time, and shifts can range from daily fluctuations to interannual variation (Peterson et al., 2007). For example, daily tidal fluxes influence water quality patterns (i.e. temperature, salinity, and dissolved oxygen), while interannual cycles such as the El Niño Southern Oscillation can impact long-term estuarine mixing and temperature regimes (Wooldridge and Deyzel, 2012; Sutherland and O'Neill, 2016; Possamai et al., 2018). Together, these spatio-temporal processes shape estuarine habitats into highly complex and dynamic systems.

Water temperature is a key dimension of the estuarine habitat mosaic (Fulford et al., 2011). Many processes govern estuarine water temperature—including river flows and temperature, meteorologic conditions, and ocean temperature and tides—which together drive dynamic spatio-temporal patterns (Schumann, 2000; Brown et al., 2016; Marin Jarrin et al., 2022). Across aquatic systems, water temperature patterns can influence many biological processes including organismal physiology, species distributions, and community composition (Sanford, 1999; Perry et al., 2005; Eliason et al., 2011). For example, the growth potential and physiological performance of fishes is temperature dependent—growth increases as temperatures rise, but declines precipitously when temperatures exceed thermal optima (Beauchamp, 1989; Hanson et al., 1997). Within river networks, cold-water fishes have been shown to track optimal growth temperatures between seasons, exploiting different habitats over the year, and even complete daily migrations across temperature gradients (Armstrong et al., 2013; Armstrong et al., 2021, Hahlbeck et al., 2022). These and other studies have increasingly revealed how fish rely on both broad- and fine-scaled spatio-temporal variability in freshwater temperatures; however, few studies have examined these temperature dynamics in estuaries (Welsh et al., 2001; Kaylor et al., 2021). Investigating fine-scaled temperature variation across both space and time is therefore an important step towards understanding and predicting key biological processes in estuaries (Wagner et al., 2011; Marin Jarrin et al., 2022).

Estuarine systems can support many important species, including anadromous fishes like Pacific salmon (*Oncorhynchus* spp.). Juvenile salmon transit through estuaries during seaward migration in the spring, but may also rely on these systems as nursery grounds prior to ocean entry (Magnusson and Hilborn, 2003; Weitkamp et al., 2014; Moore et al., 2016; Sharpe et al., 2019; Woo et al., 2019). The duration of estuary residency varies considerably within and between species. For example, Chinook salmon (*O. tshawytscha*) are known to rear extensively in estuaries, while pink salmon (*O. gorbuscha*) typically pass through rapidly (Bottom et al., 2005; Moore et al., 2016; Quinn, 2018; Chalifour et al., 2021). During estuarine residency, spatio-temporal temperature dynamics mediate key physiological and ecological processes for juvenile salmon including growth, survival, movement, and prey availability (Cordell et al., 2011; David et al., 2014; Davis et al., 2019; Davis et al., 2022). Estuarine growth can be relatively rapid compared to upstream habitat, and this growth can have subsequent benefits for marine survival (Bond et al., 2008; Duffy and Beauchamp, 2011, Sawyer et al. in press). For example, Sawyer et al. (in press) estimated that estuarine growth improved marine survival by 31-47% for juvenile coho salmon (*O. kisutch*) on the Central Coast of British Columbia and that growth was substantially higher in a year with warmer temperatures. On the other hand, observations from an estuary lagoon in California suggest that excessively high estuary temperatures can limit rearing habitat and drive diel movements for juvenile steelhead and coho salmon (Osterback et al., 2018; Bond et al., 2022). Thus, navigating mosaics of temperature in estuaries and the associated growth opportunities can have important consequences for juvenile salmon during estuary rearing and seaward migration.

Understanding the spatial and temporal dynamics of temperature in estuaries is particularly important given oncoming climate change. Depending on the emissions scenario, sea-surface temperatures are expected to increase anywhere from 1.3-4.4°C in the northeast Pacific Ocean between 2010-2099 (Hoegh-Guldberg et al., 2014). In addition, global river temperatures are projected to increase by several degrees by 2100 relative to 1971-2000, also dependent on emissions, location, and river water source (van Vliet et al., 2013) (e.g., up to 6°C increase in annual maximum temperature by the 2080s relative to the 1980s in the Pacific Northwest, Mantua et al., 2010). These shifts, along with changes to other climatological processes like precipitation, will likely drive increases in estuarine water temperature (Wagner et al., 2011; Cho and Lee, 2012; Brown et al., 2016; Davis et al., 2022). Shifting temperature mosaics will transform growth opportunities for fishes across estuarine systems (Harley et al., 2006). For juvenile salmon, this could have cascading impacts including changes in marine survival and migration phenology (Pörtner and Peck, 2010; Gillanders et al., 2011; Wilson et al., 2021; Davis et al., 2022; Wilson et al., 2023). Therefore, predicting shifts in growth potential is a key step towards understanding Pacific salmon vulnerability to increased estuarine temperatures, which can in turn help inform conservation and management strategies (Griffiths and Schindler, 2012; Davis et al., 2022; Spanjer et al., 2022).

Here we aim to quantify estuary temperature mosaics and their implications for nursery function for salmon in this era of climate warming. Specifically, we (1) assess spatial and temporal patterns of summer temperatures across different habitats within two contrasting estuaries on Vancouver Island, BC, (2) use this data to explore juvenile Chinook salmon growth potential across each system using bioenergetics modeling, and (3) investigate changes in growth potential under a simple scenario of increased temperature. Collectively, we discovered high variation in water temperatures and associated growth opportunities across both space and time that suggests key linkages between estuarine habitat complexity and oncoming vulnerability to climate warming.

2 Methods

2.1 Study systems

We performed this study in the estuaries of two salmon-bearing rivers, the Englishman and Salmon, on the eastern side of Vancouver Island, British Columbia, Canada. This work is a part of a large-scale collaborative initiative—Estuary Resilience project—led by The Nature Trust of British Columbia (NTBC), in collaboration with coastal First Nations and other organizations. Both the Englishman and Salmon Rivers and estuaries support all five species of Pacific salmon in addition to sea-run dolly varden (*Salvelinus malma*), cutthroat trout (*Oncorhynchus clarkii*), and anadromous steelhead trout (*Oncorhynchus mykiss*) (Silvestri, 2007; Lament et al., 2015). These two estuaries contrast in their size, local climate setting, and degree of anthropogenic alteration. The Salmon River estuary is larger and relatively intact with cooler and less variable climatic patterns. Contrastingly, the Englishman River estuary is smaller and highly altered by residential developments, flow modification, and land-use conversion, and experiences warmer and more seasonally variable climatic conditions.

The Salmon River estuary is located on the ancestral territory of the K’ómoks First Nation, who know this area as X’wésam. The estuary encompasses approximately 8.4 km^2 of wetlands, bordering the small town of Sayward to the west, forested mountains to the east, and draining into Johnstone Straight (GPS: 50.39N, 125.95W) (Figure 1). Johnstone Strait is a deep (e.g. over 500 m in some sections) and narrow (e.g. 4.5-2.5 km wide) channel that experiences rapid tidal streams and high winds. Thus, water is vertically well-mixed and typically remains relatively cool year round (Thomson, 1981). The Salmon River watershed is 1210 km^2, and the river is 208 km long (Atagi, 1994). This is a rainfall-

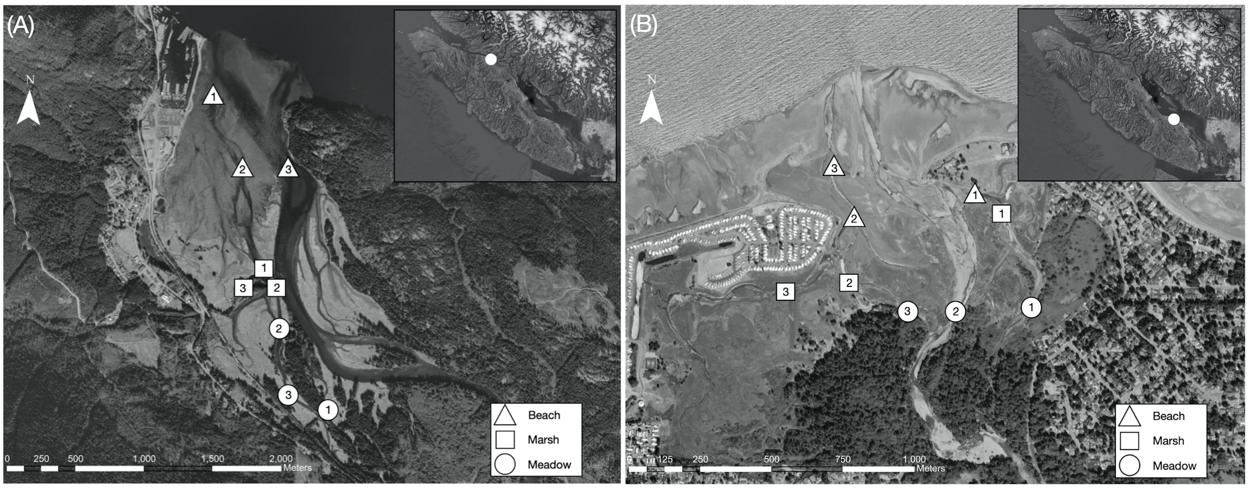

FIGURE 1
(A) Map of the Salmon River estuary. Temperature logger locations are indicated by the shapes, with each shape corresponding to a habitat type as indicated by the key. Sites are numbered 1-3 within each habitat type. The white dot on the inset indicates the location of the Salmon River estuary on Vancouver Island. **(B)** Map of the Englishman River estuary. Temperature logger locations are indicated by the shapes (triangles are beach habitats, squares are marsh habitats, and circles are meadow habitats). Sites are numbered 1-3 within each habitat type. The white dot on the inset indicates the location of the Englishman River estuary on Vancouver Island.

dominated system, with the highest discharge in fall and winter (Environment and Climate Change Canada (ECCC), 2023a). The estuary sits within the Coastal Western Hemlock (CWH) biogeoclimatic zone, which is characterized by cool summers and mild winters (Pojar et al., 1991). The Salmon River watershed has a long history of logging, and a log-sort continues to operate in the northwest corner of the estuary, separated from the system by a narrow jetty (Baldwin and Bradfield, 2010).

The Englishman River estuary is in southeastern Vancouver Island on the ancestral territory of the Snaw'naw'as First Nation, who know this area as Kw'a'luxw. The system sits within the city of Parksville and includes about 3.7 km^2 of wetlands that are almost entirely surrounded by residential developments (GPS: 49.33N, -124.29W) (Figure 1). Thus, the estuary is less than half the size of the Salmon River estuary. The Englishman watershed is 319 km^2, and the river runs for 40 km before entering the estuary and Strait of Georgia (Bocking and Gaboury, 2001). The Strait of Georgia is shallower (e.g. average depth is 155 m) and wider (e.g. average width is 28 km) in comparison to Johnstone Strait, with strong year round vertical stratification. In the Strait of Georgia, water temperature in the upper layer displays strong seasonal variation, with summer temperatures exceeding 20°C in some places (Thomson, 1981). The Englishman River is rainfall-dominated and is generally characterized by lower discharges than the Salmon River (Environment and Climate Change Canada (ECCC), 2023b). A dam operates 34 km above the estuary in the headwaters. The estuary is also within the CWH biogeoclimatic zone (Pojar et al., 1991). However, the system typically experiences higher summer temperatures and less annual precipitation in comparison to the Salmon River estuary (Environment and Climate Change Canada-Meteorological Service of Canada (ECCC-MSC), 2023a; Environment and Climate Change Canada-Meteorological Service of Canada (ECCC-MSC), 2023b). Many land-use activities impact the Englishman River watershed, including logging, agriculture, and residential developments (Boom and Bryden, 1994). Similarly, the estuary has been altered substantially by development, although there have been recent restoration efforts.

2.2 Field methods

To obtain temperature data across a range of estuarine habitat conditions, we deployed ten temperature loggers (HOBO TidbiT v2) in each estuary from May-August, 2022. Logger sites were chosen to cover three broad estuarine habitat types—beach, marsh, and meadow (Figure 1). These classifications span a range of vegetation, geomorphology, and tidal influence, thus representing a mosaic of available juvenile salmon estuarine habitat (Levings, 2016; Woo et al., 2019). More specifically, beach habitats are predominantly marine influenced with sandy and rocky shorelines and some marine macroalgae (e.g., *Fucus* spp.). Estuarine marshes are diurnally tidally influenced and dominated by salt tolerant plants such as Lyngbye's sedge (*Carex lyngbyei*). Last, meadow habitats are generally highest and furthest upstream in the estuary, experiencing less frequent tidal inundation and featuring diverse plant communities (MacKenzie and Moran, 2004). We chose three sites within each habitat type based on accessibility and variability in characteristics such as water flow, depth, and vegetation. The tenth logger was placed upstream in the mainstem river channel above tidal influence to record freshwater inflow temperatures. Loggers were set to record at fifteen-minute intervals and deployed at every site between April 30-May 4, 2022. Rebar was hammered into the substrate, and loggers were connected using zip-ties to sit 15cm above the bottom. Although loggers were not deployed within a protective housing, research suggests that loggers at sites with continuous flow, turbid water, and/or shading (i.e. riparian or aquatic vegetation) experience much less heating from direct solar radiation. All of our deployment sites were characterized by at least one of these conditions, so we suggest that the lack of housings does not significantly impact our results (Johnson and Wilby, 2013; Caissie and El-Jabi, 2020). We downloaded and redeployed all loggers at the beginning of July with final retrieval on August 27-28, 2022. Throughout this field work, members of the K'ómoks and Snaw'naw'as First Nations joined us to share guidance on site selection and assist with field operations.

2.3 Analysis

Temperature recordings taken during dewatered periods were removed from each dataset. This included readings taken during initial deployment, the mid-summer logger check, and final retrieval. In addition, two loggers in the Salmon River estuary (Marsh 2 and Beach 3) were found dewatered when retrieved in August due to lower water levels. We visually inspected these temperature time-series for increased daily variance, which indicates that the loggers were recording air temperature, and removed data accordingly. Data from all other loggers was also examined to check for dewatered periods, but none were identified. During the mid-summer check, one logger in the Salmon River estuary was missing (Meadow 2). A new logger was deployed at this time, so data for this site is limited to July-August.

We used generalized additive models (GAMs) to quantify variation in summer water temperatures between habitat types across each estuary. For each system, we modeled daily average water temperature against a factor-smooth interaction between day (an integer ranging from 1-119) and habitat type (beach, marsh, and meadow) using a Gaussian distribution. Factor-smooth interactions fit separate smooths for each level of a factor, which allows for *post-hoc* comparisons between these different levels (Pedersen et al., 2019). We fit the factor-smooth interaction between day and habitat type using thin-plate regression splines with forty knots. Habitat type was also added as a random effect to allow for varying intercepts. In addition, site was included as a random effect to account for variation between temperature loggers. Both models were fit with restricted maximum likelihood estimation (REML) using the R software package "mgcv" (R Core Team, 2022, R version 4.2.1 [2022-06-23], Wood, 2017). After models were fit, we used the "plot_differences" function from the R package "gratia" to examine pairwise differences between habitat-level smooths for each model (Simpson, 2023). This function calculates pairwise difference smooths with 95% credible intervals for every combination of factors in a factor-smooth interaction. We concluded that daily water temperature differed significantly between habitat types when the 95% credible interval for the difference smooth did not include zero.

For further data visualization and analysis, we used tide predictions from the nearest Fisheries and Oceans Canada stations, regional ocean temperatures from the nearest Fisheries and Oceans Canada lighthouse stations, and air temperature data from the nearest Meteorological Service of Canada weather stations (Department of Fisheries and Oceans Canada (DFO), 2023c—Tides, currents, and water levels for Kelsey Bay-08215 [data for the Salmon River estuary], Department of Fisheries and Oceans Canada (DFO), 2023d—Tides, currents, and water levels for Nanoose Bay-07930 [data for the Englishman River estuary], Department of Fisheries and Oceans Canada (DFO), 2023b—British Columbia Lightstation Sea-Surface Temperature and Salinity Data (Pacific), 1914-present for Pine Island [data for the Salmon River estuary], Department of Fisheries and Oceans Canada (DFO), 2023a—British Columbia Lightstation Sea-Surface Temperature and Salinity Data (Pacific), 1914-present for Departure Bay [data for the Englishman River estuary], Environment and Climate Change Canada-Meteorological Service of Canada (ECCC-MSC) (2023a) [data for the Salmon River estuary], Environment and Climate Change Canada-Meteorological Service of Canada (ECCC-MSC) (2023b) [data for the Englishman River estuary]).

2.4 Bioenergetics

We used bioenergetics models to explore the implications of temperature mosaics on potential growth of juvenile salmon given simple assumptions. Specifically, we used the Wisconsin Bioenergetics model to simulate growth of juvenile Chinook salmon at each temperature logger site from May-August (Hewett and Johnson, 1987; Hewett and Johnson, 1992; Hanson et al., 1997). We focused on Chinook salmon given their cultural importance, imperiled conservation status, estuary-dependent life-histories, and available bioenergetic parameters (Plumb and Moffitt, 2015; Price et al., 2017; Atlas et al., 2021; Chalifour et al., 2021). The Wisconsin model is an energy balance equation where energy consumed by a fish is balanced against metabolism, waste losses, and growth (Deslauriers et al., 2017). Model inputs of water temperature, prey energy density (ED_{prey}), predator energy density (ED_{fish}), starting weight, and the proportion of maximum consumption (P_{cmax}) can be used to estimate fish growth. We ran models on a daily time-step with inputs of daily-averaged water temperature and constant values of P_{cmax}, ED_{prey}, ED_{fish}, and starting weight with an output of weight per day. A separate model was run with each full temperature logger dataset to examine differences in juvenile Chinook salmon growth under different thermal regimes across the two estuaries. We did not run a model for the Salmon River estuary site with a July-August dataset (Meadow 2) to maintain consistency in start timing.

A starting weight of 5 grams was chosen to represent sub-yearling fish entering the estuary in early May (Davis et al., 2019). ED_{prey} was set to 4000J based on recent values from bomb-calorimetry studies of juvenile Chinook salmon estuarine diets (David et al., 2014; Davis et al., 2019). ED_{fish} was calculated as a function of body mass (Stewart et al., 1983). We set P_{cmax} to 0.6, which is an ecologically plausible consumption rate for juvenile Chinook salmon in estuaries (Davis et al., 2019, Kaylor et al., 2021). Physiological parameters for juvenile Chinook salmon were used in all simulations, which sets the thermal optimum for consumption at 20.93°C (Stewart and Ibarra, 1991; Plumb and Moffitt, 2015). All models were run with the R shinyApp program Fish Bioenergetics 4 (Deslauriers et al., 2017). The model outputs of daily weight were used to calculate daily growth rate potential (GRP) as follows, where t1 and t2 are on daily time increments:

$$\frac{\%\ change\ in\ body\ mass}{day} = \frac{weight_{t2} - weight_{t1}}{weight_{t1}} \times 100\,\%$$

We calculated average monthly GRP for each site from May-August to compare relative growth between sites over the summer.

An increase of 2°C was applied to all temperature datasets to simulate a simplistic end-of-century climate change scenario. We chose 2°C given end-of-century predictions for sea-surface (1.3-4.4° C from 2010-2099 in the northeast Pacific Ocean) and river (several degrees) temperature increases, although we recognize the limitations and assumptions of this method, as further detailed in the discussion (Mantua et al., 2010; van Vliet et al., 2013; Hoegh-Guldberg et al., 2014). Keeping all other parameters constant, we re-ran the bioenergetics models for each logger site under the increased temperature scenarios to investigate shifts in juvenile Chinook salmon GRP patterns.

3 Results

3.1 Water temperature

Water temperatures generally increased from May-July across both estuaries, although the Englishman River estuary reached substantially warmer temperatures than the Salmon River estuary. At all Englishman River estuary sites, water temperature peaked in late July before decreasing slightly and roughly plateauing through August (Figure 2). For example, at a marsh site (Marsh 2), weekly mean temperature increased from 11.6°C in early May (May 5-11) to 22.9°C in late July (July 25-31). Mean weekly temperature at the end of August (Aug 20-26) was 21.7°C (Supplementary Figure 1). In comparison to the Englishman River estuary, Salmon River estuary temperatures followed a similar pattern, although May-July increases were generally smaller (Figure 2). For example, at a marsh site (Marsh 3), weekly mean temperature increased from 9.4°C (May 5-11) to 14.0°C (July 25-31). August temperatures in the Salmon River estuary displayed a steady trend with a mean of 13.5°C in late August (Aug 20-26) (Supplementary Figure 1). Thus, estuary temperatures generally increased during the spring to summer, but reached substantially warmer temperatures in the Englishman River estuary relative to the Salmon River estuary.

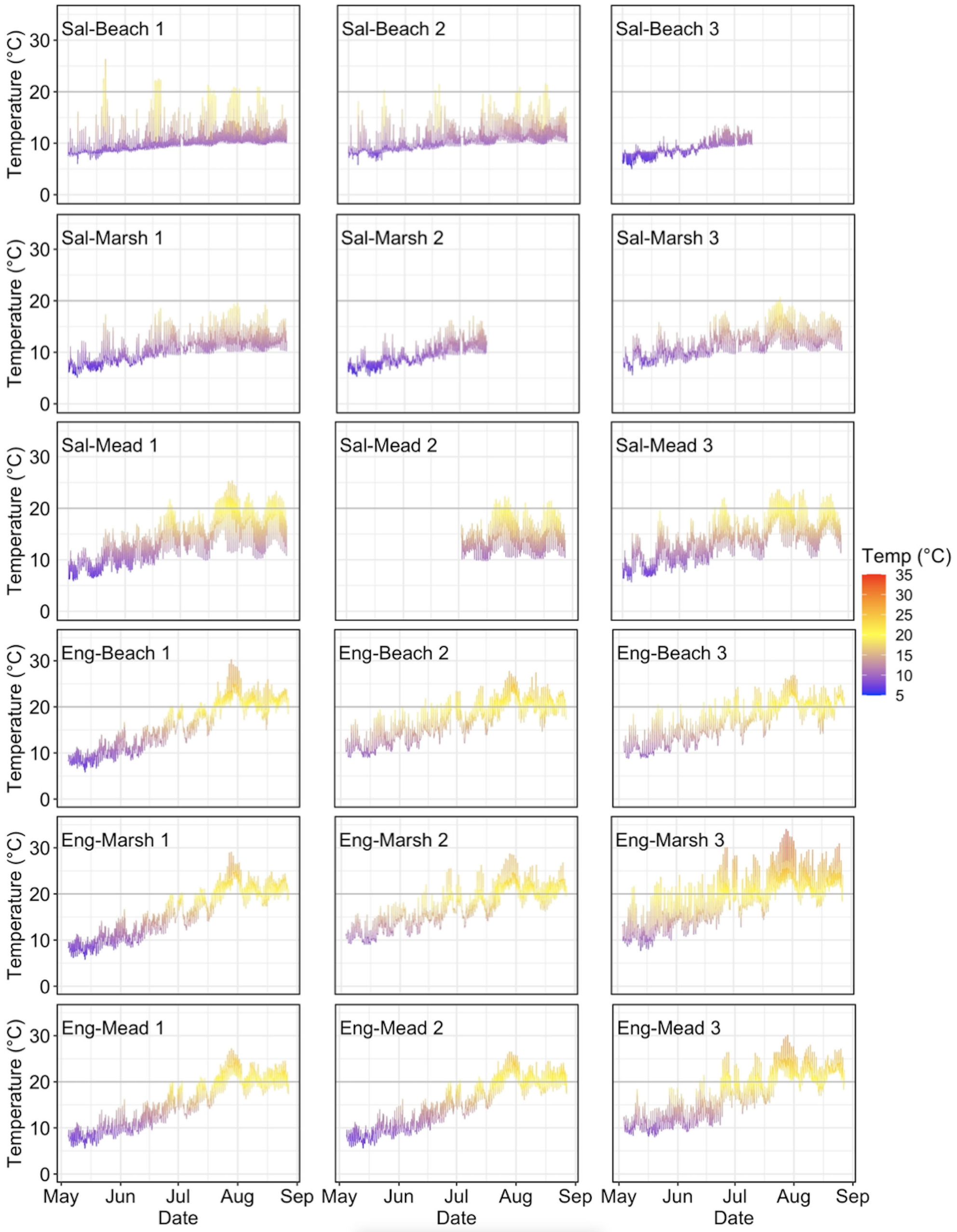

FIGURE 2
May-August water temperature for each temperature logger site in the Salmon and Englishman River estuaries. Each panel displays temperature from one temperature logger. Water temperature is color-coded by value, with the scale bar to the right of the panels. The horizontal gray line in each panel indicates the 20°C isoline to ease comparability between each plot.

Temperatures varied across different estuary habitats through time, although this thermal diversity was greater in the Salmon River estuary compared to the Englishman River estuary. The Salmon River estuary GAM and pairwise difference smooths indicated that all habitat-level smooths differed significantly from each other at more than one time throughout the summer (Figure 3). Broadly, meadow habitat had significantly lower early-summer temperatures and significantly higher late-summer temperatures compared to both beach and marsh habitats. Differences between marsh and beach habitat temperatures were smaller, but marsh temperatures were significantly lower in parts of May-June and significantly higher in parts of July. As an example, at the end of July (July 25-31), weekly mean temperatures were 11.8°C (beach), 13.4°C (marsh), and 17.9°C (meadow) (Supplementary Figure 1). In the Englishman River estuary, the GAM and pairwise difference smooths showed that only meadow habitat differed significantly from the beach and marsh habitats over the summer (Figure 3). Meadow habitat had significantly lower temperatures in parts of May-June, and significantly higher temperatures in parts of July-Aug compared to marsh and beach habitat, although differences were smaller than in the Salmon. For example, weekly mean temperatures at the end of July (July 25-31) were 22.9°C

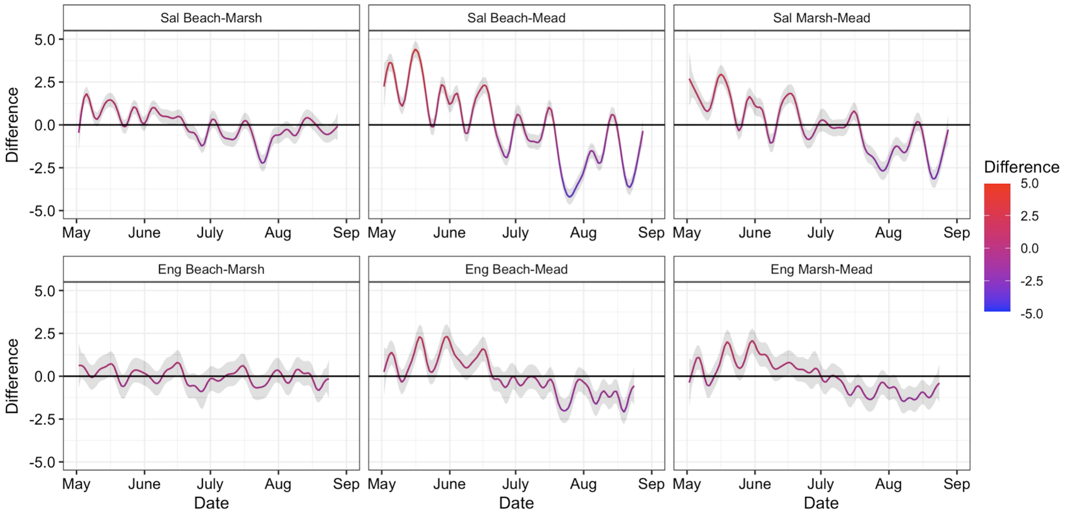

FIGURE 3
Difference smooths for each pairwise habitat type combination from the factor-smooth interactions of day and habitat type in the GAMs for the Salmon and Englishman River estuaries. Each panel displays the difference between the two habitat-level smooths indicated in the title from May-August, with the 95% credible interval included as a gray ribbon. Pairwise differences from the Salmon River estuary are displayed in the first row, with pairwise differences from Englishman River estuary below. Where the credible interval does not include zero, the pair of habitats have significantly different temperatures for that date.

(beach), 24.0°C (marsh), and 23.6°C (meadow) (Supplementary Figure 1). Therefore, different habitats had diverse temperatures that were asynchronous through time, with the Englishman River estuary having a warmer and more homogenous temperature mosaic than the Salmon River estuary.

Estuary temperature dynamics across time appeared to be driven in part by two key processes: first, there was a seasonal reversal in the temperature differences between ocean and freshwater inputs; second, tidal fluctuations controlled fine-scaled temperature patterns. Across both estuaries, the relationship between tide height and water temperature displayed a clear daily pattern that shifted seasonally at some sites. In early summer, high tide corresponded with warmer temperatures, but by mid-late summer, cooler temperatures were observed at high tides. This pattern suggests that sea-surface temperature (SST) is initially warmer than river temperature—thus, tidal influxes bring warmer water into the system—before reversing at some point over the summer. Indeed, this reversal is evident through a comparison of regional ocean and river temperature data for both systems, where river temperatures are initially cooler in early summer before exceeding more stable ocean temperatures (Supplementary Figure 3). Interestingly, the timing of this switch differed between estuaries. For example, a beach site in the Salmon River estuary (Beach 3) displayed the change about a month earlier than an Englishman River estuary beach site (Beach 1), reflecting differences in river and ocean temperature trends between the systems (Figure 4, Supplementary Figure 2, Supplementary Figure 3). On a larger spatial scale, between-habitat temperature differences in both estuaries also illustrate this shifting pattern between ocean and river temperatures—in early summer, river-dominated meadow habitat was generally cooler than beach and marsh habitats before switching in July (Figure 3). However, this seasonally shifting pattern was not evident across all sites. For some sites with limited freshwater influence (e.g. Sal-Beach 1 and Eng-Beach 3), high tide always corresponded with lower water temperatures. In addition, not all sites showed a clear link between water temperature and tide (e.g. Eng-Marsh 3). Instead, water temperature at these sites consistently peaked in the afternoon alongside air temperature, suggesting that these sites are likely more isolated from tidal flushing. Together, these complex temporal patterns of estuary temperatures suggest that rivers switch from being a source of cooler water to warmer water compared with the more stable ocean water temperatures over the summer, and that the magnitude and timing of tidal ebb and flow drives temperatures on a fine scale, all mediated by habitat complexity.

3.2 Bioenergetics

The complex temperature mosaics within estuaries led to diverse growth opportunities for juvenile Chinook salmon across space and time, with temperatures ranging from colder-than-optimal, optimal, and excessively hot. Under present conditions, juvenile Chinook salmon GRP generally increased through early summer across both estuaries as temperatures warmed, but declined sharply in the Englishman River estuary over mid-late summer when temperatures got too hot (Figure 5). In the Englishman River estuary, average GRP was highest in June before dropping to negative values in late-July and early-August as summer temperatures peaked. This broad temporal trend was consistent estuary-wide, but spatio-temporal temperature patterns within the system generated variable growth opportunities between habitats and sites. For example, on a monthly timescale, average GRP was highest in marsh habitat in May, but highest in beach habitat from

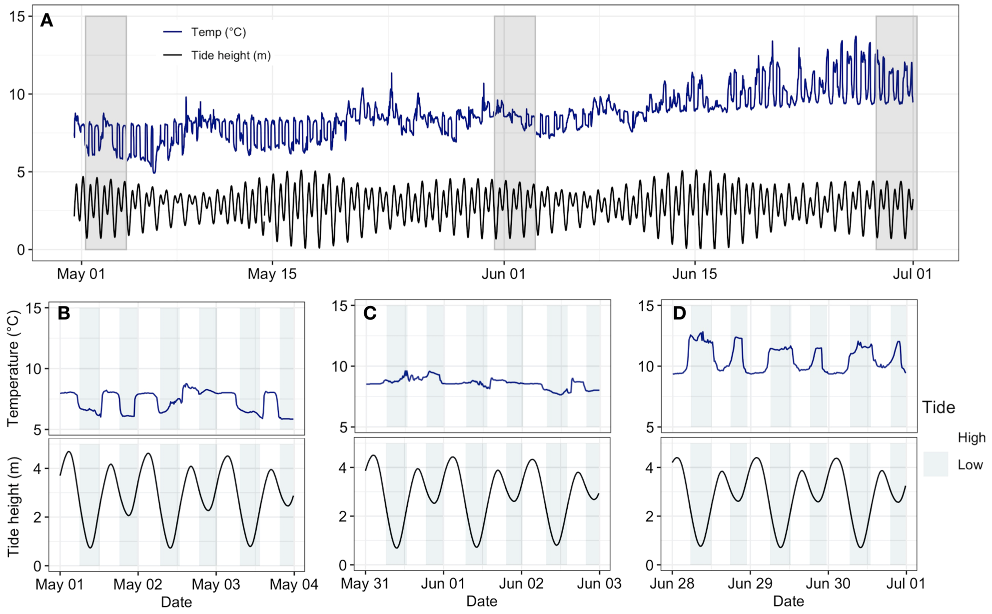

FIGURE 4
May-June water temperature (blue line) and tide height (black line) for site Beach 3 in the Salmon River estuary. Tide height data is from the nearest Fisheries and Oceans Canada station (Department of Fisheries and Oceans Canada (DFO), 2023c—Tides, currents, and water levels for Kelsey Bay-08215). **(A)** Temperature and tide height over the full May-June period. The grey bars indicate the time periods displayed in **(B–D)**. **(B)** Temperature and tide height from May 1-3. Low tide corresponds with lower water temperatures. High and low tides are indicated by light and dark blue bars in **(B–D)**. **(C)** Temperature and tide height from May 31-June 2. Water temperature shows little variation with tide height. **(D)** Temperature and tide height from June 28-30. Water temperature is higher at low tides.

June-August. In contrast, growth opportunities in the Salmon River estuary continued to increase into July and remained stable through August as water temperatures never exceeded optimal growth conditions. GRP patterns between habitats were more consistent in the Salmon River estuary, with the highest average monthly GRP in meadow habitat across all months. Comparing growth potential between the two estuaries, GRP was generally higher across the Englishman River estuary from May-June. This trend switched from July-August, with higher GRP throughout the Salmon River estuary. Thus, spatio-temporal temperature patterns led to variable growth opportunities within and between estuaries, with warmer temperatures in the Englishman River estuary leading to higher early-summer GRP but substantial declines by late-summer, while lower temperatures in the Salmon River estuary created positive, stable GRP trends through the summer.

The simple climate change scenario had variable impacts between estuaries, with GRP increases across most habitats and times in the Salmon River estuary, but consistent GRP declines through the Englishman River estuary from June-August (Figure 5). Growth opportunities in the Salmon River estuary improved across all habitats from May-June, as an increase of 2°C pushed temperature mosaics closer to optimal conditions. Average GRP in beach and marsh habitats continued to increase in July-August, while meadow habitat GRP declined in late-summer as temperatures became excessively hot. These shifting patterns drove changes in relative GRP between habitats over space and time—average growth potential was highest in meadow habitat from May-June, but switched to marsh habitat from July-August. In the Englishman River estuary, warmer temperatures drove higher GRP across habitats in May, but temperatures began to exceed optimal growth conditions by June, causing GRP declines estuary-wide through mid-late summer. Relative GRP between habitats also changed in the Englishman River estuary as temperatures reached and exceeded optimal temperatures asynchronously. GRP was highest in beach and marsh habitats in May, meadow habitat in June, beach and meadow habitat in July, and beach habitat in August. By this final month, average GRP was negative across all habitats, effectively limiting the rearing capacity of the estuary to earlier in the summer. Between the two estuaries, growth potential was similar between the Englishman and Salmon River estuaries in May-June, but consistently higher in the Salmon River estuary from July-August. Therefore, increasing temperatures by 2°C largely expanded growth opportunities across space and time in the Salmon River estuary, but constricted growth opportunities to early-summer in the Englishman River estuary, illustrating how the nursery capacity of the Salmon River estuary may be more resilient to oncoming climate warming relative to the Englishman River estuary.

4 Discussion

This study reveals how complex spatio-temporal summer water temperature patterns within and between two estuaries on Vancouver Island, BC provide rich mosaics of growth opportunities for juvenile Chinook salmon that may be challenged by climate warming. Different habitats had different water temperatures. Multiple processes likely drove these

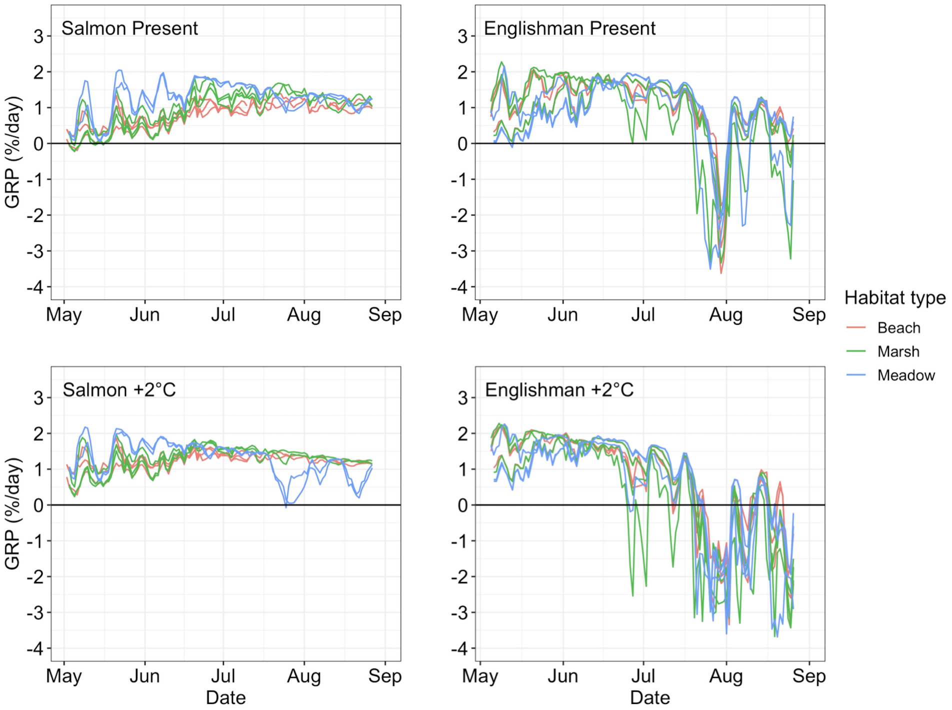

FIGURE 5
Juvenile Chinook salmon growth rate potential (GRP) for the Salmon and Englishman River estuaries under present and +2°C scenarios from May-August. Present GRP trends are shown in the top two panels for each estuary, while +2°C GRP trends are displayed below. The individual lines represent GRP at each temperature logger site, and these lines are color-coded by habitat type with the key to the right of the panels.

temperature patterns, including local climate setting, tidal influence, seasonally changing river and ocean temperatures, and habitat processes that together generated asynchronous temperature dynamics between habitats and sites over time. These dynamic temperature patterns drove shifting mosaics of growth opportunities. In the smaller, more degraded estuary with warmer and more variable climatic patterns (Englishman), temperatures reached excessively hot temperatures at some habitats and times, leading to substantial declines in growth opportunities over the summer. These declines were exacerbated in the simplified climate change scenario, further limiting favorable growth opportunities to early-summer. Water temperatures in the larger, more intact system with cooler and more stable climatic influences (Salmon) never exceeded optimal growth conditions, creating a mosaic of positive growth opportunities across the summer that was largely enhanced by increasing temperatures. Therefore, this study illustrates how modest levels of climate change may increasingly limit estuarine nursery capacity across some habitats and times—but expand it in others—dependent on the underlying spatio-temporally complex temperature patterns and associated portfolios of growth opportunities.

The dynamic temperature patterns across both systems implicate several key underlying processes. First, at the interface between rivers and oceans, estuarine temperatures are shaped by interactions between ocean and river temperatures (Thomson, 1981; Wooldridge and Deyzel, 2012; Khadami et al., 2022). In both the Salmon and Englishman River estuaries, this was evident when predominantly river-influenced meadow habitats were coolest in early summer but warmest in late summer, reflecting a pattern where river temperatures warm and eventually exceed more stable ocean temperatures through the summer (Hall et al., 2018). The timing of this pattern varied between systems, likely driven by differing river and regional ocean temperatures. For example, mean weekly stream temperature from May 5-11 was 6.6°C in the Salmon River *vs.* 7.2°C in the Englishman River, and regional ocean temperature for the same period was 9.65°C in Johnstone Strait and 10.17°C in the Strait of Georgia (Department of Fisheries and Oceans Canada (DFO), 2023b—British Columbia Lightstation Sea-Surface Temperature and Salinity Data (Pacific), 1914-present for Pine Island [data for the Salmon River estuary], Department of Fisheries and Oceans Canada (DFO), 2023a—British Columbia Lightstation Sea-Surface Temperature and Salinity Data (Pacific), 1914-present for Departure Bay [data for the Englishman River estuary]). Regardless, the seasonal reversal in temperature gradient across estuaries is an intriguing and likely widespread phenomenon at these latitudes. Second, tidal inundation interacted with these river and ocean temperature patterns to shape daily temperature fluctuations (Schumann, 2000; McKay and Iorio, 2008). At some sites, cyclic patterns reflected river and ocean temperature dynamics where lower temperatures occurred at high tide before reversing later in the summer, but this only occurred where there was substantial oceanic and freshwater mixing. In addition, temperature variability was likely also influenced by local habitat and site-specific features including flow patterns, aquatic and riparian vegetation, and channel connectivity (McKay and Iorio, 2008; Fogarty et al., 2018). For example, one of the Englishman

River estuary meadow sites (Mead 3) is in a pool that disconnects from the channel at low tide—therefore resulting in stagnant flows—which may have contributed to higher temperatures relative to the other meadow sites that are both in higher flowing freshwater tributaries. Last, meteorological patterns obviously controlled water temperatures. For example, a heat dome occurred across Vancouver Island in late July, driving air temperatures in the Englishman River estuary up to 32°C and resulting in water temperatures in excess of 30°C at some estuary sites (Environment and Climate Change Canada-Meteorological Service of Canada (ECCC-MSC), 2023b). In comparison, air temperatures in the Salmon River estuary reached 22°C and water temperatures at some sites exceeded 20°C (ECCC-MSC 2023—Historical Climate Data for Fanny Island, British Columbia). Thus, these data reveal the underlying processes that generate spatio-temporal temperature dynamics within each system, working alongside key between-estuary differences in climate, oceanography, complexity, and degradation.

One of the striking patterns in this study was the degree to which one estuary (Englishman) had warmer and more homogenous water temperatures than the other (Salmon), which remained cool and more variable over space. We recognize that a comparison of only two estuaries offers limited inference, but suggest that these patterns bear careful consideration. First, the Englishman River estuary experiences warmer and more variable climatic patterns relative to the Salmon River estuary, which is likely driven in part by differing oceanographic patterns between the systems. Johnstone Strait (Salmon) has relatively cool and stable year-round temperatures with consistent vertical mixing, while the Strait of Georgia (Englishman) displays strong seasonal variability, year round vertical stratification, and warmer summer temperatures. These differences likely influence local climate patterns including air temperatures and fog frequency (Thomson, 1981, Supplementary Figure 3). Therefore, marine and climatic influences in each system vary considerably. In addition, the Englishman River has warmer water temperatures and lower discharge in the spring-summer relative to the Salmon River, which together brings warmer freshwater inputs into the Englishman River estuary [Supplementary Figure 3; Environment and Climate Change Canada (ECCC), 2023b); Environment and Climate Change Canada (ECCC) (2023a)]. Together, these differing atmospheric, terrestrial, and marine inputs may help explain the cooler summer water temperatures across the Salmon (Thomson, 1981; Vaz and Dias, 2008; Roegner et al., 2011; Cho and Lee, 2012). Additionally, the Salmon River estuary is a larger and more complex system, with over twice the area of the Englishman River estuary and more intact estuary habitats. Estuary size and morphology are known to impact mixing patterns and heat dispersion, where smaller systems are usually more well-mixed (McKay and Iorio, 2008, Webb, 2020). The Englishman River estuary is also more degraded, with a dammed and heavily urbanized upstream river that often runs at minimum baseflows throughout the summer that could more easily reach radiative equilibrium with the atmosphere, agriculture and logging across the watershed, and encroaching residential developments constraining the estuary (Boom and Bryden, 1994, Environment and Climate Change Canada (ECCC), 2023b); Sutherland, 2014). These characteristics have been linked to warmer and more homogenous temperature regimes in river systems (Olden and Naiman, 2010; Somers et al., 2013; Juracek et al., 2017; Cunningham et al., 2023). We suggest that understanding the impact of watershed and estuary degradation on estuary temperature mosaics is a key research priority for future work.

The complex summer temperature patterns across both estuaries generated shifting spatio-temporal mosaics of growth opportunities for juvenile Chinook salmon. Water temperatures fluctuated above and below the thermal optimum for consumption (20.9°C) at differing magnitudes and times between estuaries, habitats, and sites—thus, while growth opportunities shared similar seasonal trends across each system, they also varied at smaller habitat and site-level scales (Plumb and Moffitt, 2015). These multiple scales of variability generated portfolios of potential growth across the estuaries, which would be expected to drive several important responses in juvenile Chinook salmon (Greene et al., 2021; Davis et al., 2022). In both freshwater and estuarine systems, for example, water temperature has been shown to direct movement and habitat use patterns, where juvenile salmon will select for metabolically favorable conditions (Armstrong and Schindler, 2013; Matsubu et al., 2017; Morrice et al., 2020). In addition, estuarine water temperatures have been linked to the duration of estuary residency (Greene et al., 2021). For example, when temperatures exceeded tolerable rearing conditions, juvenile Chinook salmon have been found to spend less time in estuarine habitats before outmigrating and entered the ocean at smaller sizes (Munsch et al., 2019). These changes could have cascading impacts on subsequent marine survival (Sawyer et al. in press). Thus, our study serves as a first step towards understanding and predicting these key physiological and ecological responses to temperature mosaics, which may have important consequences for juvenile salmon during this life-history transition to sea.

The simplified warming scenario illustrated how forthcoming climate warming may have diverging impacts on estuarine growth opportunities for juvenile Pacific salmon, dependent on baseline temperatures and habitat complexity (Nielsen et al., 2013; Zhang et al., 2019). Our study was performed with a single year of temperature data and simple warming assumptions—climate change will undoubtedly manifest with more unpredictability across time given complex climatic processes and ecological patterns. That being said, our study did reveal several key findings that we anticipate will be robust to these study limitations. First, excessively warm temperatures have already made some estuarine habitats unsuitable at certain times, and climate warming will further constrict growth opportunities for cold water fishes such as salmon over space and time. Second, estuaries and habitats have differing vulnerabilities to these impacts—in some cases, rising temperatures may actually expand summer growth opportunities across cooler and more heterogenous systems like the Salmon River estuary over the next few decades, depending on climate change. However, these gains will have a finite temporal window—as temperatures continue to rise beyond a few degrees and exceed thermal tolerances, portfolios of growth opportunities will collapse. As temperature mosaics approach and exceed these tolerances, juvenile salmon will likely face several physiological and ecological consequences. For example, Marine and Cech (2004) found that juvenile Chinook salmon experimentally reared in 21-24°C experienced significantly decreased growth, impaired smoltification indices, and increased predation vulnerability in estuaries compared to fish reared at lower temperatures. In addition, the timing and duration of estuary migration could start to shift as temperatures rise, which may lead to phenological mismatches in marine prey availability (Visser and Both, 2005; Crozier et al., 2008; Wilson et al., 2021; Wilson et al., 2023). Our study suggests that juvenile salmon in warmer systems like the Englishman River estuary may face these consequences more acutely and rapidly, while growth opportunities may increase before losses occur in systems like the Salmon River estuary that are not as far along in this trajectory of warming.

Our bioenergetics modeling approach entailed assumptions and simplifications that are important to consider. Throughout all simulations, we held prey energy density and the proportion of maximum consumption at constant literature-obtained values given our lack of empirical data. However, numerous studies have shown that prey communities vary over space and time across estuaries (Arbeider et al., 2019; Davis et al., 2019; Woo et al., 2019; Weil et al., 2020). In addition, prey community dynamics are expected to shift under climate change, which we did not account for in our climate change scenario (Daufresne et al., 2004; Hallett et al., 2018; Woodland et al., 2021). Given this variability in prey resources, the proportion of maximum consumption for juvenile salmon could also vary spatio-temporally, and potentially shift with climate change (Beauchamp, 2009; Davis et al., 2019; Kaylor et al., 2021). Therefore, further work is needed to understand how prey mosaics shape present and future growth opportunities across these systems, but we suggest that the reasonable prey and consumption parameters we selected nonetheless generated useful estimates of growth potential. Our approach of applying a 2°C increase to temperature across all sites based on a single year of temperature data for the climate change scenario is also a major simplifying assumption. While this methodology allowed for a simplistic evaluation of potential impacts on juvenile Chinook salmon GRP, water temperature will not increase uniformly over space and time in estuaries. Process-based and statistical models of water temperature have the ability to account for some of this variability, and could therefore be used to improve estimates of future GRP (Wagner et al., 2011; Brown et al., 2016; Davis, 2019; Des et al., 2020).

In addition to water temperature, climate change will drive shifts in other key estuarine conditions that may impact the nursery quality of estuaries for juvenile salmon. Over the coming century, sea level rise (SLR) is projected to transform estuarine habitat mosaics, and systems constrained by coastal development may disappear entirely without the ability to migrate inland (Craft et al., 2009; SChile et al., 2014; Thorne et al., 2018). These changes are expected to impact habitat availability, connectivity, and growth opportunities for juvenile salmon (Fulford et al., 2014; Torio and Chmura 2015; Flitcroft et al., 2018). For example, Davis et al. (2022) found that under end-of-century SLR and temperature scenarios, juvenile Chinook salmon are predicted to experience decreased summer growth in the Nisqually River estuary, WA, USA. In addition to rising sea levels, many other climate change-induced shifts including ocean acidification, extreme river flows, and more frequent and intense storm activity will potentially impact estuarine habitat structure and quality (Lee et al., 2016; Munsch et al., 2019; Scanes et al., 2020; Lonsdale et al., 2022). These climatic changes will occur alongside growing anthropogenic pressures such as pollution and habitat alteration, which together may have cumulative or interacting effects on estuarine nursery capacity (Lotze et al., 2006; Healey, 2011; Jorgensen et al., 2013; Toft et al., 2018; Hodgson et al., 2020; Tulloch et al., 2022). Thus, investigating changes in individual conditions such as water temperature is an important piece of the puzzle, but future work is needed to continue building an understanding of more comprehensive shifts in estuary quality and function for juvenile salmon with global change (Hodgson et al., 2020).

Our study demonstrates how variability in a key estuarine habitat condition, water temperature, shapes diverse growth opportunities for juvenile Chinook salmon in two contrasting estuaries. Across both systems, growth potential shifted across habitats and sites through the summer, suggesting that juvenile Chinook salmon could increase their growth by using different estuarine habitats over time (Greene et al., 2021). These portfolios of growth and habitat use may also confer resiliency to estuarine systems, as high GRP in some habitats can compensate for lower GRP across others (Harley et al., 2006; Peirson et al., 2015; Greene et al., 2021). However, we illustrate that as temperature increases across a smaller system with more homogenous spatial temperature patterns like the Englishman River estuary, growth opportunities faced consistent declines estuary-wide. In contrast, when temperatures were increased across a cooler and more complex system like the Salmon River estuary, only some sites faced decreased growth opportunities while others remained stable or increased given higher spatial heterogeneity within the estuary. Together, this underscores the importance of maintaining diverse temperature mosaics across estuaries, which will be especially important for creating and sustaining thermal refuges as temperatures continue to rise (Waples et al., 2009; Wade et al., 2013). Therefore, looking ahead, conservation and management initiatives that aim to maintain spatio-temporal habitat complexity and connectivity among these habitats can serve to support diverse growth opportunities and other key ecological functions for important species like Pacific salmon in this era of climate change (Beck et al., 2001; Schindler et al., 2010; Nagelkerken et al., 2015; Sheaves et al., 2015; Moore and Schindler, 2022).

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.5281/zenodo.8033874.

Author contributions

PG: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. JG: Investigation, Methodology, Writing – review & editing. DS: Investigation, Methodology, Writing – review & editing. JM: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. CoF: Investigation, Methodology, Writing – review & editing. CeF: Investigation, Methodology, Writing – review & editing. CM: Investigation, Methodology, Writing – review & editing. CB: Investigation, Methodology, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1278810/full#supplementary-material

SUPPLEMENTARY FIGURE 1
Violin plots illustrating the distribution of water temperature data from every temperature logger site over three one-week periods between May-August. Abbreviations E and S indicate the Englishman and Salmon River estuaries, respectively, and abbreviations B, Ma, and Me indicate beach, marsh, and meadow habitat types, respectively. **(A)** Water temperature distributions from May 5-11 for each site. **(B)** Water temperature distributions from July 25-31 for each site. **(C)** Water temperature distributions from August 20-26 for each site. Across all panels, the black dot indicates the mean temperature for each site for the respective week.

SUPPLEMENTARY FIGURE 2
May-August water temperature (blue line) and tide height (black line) for site Beach 1 in the Englishman River estuary. Tide height data is from the nearest Fisheries and Oceans Canada station (Department of Fisheries and Oceans Canada (DFO), 2023d—Tides, currents, and water levels for Nanoose Bay-07930). **(A)** Temperature and tide height over the full May-August period. The grey bars indicate the time periods displayed in **(B–D)**. **(B)** Temperature and tide height from May 11-13. Low tide corresponds with lower water temperatures. High and low tides are indicated by light and dark blue bars in **(B–D)**. **(C)** Temperature and tide height from July 13-15. Water temperature shows little variation with tide height. **(D)** Temperature and tide height from August 15-17. Water temperature is higher at low tides.

SUPPLEMENTARY FIGURE 3
Air temperature (red lines), river temperature (light blue lines), regional ocean temperature (dark blue lines) and river discharge (green lines) for the Englishman (left) and Salmon (right) River estuaries. River and regional ocean temperature data is plotted together to illustrate the seasonal reversal in relative temperature. Air temperature data is from the nearest Meteorological Service of Canada weather stations (Environment and Climate Change Canada-Meteorological Service of Canada (ECCC-MSC), 2023a [data for the Salmon River estuary], Environment and Climate Change Canada-Meteorological Service of Canada (ECCC-MSC), 2023b [data for the Englishman River estuary]), regional ocean temperature data is from the nearest Department of Fisheries and Oceans lighthouse stations (Department of Fisheries and Oceans Canada (DFO), 2023b—British Columbia Lightstation Sea-Surface Temperature and Salinity Data (Pacific), 1914-present for Pine Island [data for the Salmon River estuary], Department of Fisheries and Oceans Canada (DFO), 2023a—British Columbia Lightstation Sea-Surface Temperature and Salinity Data (Pacific), 1914-present for Departure Bay [data for the Englishman River estuary]), and river discharge data is from Environment and Climate Change Canada maintained hydrometric stations (Environment and Climate Change Canada (ECCC), 2023b [data for the Englishman River estuary], Environment and Climate Change Canada-Meteorological Service of Canada (ECCC-MSC), 2023a [data for the Salmon River estuary).

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