

Examining Environmental and Morphological Impacts on Rainbow Smelt (*Osmerus mordax*) Spawning Behavior

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Introduction

Movement, or the ability of an organism to alter its location in response to stimuli, can play a major role in determining the fitness of individuals, dynamics of populations, and the ability to adapt to localized change. Driven by various environmental and physiological processes, these directed responses to stimuli allow organisms to take advantage of habitat variation, follow food resources, and avoid competition (Nathan et al., 2008). With anthropogenic activities increasing the frequency of habitat fragmentation and rapid environmental change, populations are under strong selection to move or quickly adapt to survive. Understanding the mechanisms and consequences of movement is vital to successful management and restoration of ecosystems (Nathan et al., 2008).

Anadromous fish move in large numbers from the ocean to freshwater to spawn in optimal habitat. During these migrations, fish are exposed to intense selective pressures such as seasonal time constraints, varying environmental conditions, and differences in physiological capabilities that may affect an individual's ability to complete their life history. This ability to move and interact with other species in the ecosystem contributes to anadromous fish ecosystem services such as nutrient cycling, food web regulation, habitat formation, biological diversity, human consumption, and cultural importance for many indigenous communities (Ouellet et al., 2022). Anadromous fish used to run through river systems in the millions, however, recently the abundances of these fish have diminished due to a loss of ecosystem connectivity from large scale environmental changes and human activities (Saunders et al, 2006).

In the Northern Atlantic, rainbow smelt (*Osmerus mordax*) are listed as an anadromous "species of concern" (NOAA, 2004). Historically, rainbow smelt were present in high numbers and supported major ice fisheries in New Hampshire and Maine. With the reduction in ice cover and fish abundance in these areas, ecosystem services provided by rainbow smelt have become limited. For example, it is hypothesized that declines in rainbow smelt populations may have been a major factor in the low population estimates of Atlantic salmon spawners as they

are an important prey resource in the spring (Saunders, 2006). The factors that contribute to this major decline in rainbow smelt populations are not fully understood, however it has been hypothesized to be a combination of degradation of spawning habitat, stream obstructions, declines in water quality, fishing pressure, and predator-prey relationships (Enterline, 2013). Identifying major threats, habitat preferences, and population structure may aid in conservation and management efforts.

Rainbow smelt undergo spawning migrations in the early spring and timing varies latitudinally as the ice begins to recede. In Great Bay Estuary in New Hampshire, rainbow smelt are found to migrate upstream to spawning sites in mid-March. The timing of post-spawning migrations is not well known, but recent studies predict adult emigration in the southern part of their range to be sometime in mid-May (Pearson et al, 2024). Site fidelity has been reported to be low for specific tributaries, however, most individuals return to their natal estuaries to spawn (Bradbury et al, 2011). Once adults reach spawning grounds, they deposit their eggs into the substrate, and depending on temperature, they will hatch 1-3 weeks later. Downstream larval dispersal relies heavily on the hydrography of the region (Kovach et al., 2012). Juveniles will remain in the estuary or coastal area throughout the summer and into the early fall.

Recent research has begun to explore some of the environmental and morphological factors that contribute to the success of rainbow smelt spawning and survival. Rainbow smelt migrate into estuarine and river systems in search of optimal environmental conditions to spawn. Across their geographic range, anadromous rainbow smelt optimal spawning temperatures vary. In Massachusetts and New Hampshire, rainbow smelt tend to start their spawning season when temperatures reach 3.5°C to 6.3°C and runs span three to six weeks (Chase, 2006). Rainbow smelt almost never exceed 250mm in length and are short-lived, often not surviving past 5 years. By age 2, they are fully mature and ready to undergo migrations to spawning grounds. Age-1 rainbow smelt are found at spawning grounds in higher numbers in Massachusetts, New Hampshire, and southern Maine in comparison to areas further north into Canada. Most of these age-1 migrating fish tend to be males following the masses of adults up the river to spawn (Enterline et al., 2012).

Using annual fyke net data collected by New Hampshire Fish and Game from three rivers in the Great Bay Estuarine River system, the current paper aims to assess environmental and morphological factors that may contribute to Rainbow smelt migratory behavior and spawning habitat selection. Specifically, we will assess 1) the water temperature variation between the Winnicut, Squamscot, and Oyster rivers in Great Bay, NH over time and whether there is an optimal temperature range across all three rivers for peak rainbow smelt spawning, 2) the relationships between length and age classes of rainbow smelt with spawning behavior in the three rivers and over time. These analyses may help us predict what temperature, size, and age class can tell us about migration timing and future population resiliency.

Methods

Field work was performed between mid-March and early April from 2019 to 2023 by New Hampshire Fish and Game in Great Bay Estuary, NH. Sampling took place at sites in the Oyster, Squamscott, and Winnicut rivers that were representative of a range of watershed conditions known to support rainbow smelt spawning behavior. Additional spawning has been observed in the Bellamy, Salmon Falls, and Lamprey rivers however these rivers are not currently being monitored (Enterline et al., 2012).

Fyke nets were deployed in the mid-channel zone of each river downstream of the limit of rainbow smelt egg deposition. Nets were set for three nights each week during overnight low tides. On the next low tide, nets were checked, and contents were emptied into buckets with aerators depending on the size of the catch. Total lengths of up to 100 male and 100 female rainbow smelt were measured in millimeters. All remaining smelt were counted and sexed. Fin clips were also taken to track recaptures. Bycatch species were identified and up to 25 fish per species were measured in each sample.

Over the course of sampling, scale samples for each centimeter size class for each sex were collected from Rainbow smelt to assess age. Approximately 10 scale samples were collected for each centimeter size class. All scales were placed in a 1.5 mL micro-centrifuge tube with 2% pancreatin solution to remove the mucus membrane. Scales were aged using a QImaging microscopy camera and Image-pro software by two different readers to account for discrepancies and increase accuracy.

Environmental data was collected using a YSI 6920v2 to record daily snapshots of the pH, temperature, specific conductivity, dissolved oxygen, and turbidity at each site below spawning locations where fyke nets were set. Environmental data was paired with catch data to assess the impact of external factors on the timing of rainbow smelt movements.

To analyze the impacts of environmental and morphological factors on rainbow smelt spawning behavior, we used the software, R v. 4.4.1 (R Core Team, 2020). To examine the environmental data and determine if there were differences in the water temperatures between rivers and throughout the study period, we used an ANOVA test. The first model included the water temperatures recorded throughout the five years in each of the three rivers, Winnicut, Squamscot, and Oyster and the second model included the water temperatures recorded using the YSI during each haul date for each of the five years of the study. To observe if there was an optimal temperature difference for fish catches between years and between rivers, we determined the peak temperatures and used an ANOVA.

To examine morphological data and determine if there were differences in the lengths of rainbow smelt between rivers during the timeframe of this study, the Kruskal Wallis test was used due to unequal variances. A linear model was run to observe the relationship between fish length (mm) and calendar day to see if there was any relationship between the size of the fish and when they begin their migrations into tributaries to spawn. To determine if there was a difference in the proportion of age classes between years we used a chi-squared test. Finally, a linear model

was run to observe the relationship between age and calendar day to validate the relationship in the previous linear model.

Results

To observe the change in total rainbow smelt counts between 2019 and 2023 we used total catch data from each of the three rivers (Oyster, Squamscott, Winnicut) (Figure 1). The highest total catch was in 2022 ($n=2375$) and the lowest total catch was in 2019 ($n=844$). Over the five years, most rainbow smelt were caught in the Winnicut River ($n=3299$) followed by the Squamscott ($n=2755$) and Oyster Rivers ($n=902$).

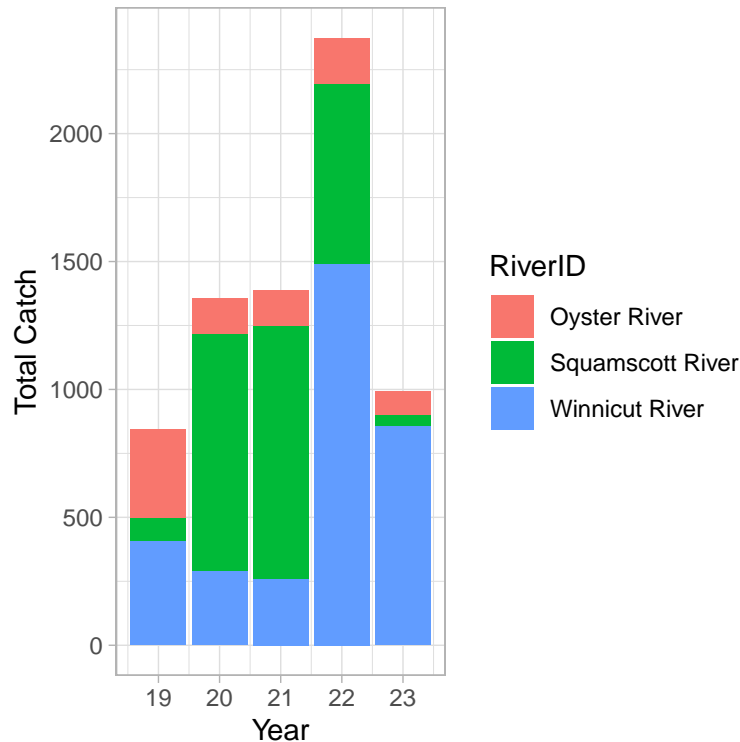


Figure 1: Stacked bar graph depicting total rainbow smelt catch in each of the three rivers over the five years of the study.

Temperature

Water temperatures did not vary significantly between the Winnicut, Squamscot, and Oyster rivers or between the five years of the study in Great Bay, NH (ANOVA; $F= 2.147$, $p=0.12$; $F= 2.881$, $p=0.09$; respectively; Figure 2). Average temperature for the five years was 5.6°C with a range of temperatures from 0.05 - 12.38°C from late February through April.

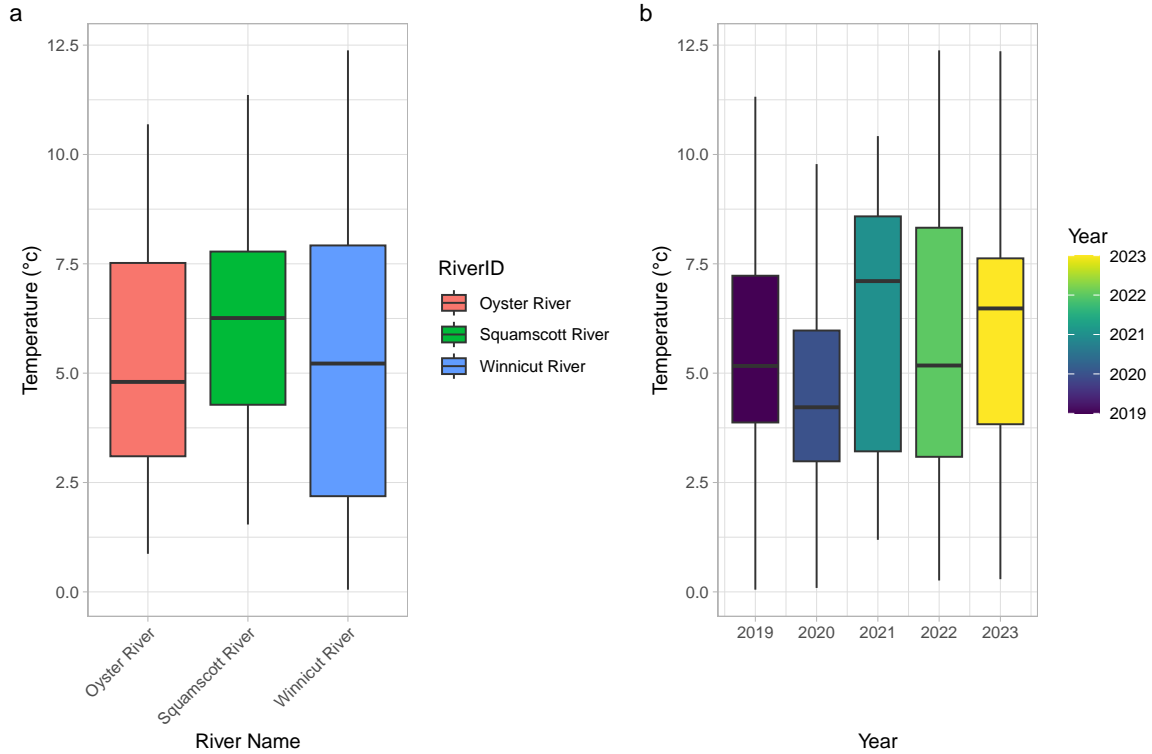


Figure 2: Boxplots of recorded temperature (°C) in (a) each river and (b) over the five years.

To determine if there was an optimal temperature range for rainbow smelt spawning, we calculated the temperature at peak catch for each river and year. Using an ANOVA we determined there was not a statistically significant difference in the temperatures at peak catch for each river or between years ($F=3.154$, $p=0.076$; $F=0.402$, $p=0.536$; respectively; Figure 3). Due to the lack of difference between rivers and years we were able to determine that the optimal temperature range for spawning between 2019 and 2023 was between 1.74°C and 4.55°C .

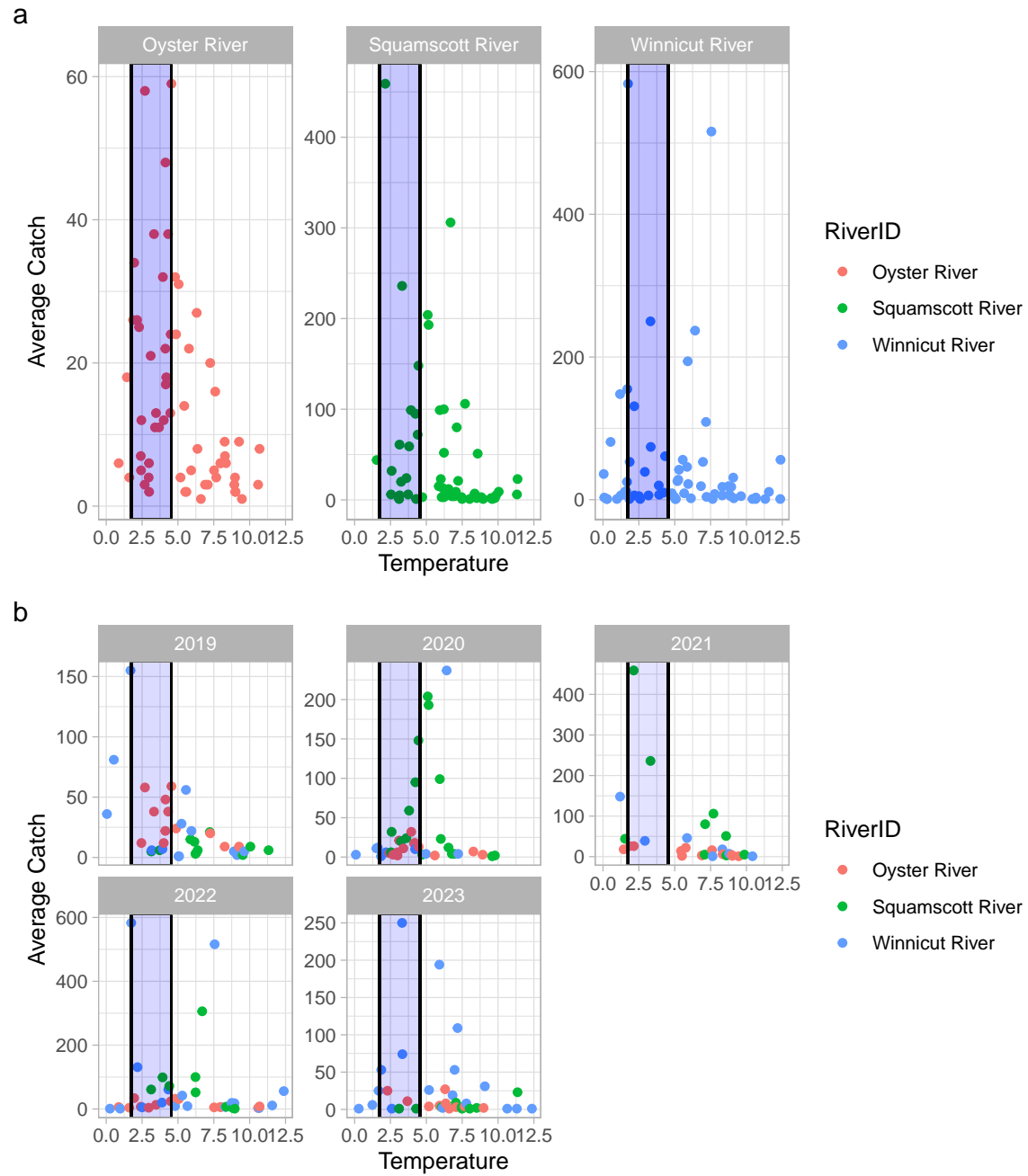


Figure 3: Optimal spawning temperatures in (a) each river and (b) over the five years. The shaded blue regions represent the average optimal spawning temperature based on the model (1.74-4.55(°c)). The y-axis is adjusted to each treatment to better observe the trends.

Age Class

The changes in the mean age of rainbow smelt during spawning displayed a seasonal pattern with the oldest, repeat spawners dominating at the start of spawning season, and first-time spawning individuals dominating at the end of the season (ANOVA; $p < 0.001$). Proportions of each rainbow smelt age class in each year were determined using age data from scales. Of the 1,747 fish that were sampled during migration, most fish in the spawning grounds were age-1 and age-2. Results from the Chi Squared Test determined that there was a statistically significant difference in age classes at spawning grounds over the four years ($p = 0.0005$; Figure 4).

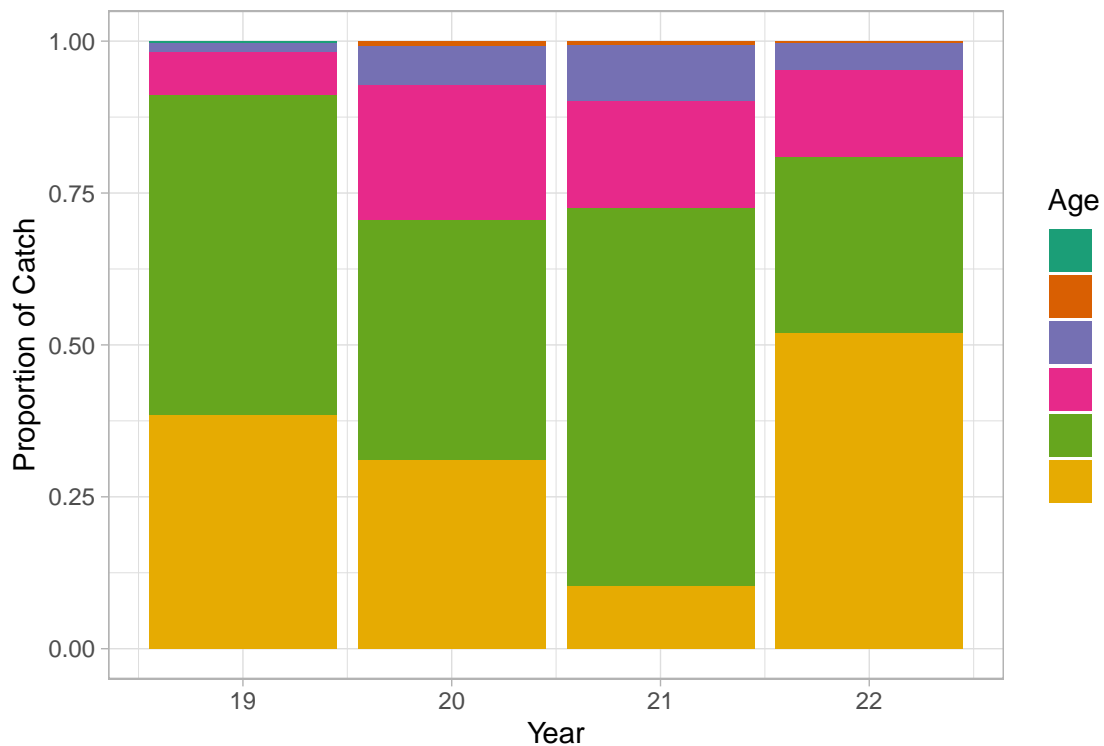


Figure 4: Percent contribution of each age class of rainbow smelt to the total of those aged via scales. The data is aggregated for all three rivers (Oyster, Squamscott, and Winnicut Rivers).

Length

We found there was a significant effect of the three different rivers on the lengths of smelt that visited each site during spawning season. The Oyster River tended to attract slightly smaller smelt than the Squamscott or Winnicut Rivers (Kruskal-Wallis Test; $p < 0.001$; Figure 5). As

predicted, larger smelt arrived earlier in the spawning season and when the temperatures were colder compared to the smaller sized smelt (ANOVA; $p < 0.001$).

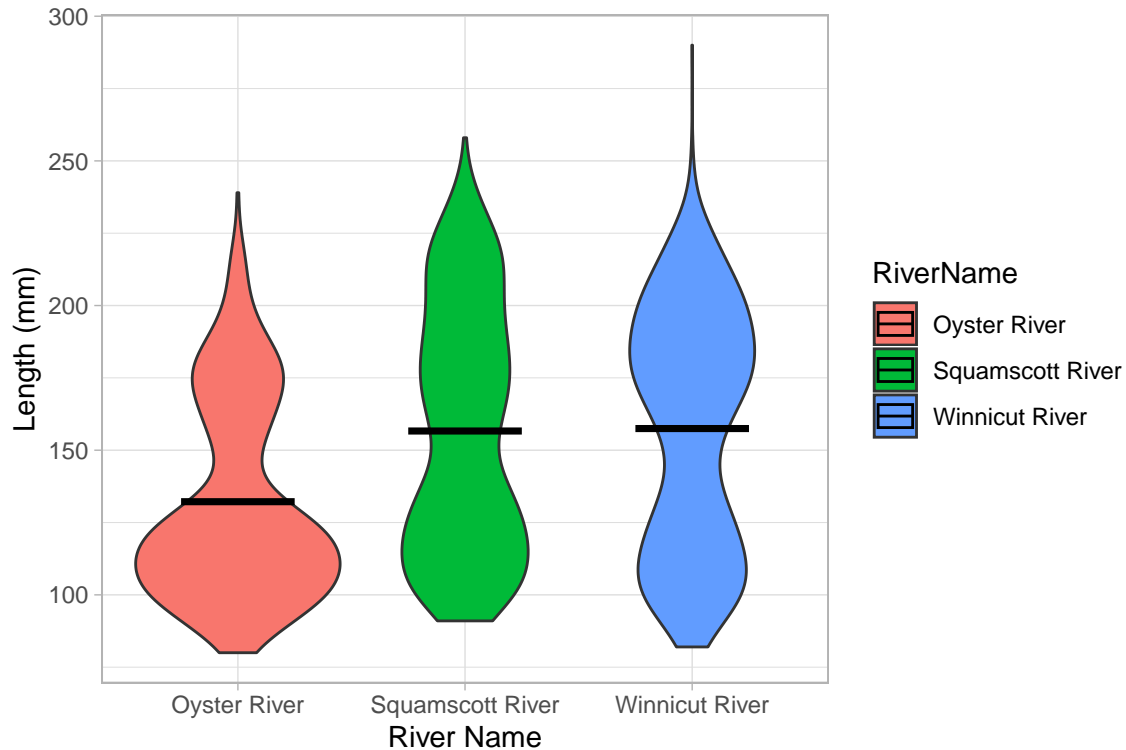


Figure 5: Violin plot of the distribution of lengths over the five year study in each river. Black crossbars represent the mean lengths.

Discussion

We determined that both temperature and morphology played a role in preferred spawning grounds for rainbow smelt in Great Bay, NH. Similar to previous studies on rainbow smelt thermal preferences, we found that the optimal temperature for spawning was between approximately 2°C and 5°C and there was no difference across years or rivers (Chase, 2006). In terms of morphology, we found that larger, older smelt arrived at spawning grounds earlier than smaller, younger smelt (Quinn et al., 2016). Lastly we identified a difference in the proportion of age classes that spawned over the course of the study.

Determining an optimal spawning temperature can help predict future population resiliency in a changing climate, inform management of habitat, and maintain the recreational freshwater fishery. A recent study found that changes to the optimal thermal environment for rainbow smelt may affect muscle function (Shuman & Coughlin, 2018). While rainbow smelt were

able to acclimate to colder waters more easily than trout species, the authors predicted that rainbow smelt will be particularly stressed by warming environments. This predicted response is likely a result of reduced smelt physiology, changes in hydrography, and shifts in community dynamics due to the invasion of warm water species (Paukert et al., 2017). Management solutions that maintain water quality and temperatures at optimal ranges will help to restore and maintain populations.

Understanding the relationships between size classes and spawning times can be valuable for ensuring management windows are representative of all sizes for future population resiliency. These relationships can also help researchers observe the potential impacts of environmental changes on migration timing and increase the success of tagging studies to better inform our understanding of population dynamics. Similar to our findings, previous research has suggested that premature spawning timing, or spawning early when conditions may be less favorable, is more common with larger anadromous fish (Quinn et al., 2016). Two potential explanations for this relationship are (1) that larger fish would not benefit from more time at sea to grow and (2) they can withstand stronger currents and colder waters, which are more common earlier in the season. This is an important evolutionary trade off because less time spent at sea means less risk of mortality (Quinn et al., 2016). The staggered timing of migrations helps to preserve phenotypic diversity and increase population resilience.

Age class dynamics within a population provide insight into mortality rates and recruitment rates which are important for predicting population resilience. In our study, rainbow smelt aged 4-6 years old had the lowest proportions in the catch data which may indicate high at sea mortality among older age groups (Furey et al., 2023). In the third year (2021) of the study there was an increase in age-2 fish compared to the previous and subsequent years. This may be due to a good spawning year in 2020 and potential resilience in the juvenile population. However, the higher proportion of 2 year olds to 1 year olds may be due to poor spawning effort or poor juvenile survival rates (Furey et al., 2023). More data is necessary to fully understand these dynamics.

Rainbow smelt populations have declined or become extirpated in recent years (Enterline et al., 2012). This current study illustrates the importance of collecting environmental and morphological data over time for informing mitigation decisions and predictors for future population and ecosystem health. Restoration efforts such as increasing shade to provide habitat and maintain optimal thermal temperatures as well as mitigation efforts to lower fishing pressure and reduce at sea mortality rates would benefit not only rainbow smelt, but a host of other diadromous fish species (Saunders et al., 2006). Rainbow smelt have important ecological roles such as increasing the trophic levels of the food web and providing an important prey resource for larger diadromous fish due to their spawning timing and life history (Saunders et al., 2006). With continued monitoring efforts to validate sampling trends and engagement from local communities, rainbow smelt populations could rebound (Enterline et al., 2012).

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