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Life history differences between 2 anadromous populations of the northern form of the Dolly Varden (*Salvelinus malma malma*) in Bristol Bay in southwestern Alaska

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Abstract—The Dolly Varden (*Salvelinus malma*), an iteroparous, facultatively anadromous Pacific salmonid, displays diverse life history and migration patterns. Using otolith microchemistry, we inferred that individuals sampled in the Nushagak Commercial Salmon Fishery Management District, Alaska (sample size [*n*]=30; mean fork length=597 mm), had entered saltwater at ages 4–7 and were in their first (26%) or second (74%) summer at sea. Most (88%) of the fish that had spent 2 summers at sea migrated in consecutive years, but 2 of them skipped a migration to marine waters, remaining in fresh water for an additional year after migrating to sea in their first year. Only 15% of the individuals with 2 summers at sea had anadromous mothers. In contrast, conspecifics sampled on the other side of Bristol Bay in the Egegik Commercial Salmon Fishery Management District started migrating at an earlier age, migrated more often, and more often had anadromous mothers. Together, these results highlight the differences in life history among Dolly Varden and indicate that freshwater rather than marine conditions influence life history patterns, at least for fish within the Nushagak District.

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Salmonids exhibit a wide variety of migratory patterns, among and within species (Klemetsen et al., 2003; Quinn, 2018). Some species reside in small streams, whereas others migrate between streams and larger rivers (Northcote, 1997), migrate between streams and lakes (Arostegui and Quinn, 2019), or are anadromous and spend weeks, months, or years at sea (Quinn and Myers, 2004). Anadromous salmonids that are iteroparous may vary in age of first marine migration (Swanson et al., 2010; Bond et al., 2015) and in the number or sequencing of those migrations (Spares et al., 2015). This variation is especially marked in the char species (*Salvelinus* spp.) (Dunham et al., 2008), with anadromy positively associated with key life history traits, such as growth rate, age at first spawning, fecundity, and longevity (Tallman et al., 1996), but also with high mortality (Brown et al., 2019).

The Dolly Varden (*S. malma*) is an iteroparous char species of the North Pacific Rim with 3 subspecies (Taylor and May-McNally, 2015), and there are fluvial (Denton et al., 2010; Ayer et al., 2018), adfluvial (Markevich et al., 2018), and anadromous or partially anadromous populations of this species (Bond and Quinn, 2013; Morrison et al., 2021). Anadromy is known for the 2 North American subspecies or forms in Alaska. The southern form of Dolly Varden, *S. m. lordii*, found south of the Alaska Peninsula, inhabits estuarine and nearshore habitats (Bond et al., 2014a) and may overwinter in marine waters (Bernard et al., 1995). In contrast, the northern form, *S. m. malma*, found north of the Alaska Peninsula, makes more extensive marine migrations (Morita et al., 2009; Courtney et al., 2018) and typically overwinters in fresh water after spawning and then migrates to sea annually; however, individuals of this subspecies may skip a year between migrations, remaining in freshwater habitats (Gallagher et al., 2018).

In Bristol Bay, in southwestern Alaska, populations of the northern form of Dolly Varden may be non-anadromous

(Denton et al., 2010) or partially anadromous, as has been inferred from catches at weirs (Lisac[1]) and from microchemical analysis of otoliths taken from fish sampled in marine waters at the mouth of the Egegik River (Hart et al., 2015) and taken in fresh water (Scanlon, 2000). Herein, we report life history data (size, total age, age at first migration, migration frequency, and maternal anadromy) on anadromous individuals of the northern subspecies of Dolly Varden sampled from the Nushagak Commercial Salmon Fishery Management District (hereafter, referred to as the *Nushagak District*), a commercial fishing zone within the Nushagak Bay estuary that opens into Bristol Bay. We compare them to data on conspecifics similarly sampled from the Egegik Commercial Salmon Fishery Management District (hereafter, referred to as the *Egegik District*) in the northeastern arm of Bristol Bay (Hart et al., 2015). The fish have access to common feeding areas, with the mouths of the rivers that drain into these bays only ~70 km apart (Fig. 1), allowing us to assess differences that might result from their respective freshwater ecosystems in the same region.

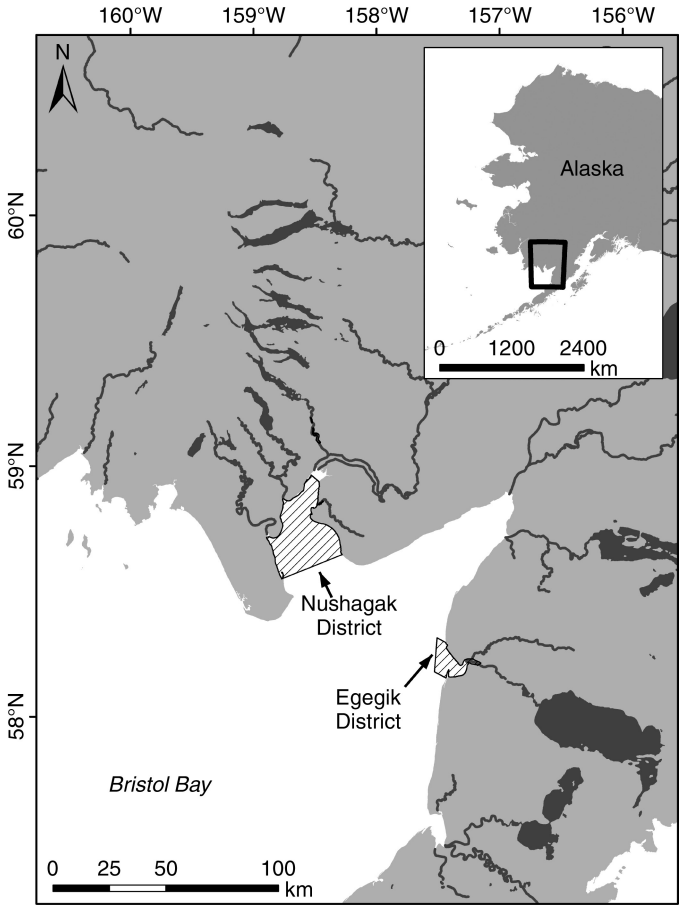

Figure 1

Map of the 2 locations in southwestern Alaska where individuals of the northern subspecies of Dolly Varden (*Salvelinus malma malma*) were taken as bycatch in the commercial gillnet fishery for sockeye salmon (*Oncorhynchus nerka*). Samples were collected from the Nushagak Commercial Salmon Fishery Management District on 25 June 2018 for this study, and comparable samples of the same subspecies of Dolly Varden were collected in the Egegik Commercial Salmon Fishery Management District by Hart et al. (2015) on 22 June and 2 July 2013.

Materials and methods

On 25 June 2018, 30 fish identified as the northern form of Dolly Varden (Taylor and May-McNally, 2015) by. E. Taylor[2], of the University of British Columbia, were taken as bycatch in the commercial gillnet fishery for sockeye salmon (*Oncorhynchus nerka*) in the Nushagak District (Salomone et al.[3]). The use of the samples examined in this study was permitted by the Alaska Department of Fish and Game. These fish could not be sold as food and would have been discarded if they had not been made available to us for study. The fish were frozen and later thawed, measured (fork length [FL]), and weighed. Paired *t*-tests were used to detect statistically significant differences between fish from the Nushagak and Egegik Districts.

Otoliths were removed for determination of life history characteristics by using visual and microchemical analyses. These analyses followed procedures used on conspecifics also taken as bycatch in the gillnet fishery between 22 June and 2 July 2013 in the Egegik District, on the opposite side of Bristol Bay from the Nushagak District (Hart et al., 2015). The similarities in gillnet mesh size (typically a mean diameter of 12.7 cm [standard deviation (SD) 0.3]) and in the times when these fisheries are open made it possible for us to compare life history patterns between these 2 collections. It is important to note, however, that neither collection fully represents the population in the district from which it was sampled owing to the limited collection dates and large basins from which these specimens may have originated, basins that include not only the basins of the Nushagak and Egegik Rivers but also other basins throughout Bristol Bay and southwestern Alaska.

Otoliths were extracted, sectioned, mounted, polished to expose the core and surrounding matrix, and aged visually by using reflected light. A subset of otoliths (sample size [*n*]=23) was selected for microchemical analysis on the

[1] Lisac, M. J. 2010. Abundance and run timing of Dolly Varden in the Middle Fork Goodnews River, 2008 and 2009. Alsk. Fish. Data Ser. Rep. 2010-13, 14 p. [Available from Togiak Natl. Wildl. Refug. Off., 6 Main St., Dillingham, AK 99576-0270.]

[2] Taylor, E. 2018. Personal commun. Dep. Zool., Univ. British Columbia, Beaty Biodivers. Cent., Rm. 310, Vancouver, Canada V6T 1Z4.

[3] Salomone, P., T. Elison, T. Sands, J. Head, and T. Lemons. 2019. 2018 Bristol Bay annual management report. Alsk. Dep. Fish Game, Fish. Manag. Rep. 19-12, 64 p. [Available from website.]

basis of the clarity of the preparation and ease of determination of the otolith's core from the surrounding area. Strontium (Sr) and barium (Ba) are incorporated into fish bony structures relative to their concentrations in the surrounding water. The concentration of these elements is typically correlated with salinity (Elsdon et al., 2008) and is highly conserved in fish otoliths (Kraus and Secor, 2004). Normalized to calcium (Ca) levels, Sr and Ba concentrations in otoliths have been used to indicate migratory patterns and life history in diadromous fish species (Walther, 2019) and especially in salmonids (Swanson et al., 2010; Bond et al., 2015; Austin et al., 2019).

Laser-ablation mass spectroscopy of otoliths was conducted with an iCap RQ ICP-MS[4] (Thermo Fisher Scientific, Waltham, MA). Element concentrations, adjusted to NIST-612 standards, were converted to molar mass ratios of ^{86}Sr:^{43}Ca and ^{138}Ba:^{43}Ca, presented as millimoles per mole and micromoles per mole, respectively. Winter annuli were visually identified by using dark growth rings and were measured from the core along the ablated transect. These measurements were then converted to a ratio of the total transect measured, and the corresponding ratio of lengths along the transect were overlaid onto a 9-point rolling mean of Sr:Ca and Ba:Ca ratios for individual otoliths to infer initial age of migration and annual migratory and overwintering patterns. Maternal anadromy was identified when core Sr:Ca ratios were elevated above the surrounding freshwater signals, reflecting the concentrations in the female during egg production (Kalish, 1990). Similarly, anadromy was inferred when the Sr:Ca ratio was >3 mmol/mol and the Ba:Ca ratio was <6 µmol/mol (Bond et al., 2015). In all cases, there was agreement between Sr:Ca and Ba:Ca ratios, indicating anadromy. The life history and microchemical data from our study can be accessed from GitHub.

Results and discussion

The Dolly Varden sampled from Nushagak District had an average length of 597.1 mm FL (SD 40.6), with a range of 522–690 mm FL, and an average mass of 2.16 kg (SD 0.42), with a range of 1.63–3.25 kg. Both of those means are greater than those of the fish caught in the Egegik District at essentially the same time of year, with a mean length of 509.0 mm FL (t=10.0, P<0.001) and a mean mass of 1.49 (t=4.1, P<0.001). However, the mean age of 6.1 years (range: 5–8 years) for fish from the Nushagak District did not differ from the mean age of 5.7 years (range: 4–9 years) for fish from the Egegik District (t=1.75, P=0.09) (Suppl. Table). These length and age values are comparable to those for conspecifics at similar latitudes (Maekawa and Nakano, 2002), although older individuals occur in Arctic populations (Stolarski and Sutton, 2013; Gallagher et al., 2016).

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Morrison et al. (2021) reported that rapid growth in fresh water was associated with early age at first migration in Dolly Varden and that growth rate in fresh water is typically inversely related to smolt age in salmonids (McCormick et al., 1998; Quinn, 2018). In contrast to the modest differences in size and age between the populations on opposite sides of Bristol Bay, a clear difference in age at migration was observed. The fish sampled from the Nushagak District first migrated to sea much later in life than the fish sampled from the Egegik District, with mean ages at migration of 5.2 years (range: 4–7) and 2.5 years (range: 2–3), respectively (t=15.33, P<0.001), indicating that the fish from the Nushagak District grew at a slower rate than the fish from the Egegik District. Similarly, a population of the southern subspecies of Dolly Varden along the southern Alaska Peninsula also migrated to sea at a younger age, although at a smaller body size at that age of migration (Bond et al., 2015). Dolly Varden at the northern end of their range also smolt at a younger age than the fish sampled from the Nushagak District (Morrison et al., 2021).

In addition to the difference between populations in age at first migration, 6 of the fish from the Nushagak District were in their first summer at sea, and the other 17 fish were in their second summer (mean age: 1.7 years) compared with the mean of 4.2 summers at sea (range: 3–8 summers) for the fish from the Egegik District.

Skipped migrations (i.e., remaining in fresh water for 2 winters rather than 1 winter between migrations) (Fig. 2A) were not common. Examining fish with multiple seasons at sea, we found that only 2 of 17 fish from the Nushagak District had skipped a migration to sea and that no fish from the Egegik District had skipped a marine migration. Skipped migrations were much more common (76% of the sample) in a study of fish sampled from an Arctic river that had a long (~800 km roundtrip) migration route (Gallagher et al., 2018). In comparison, the mouth of the Egegik River is only 45 km from Lake Becharof. Individuals from the Nushagak District migrate an unknown distance but likely less than the 450-km length of the Nushagak River because the Dolly Varden is common in the basin closer to Bristol Bay (May-McNally et al., 2015).

Finally, the incidence of maternal anadromy in our sampled individuals differed greatly (e.g., as evident in the data for 2 specimens shown in Figure 2, A and B): only 3 of 20 fish from the Nushagak District had mothers that migrated to sea in the season before spawning compared with 14 of 25 fish from the Egegik District having such mothers, yet all samples were collected in marine waters.

A skipped migration would create a freshwater chemical signal in a female that would not be distinguishable from a non-anadromous fish. In our sample, skipped migrations were rare; therefore, our results indicate that, in both populations, maternal migrations may not be common. However, a sample of juvenile Dolly Varden from tributaries of Lake Aleknagik, in the Wood River system of the Nushagak River basin, contained only individuals

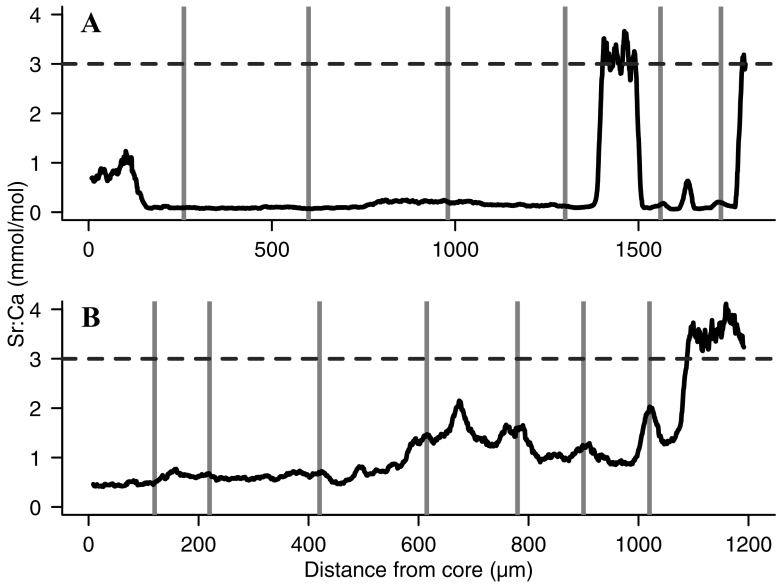

Figure 2

Profiles of the ratio of strontium to calcium (Sr:Ca) for otoliths from 2 Dolly Varden (*Salvelinus malma*) sampled on 25 June 2018 from the Nushagak Commercial Salmon Fishery Management District in southwestern Alaska, truncated to show the core at the origin. The vertical gray solid lines indicate the approximate positions of annuli. The horizontal dark gray dashed lines indicate the Sr:Ca threshold for interred marine residence (3 mmol/mol). (**A**) The top profile indicates maternal anadromy (elevated Sr:Ca at the core) and a year in freshwater between anadromous migrations (i.e., a skipped migration) at ages 4+ and 6+. (**B**) The bottom profile has no indication of maternal anadromy and indicates capture during the initial migration of the fish at age 7+. For clarity of the graphs, values of the ratio of barium and Ca are not shown.

whose mothers had been to sea in the summer prior to spawning (Dennert et al., 2016). The apparent differences among these results likely reflect the range of life history patterns of Dolly Varden in these large basins and the fact that our samples likely did not fully capture this variation. These variable life history patterns likely arise from differential survival and reproductive success, and therefore from differences in life history traits, across the heterogeneous freshwater landscape within the Nushagak River basin. These varied freshwater conditions may have more influence on the survival and reproductive success of fish migrating from the basin than the marine conditions to which all fish that migrate to sea are exposed. Regardless of the causes, however, the results indicate that the life history of the mother often differs from that of her offspring.

The fish used in this study were taken in gill nets that are size-selective (Todd and Larkin, 1971), affecting the range of phenotypes observed in a sample. Moreover, fishing mortality in general reduces age and longevity in populations (Sharpe and Hendry, 2009). Therefore, we cannot infer that fish smaller than the fish in our study do not enter marine waters, and repeat migrations might have been more common in the absence of fishing. We also acknowledge that interpreting age and microchemical data from otoliths is not without error (Stolarski and Sutton, 2013). For example, exposing otolith cores can be less reliable for adults than for juveniles, diluting or masking the core signature (Volk et al., 2000).

In addition, we made conclusions with the assumption that fish originated from the natal rivers within the district where they were caught. Dolly Varden have strong homing instincts, as indicated by results from tagging (Armstrong, 1974) and population genetics (Bond et al., 2014b) studies, but some individuals, especially those of the northern subspecies, can disperse widely (DeCicco, 1992; Morita et al., 2009). Still, the differences in life history observed in the samples from the Egegik and Nushagak Districts indicate that the examined samples did not represent a single mixed population but, rather, ones that were segregated to at least some extent. Despite issues with methods, common to the sampling of fish in both the Nushagak and Egegik Districts, and despite the access that these fish have to common, proximate foraging areas, the dramatic differences in life history of these populations indicate a dominant role of freshwater factors rather than marine factors on these traits. In this regard, the life history differences echo those found among populations of other salmonid species, including the sockeye salmon of Bristol Bay (Quinn et al., 2009).

Resumen

El salmón *Salvelinus malma*, es una especie iterópara del Pacífico, facultativamente anádroma que presenta ciclo vital y patrones de migración diversos. A partir de la microquímica de los otolitos, deducimos que los individuos muestreados en el Distrito de Administración de la pesquería comercial de salmón de Nushagak, Alaska (tamaño de muestra [*n*]=30; longitud furcal promedio=597 mm), habían entrado en el agua salada a los 4–7 años y estaban en su primer (26%) o segundo (74%) verano en el mar. La mayoría (88%) de los peces que habían pasado 2 veranos en el mar migraron en años consecutivos, pero 2 de ellos se saltaron una migración a aguas marinas, permaneciendo en agua dulce un año más después de haber migrado al mar en su primer año. Sólo el 15% de los individuos con 2 veranos en el mar tenían madres anádromas. Por el contrario, los congéneres muestreados al otro lado de la bahía de Bristol, en el Distrito de Administración de

la pesquería comercial de salmón de Egegik, empezaron a migrar a menor edad, con más frecuencia, y tuvieron más a menudo madres anádromas. En conjunto, todos estos resultados ponen de manifiesto las diferencias en el ciclo vital de este salmón e indican que son las condiciones de agua dulce y no las marinas las que influyen en los patrones del ciclo vital, al menos en el caso de los peces del distrito de Nushagak.

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