

Diversity in migration, habitat use, and growth of Dolly Varden char in
Chignik Lakes, Alaska

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Abstract

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Dolly Varden (*Salvelinus malma*) are a facultatively anadromous salmonid common around much of the north Pacific Rim, but little is known of the factors that determine their migration and life-history patterns. In the Chignik Lakes system on the Alaska Peninsula, Dolly Varden are the only large bodied resident fish species and use nearly all available aquatic habitats at different life stages. In addition, they are often the numerical dominant fish in both freshwater and estuarine habitats.

I employed a multifaceted approach to understand variation in Dolly Varden migration timing, growth, habitat use, and variation in anadromy. By integrating daily counts of Dolly Varden ascending rivers and streams throughout the migratory range over a wide temporal scale, I determined upstream migration generally occurs earlier in southern stream and later in northern streams. Interannual variation in ascent timing in southern streams is correlated with sea-surface temperatures, while in northern streams it was not.

Plasma insulin-like growth factor 1 concentrations indicate rapid summer growth in estuarine waters compared to freshwater lake habitats. However, the growth benefits of

discrete sub-regions of the estuary vary by month. Muscle tissue stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) indicate non-overlapping isotopic signatures of Dolly Varden captured at each estuary sub-region. Therefore there is behavioral spatial separation among estuarine Dolly Varden despite broadly similar body size and diet across the estuarine habitat. Finally, I employed otolith microchemistry (Sr/Ca, Ba/Ca) to evaluate the lifetime migratory history of 366 Dolly Varden captured throughout the watershed. Nearly all Dolly Varden migrate to sea at least once in their life, with most doing so at age four. However, after age four migration rates decline, to near zero by age seven. Fully resident individuals exist within marine-accessible portions of the watershed, and comprise almost 15% of fish over age six.

These data demonstrate that Dolly Varden exhibit wide diversity in movement behavior among and within watersheds. These patterns change with ontogeny, and are likely shaped by the size-specific costs and benefits of alternative habitat use and resource availability. Analogous dynamics likely drive life-history diversity in many iteroparous, facultatively anadromous species.

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Introduction

General Introduction

An emerging concept in the field of ecology is the study of the processes that lead to divergent life history trajectories. This phenomenon is especially prominent in fishes, where many life-history patterns can be observed within some populations (e.g. steelhead/rainbow trout, *Oncorhynchus mykiss*). The mechanistic drivers of life history variation range from differences in gene regulation (Nolte et al. 2009) to phenotypic plasticity (Aubin-Horth and Dodson 2004) and are often observed in the context of the physiological processes that occur when an individual initiates a switch from one life history type to another (Metcalf 1998). Because some life history types are more susceptible to anthropogenic perturbations than others (Waples et al. 2008), understanding both the causes and consequences of life history diversity has also become a key component of fish conservation (Waples et al. 2009).

There are several theories to explain niche diversification and subsequent life history variation within a given habitat. One is resource polymorphism, where disruptive selection favors fish that utilize alternate niches or resources (Smith and Skulason 1996). A second is sequential invasions, where an initial invasion of a system leads to local adaptation and divergence from subsequent invasions (e.g., threespine sticklebacks (Taylor and McPhail 1999)). Additionally, multiple life histories within a population may develop in response to a dynamic environment, where no one life history type is favored in all circumstances. Phenotypic plasticity can also produce alternate life history patterns from one genotype as a result of subtle differences in growth among individuals, leading to different trajectories. For systems where migration is possible, this can be manifested

as the maintenance of both resident and anadromous individuals within a single genetic population where a gene by environment interaction leads to differences in dominance, resource access, and ultimately growth (Metcalfe 1998, Thorpe et al. 1998, Metcalfe et al. 2002). This interaction may result in life history differences among individuals in the larger population, including partial migration, where a subset of the population initiates movement and the others do not.

The *Salvelinus* genus is known for life history variation (Noakes 2008). Most notable are the Arctic charr (*S. alpinus*) of Iceland and Scotland, where resource polymorphism is believed to drive the divergence of sympatric phenotypes (Knudsen et al. 2006, Adams et al. 2007, Adams et al. 2008). These populations often exist in land-locked species-poor lakes where divergence allows for the exploitation of novel niches (Noakes 2008).

Although low species diversity is thought to be an important driver of niche diversification within a species, charr phenotype divergence has also been observed in more speciose regions as well (Imre et al. 2002). In Iliamna Lake Alaska, Denton et al. (2010) observed diversification of both body size and rearing habitat for Dolly Varden (*S. malma*) in accessible habitats within tens of kilometers of one another. However, in only a few cases have mechanisms for the divergence been proposed (Skulason et al. 1989a). In the most famous case, Arctic charr in Thingvallavatn, Iceland, the feeding ecology and high levels of intraspecific competition for food resources is thought to maintain four distinct morphs (Noakes et al. 1989, Skulason et al. 1989b). Similar mechanisms have been proposed for charr in other lake systems outside of Iceland where divergent morphs occur (Adams et al. 2006, Adams et al. 2007).

While phenotypic diversity can be manifested as clear physical differences (Skulason et al. 1989a, Morinville and Rasmussen 2008, Noakes 2008), it is often far more subtle. For example, the distinct behavioral differences among sympatric and physically similar morphs of *O. mykiss*, which may exist as both freshwater residents and fully anadromous individuals in the same population (Thrower et al. 2004b, Narum et al. 2008). This is particularly striking because resident rainbow trout may remain within a small portion of a watershed for their entire lives, while anadromous individuals migrate long distances at sea (Myers et al. 2005). Alternatively, other salmonids of the *Oncorhynchus* genus have more discrete life histories. For example, kokanee (lake resident) and sockeye (anadromous) are two forms of *O. nerka*, yet they are typically genetically distinct, even when sympatric (Wood and Foote 1996, Wood et al. 1999). Despite years of research, little is known about what causes an individual to move down the path toward residency or anadromy. Cross breeding experiments and genetic investigations suggest that a single gene solution is not likely, and phenotypic plasticity undoubtedly plays a large role (Thrower et al. 2004a, Thrower et al. 2004b). That is, the early life history environment of the individual coupled with a particular genotype may lead to one behavior, while an alternate environment or genotype may lead to another. This level of complexity is likely responsible for the thirty-two different life history types observed in *O. mykiss* within a single population (Shapovalov and Taft 1954). Similar levels of life history diversity with respect to residency, anadromy and age of maturation are likely for Dolly Varden populations with access to the ocean. However, the body of published research on Dolly Varden life histories is poor and somewhat anecdotal (but see Armstrong 1970, Armstrong 1974, Bernard et al. 1995).

I am investigating the ongoing processes that shape the diversity of fish life histories in a location that was recently deglaciated and is volcanically active, creating a set of dynamic habitats with rapid and ongoing changes to the fish community (Westley 2007, Westley et al. 2008). The Chignik Lakes watershed in Southwestern Alaska was likely colonized through marine routes as glaciers were receding ca. 10000 BP. However, the effects of intense volcanic activity in on the Alaska Peninsula 3500-4000 BP on the current fish community are unknown, and the contemporary suite of fishes may be the result of more recent colonizations (Miller and Smith 1987). Under this scenario, all fish species within the Chignik drainage re-colonized through marine waters, necessitating a diadromous life history of colonizers. However, the current fish community includes species that rarely enter marine waters (e.g. pond smelt, *Hypomesus olidus*, ninespine stickleback, *Pungitius pungitius*) (Westley et al. 2005). This indicates a fairly rapid development of resident fishes as the offspring of marine colonizers, but the life history characteristics of Chignik fishes have not been thoroughly explored outside of the commercially exploited *Oncorhynchus* species. Intraspecific variation is also relatively common in the Chignik Lakes drainage. Three distinct morphs of Pygmy whitefish (*Prosopium coulterii*) exist within Chignik Lake (McCart 1970), and several plating forms of threespine sticklebacks (*Gasterosteus aculeatus*) (Narver 1969). Although the mechanisms leading to multiple morphs for these species are unclear, resource polymorphism is likely in a high-latitude, species poor system like the Chignik Lakes watershed.

Dolly Varden exist throughout arctic coastal Alaska and western Canada in the north, to at least Washington State in the south (Armstrong and Morrow 1980). In Asia,

they are found from the Chukhotsk Peninsula, Russia in the north to Japan and the Koreas (Armstrong and Morrow 1980). The Chignik Lakes watershed, near the middle of the range, is unusual because Dolly Varden are the only large bodied, resident fish; in other portions of the range they are often sympatric with *S. alpinus*, *O. mykiss*, *O. clarki*, *Stenodus leucichthys*, and *Thymallus arcticus*, among others. Like many of the watersheds famous for sympatric divergence of Arctic charr, the low species diversity of the Chignik Lakes system and high levels of intraspecific competition may foster niche divergence and life history variation in Dolly Varden. However, these ideas are relatively unexplored outside of Dolly Varden diet studies of the 1950's and 60's (Roos 1959, Narver and Dahlberg 1965). In fact, despite their near ubiquity in Alaskan waters, published studies of the ecology of Dolly Varden in North America are rare. The Chignik Lakes watershed provides an excellent opportunity to explore niche diversification, life history variation, and population structure of Dolly Varden. The Chignik Lake system is extremely diverse in the habitat types available to anadromous fishes with a shallow warm lake, deep cold lake, brackish lagoon, and myriad rivers and streams of varying size and gradient. In addition, the watershed is relatively small (ca. 35 km from ocean to furthest headwaters) and nearly completely accessible by small boat, making it experimentally tractable. Dolly Varden are found in nearly every below barrier habitat in the watershed (Bond, unpublished data), and are at times the numerical dominant, making them an ideal experimental organism. Their abundance, coupled with the propensity for life history diversity in the *Salvelinus* genus provides an excellent opportunity to explore the environmental mechanisms that may contribute to life history divergence, variation in anadromous behavior, habitat use and growth.

Chapter 1: Patterns and influences on Dolly Varden migratory timing in Chignik Lakes, Alaska, and comparison to populations throughout the Northeastern Pacific and Arctic oceans

Introduction

Among anadromous fishes there is considerable diversity in the timing, extent, and duration of the use of marine waters (McDowall 1988, Quinn and Myers 2004); each species employs one or more different migratory strategies to optimize the use of multiple environments. Semelparous Pacific salmon (*Oncorhynchus* spp.) acquire most of their growth at sea, timing their return to fresh waters for breeding opportunities; often leaving marine waters during a period of peak somatic growth, a trait which has evolved maximize offspring survival (Quinn 2005). Iteroparous steelhead (*O. mykiss*) and Atlantic salmon (*Salmo salar*) also return almost exclusively for reproduction as their feeding in freshwater as post-migratory adults is limited (Johansen 2001). However, for other iteroparous salmonids (e.g. cutthroat trout, *O. clarki*; bull trout, *Salvelinus confluentus*; Arctic char, *S. alpinus*; Dolly Varden, *Salvelinus malma*; and brown trout, *Salmo trutta*), anadromy is often more complicated (Armstrong 1984, Swanson et al. 2010b, Jonsson and Jonsson 2011), with some species making seasonal forays into marine environments while continuing annual use of fresh waters. For these species the return to freshwater may be driven by reproduction, feeding, the need for overwintering habitat, or a combination of needs. Therefore, the migration timing of each individual may be affected by a combination of age, size or maturational state and the relative abundance of resources in marine and fresh waters; creating a complex array of poorly understood migratory behaviors (Armstrong 1984, Quinn 2005, Jonsson and Jonsson 2011).

Latitude and migration timing are linked in many species of birds (Hagan et al. 1991) and fishes (Leggett and Whitney 1972), including salmonids (Hodgson and Quinn 2002, Spence and Hall 2010). In nearly all cases this relationship appears to be driven by the reduction of growing season, increasing severity of winter and decrease in temperature with increasing latitude. Therefore, animals must either have mechanisms to allow the precise timing of movements to coincide with optimal conditions, or evolved migration timing that best suits the average conditions. In salmonids the timing of emigration from freshwater habitats has evolved to correspond with ocean productivity, the timing of which varies with latitude (Spence and Hall 2010). Environmental conditions, which also change broadly with latitude, strongly influence return migration timing of many salmonids (e.g., sockeye (*O. nerka*), Chinook (*O. tshawytscha*), Atlantic salmon), primarily as an evolved, population-specific trait and secondarily as a proximate stimulus (Robards and Quinn 2002, Anderson and Beer 2009, Moore et al. 2012). Therefore, differences in long term average conditions among watersheds shape the differences in average run timing among populations (Hodgson and Quinn 2002, Juanes et al. 2004, Mundy and Evenson 2011), while interannual variation in stream temperature or flow drive the differences among years within populations (Quinn and Adams 1996, Hodgson et al. 2006, Jonsson et al. 2007). The effects of stream and ocean temperatures on the return timing of iteroparous species with more coastal marine distributions are less studied but many of the same processes may also modulate their migrations (Jonsson and Jonsson 2002, Moore et al. 2012). By remaining near their stream of origin, species with spatially short migrations may respond more readily to changing environmental

conditions rather than relying on a response to the long term average conditions found in far-ranging species.

Dolly Varden, a common charr species in streams and rivers of the North Pacific Rim, exhibits a wide variety of life histories through a combination of iteroparity, long lifespan (≥ 10 yrs), and facultative anadromy throughout its range (Morrow 1980). Despite its abundance and potential ecological importance, Dolly Varden have been less closely studied than many other salmonid fishes. Current knowledge of the anadromous migration timing of Dolly Varden is limited to fence counts at fixed weirs, largely in southeastern Alaskan streams (Armstrong 1970, Armstrong 1974, Bernard et al. 1995). These studies revealed complex movements among freshwater systems including movements of immature fish to non-natal streams, despite strong philopatry to natal sites for breeding (Armstrong 1974, 1984, Bernard et al. 1995). It is unclear, though, how much of the behavior observed in these systems is representative of Dolly Varden throughout the species' range (Crane et al. 2005).

The movement patterns of Dolly Varden are noteworthy because of the different evolutionary pressures on their migration compared to other salmonids. Dolly Varden smolt in the spring at age 2-4, however, their marine migration may last only 2-4 months before returning to freshwater (Armstrong and Morrow 1980), allowing them to feed on the eggs and flesh of senescent Pacific salmon, followed by spawning and overwintering in freshwater (DeCicco and Reist 1999). Alternatively, Dolly Varden may remain in marine waters well into the fall months, returning only for spawning or overwintering in freshwater habitats (DeCicco and Reist 1999). Therefore, Dolly Varden may trade off the growth opportunities of marine waters with the resources that spawning salmon provide,

while weighing the relative safety of each habitat and spreading their reproductive effort over several spawning seasons. Local environmental conditions (e.g., water temperature) influence the relative benefit of each habitat, and Dolly Varden may respond with flexibility in the timing of movements among habitats. In contrast, semelparous Pacific salmon return only for reproduction, and the timing of freshwater entry is under tight genetic control (Quinn et al. 2000, Bentzen et al. 2001, Quinn et al. 2011). In North America several species of Pacific salmon occur over a larger latitudinal range than Dolly Varden (e.g. chum salmon, *O. keta*), but few exist over the extreme range of climates that Dolly Varden inhabit (Groot and Margolis 1991, Quinn 2005). Northern populations, for example, may only have a few ice free months each year, while southern streams may remain well above freezing year round.

In this study we investigated the migration patterns of anadromous Dolly Varden on several spatial and temporal scales. First, we used acoustic tags and stationary receivers to determine whether the movements of individual fish on a single watershed scale, as they moved from marine to freshwater environments, distinguished them as discrete movement groups. We then compared the movements of tracked individuals to passage counts of Dolly Varden and also to co-occurring sockeye and Chinook salmon at a weir located in at the upper limit of tidal influence in the system. The salmon counts allowed for two distinct comparisons: whether the migratory timing of sympatric salmonids experiencing largely the same environmental conditions (e.g., local marine water temperature and tides, and river flow and temperature) were similar to Dolly Varden, and the influence of the availability of salmon-derived tissue (eggs and flesh) as food for the Dolly Varden, on their arrival timing. Third, we compared average median

weir passage dates in 18 watersheds to test for latitudinal clines in migratory timing across a large portion of the North American range (ca. 56° - 71° N) associated with diverse climatic regimes. Finally, we identified the influence of environmental and biological correlates on the interannual variability in upstream migration for 5 watersheds with long term (≥ 10 yr) weir count data.

Methods:

Dolly Varden migration timing in Chignik Lakes:

Close examination of Dolly Varden migration was conducted in the Chignik Lakes watershed on the Alaska Peninsula (Figure 1), an ideal site because they are abundant in nearly every environment within the system and the watershed is central in the species' range in the Eastern Pacific. The watershed is relatively small (1563 km² total watershed area and only 30-40 km from the headwaters to the ocean) but has habitats including small streams, large rivers, lakes (25 km² Chignik Lake, 41 km² Black Lake) estuarine (33 km² Chignik Lagoon) and marine waters. It is therefore a tractable study system where the energetic cost of migration by fish is likely low. The Alaska Department of Fish and Game (ADF&G) has been counting adult Dolly Varden ascending Chignik River through a weir (Figure 1) during summer months (ca. May 24-Sept. 4) since 1996, concurrent with the migrations of sockeye and Chinook salmon. The weir spans the Chignik River near the upper limit of tidal influence, essentially at the transition between freshwater and brackish lagoon habitats. Chignik Lagoon is a long (ca. 15 km) semi-enclosed estuary that varies in salinity from freshwater where the Chignik River enters, to full seawater (ca. 32 ‰) near its opening to the sea (Simmons et al. in press). The lagoon is generally shallow and loses nearly half of its wetted surface area

during extreme tidal exchanges (ca. 4 m) (Narver and Dahlberg 1965, Simmons et al. in press).

We used acoustic telemetry to identify upstream migration timing of anadromous individuals. V9-2L transmitters (69 kHz, 60 second nominal ping rate, Vemco Inc. Shad Bay, Nova Scotia, Canada) were chosen to optimize the balance between small size and battery life. Under ideal conditions, V-9 transmitters have a detection range of approximately 400 m, and a battery life of at least 370 days. Twenty fish were captured for tagging each summer with a 30 m beach seine over three dates (day of the year (DOY), 188, 195, 198) in two locations (Figure 1) in Chignik lagoon (salinity ca. 30‰) in 2008, and one in 2009 (DOY 217). Fish > 300 mm fork length were selected to increase post-surgery survival and decrease tagging effects; fish with visible injuries or scale loss were avoided. Each selected fish was anesthetized in buffered MS-222 (tricaine methane sulphonate, 10 mg·L⁻¹) until equilibrium was lost and measured for length and mass. A small incision (ca. 6 mm) was made in the peritoneal cavity just anterior to the pelvic fins, and a sterile acoustic transmitter was inserted. One or two synthetic absorbable sutures were used to close the wound. Following surgery, fish were placed in aerated containers until they regained orientation and began swimming normally. All fish were released within 30 min of surgery, at the capture location.

Six acoustic receivers (VR2, Vemco, Inc.) were placed throughout the watershed on stationary concrete blocks in July of 2008 to detect tagged fish (Figure 1). Due to shallowness, extensive de-watering at low tide and ice-scour, no receivers were placed in the lagoon. Data were recovered in summers of 2009 and 2010. However, in 2010 the upstream-most receiver (Black Lake outlet) and the Chignik Lake outlet receivers were

not recovered. All other receivers remained operable until they were removed in late August, 2010.

Raw data from acoustic receivers were filtered to determine the arrival and departure times of each fish at each location. If only one transmission was received, we assumed rapid movement of individuals through the detection area and that time was used for both arrival and departure. Two receivers near the weir indicated movements associated with the marine-freshwater transition. We used the filtered data to determine date and time of arrival into freshwater, overwinter freshwater duration, timing of downstream migration, and speed of migration through riverine and lacustrine portions of the migration route in $\text{km} \cdot \text{hr}^{-1}$ and body lengths per second ($\text{BL} \cdot \text{sec}^{-1}$). Additionally, we assessed the influence of both tidal height and daylight on the arrival timing of upstream migrants at the lagoon-river interface, near the limit of tidal movement. We calculated the hours of daylight for the Chignik weir location using the US Navy tables of sunrise and sunset (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). An automatic water height gauge at the Chignik weir indicated that high tides at the Chignik weir averaged 2:20 h (range 2:00-2:34) after the published high and low tides for Kodiak Island, AK (NOAA station 9457292). We used these data to estimate the arrival time for each individual at Chignik River relative to that day's high and low tides. Finally, we employed logistic regression to determine whether acoustically tagged individuals return during day or night as a function of the amount of available daylight.

In Chignik Lakes we compared the median arrival date, as well as the spread in arrival timing of Dolly Varden, sockeye and Chinook salmon over 16 years of data. The ADF&G weir operators use a video monitoring system to count all upstream moving

salmonids passing through two openings in the weir for the first 10 minutes of each hour of the day, and extrapolate counts for the entire hour. Extrapolated hourly counts are summed to provide daily return estimates. To calculate the median return DOY of Chignik Lakes sockeye salmon we used the daily catch in the Chignik salmon fishery and escapement estimates (Todd Anderson, ADF&G-Kodiak, unpublished data) from the first day of weir operation until July 4 each year, which comprises the large early run of sockeye salmon (Chasco et al. 2007). The entire annual dataset of daily weir counts was used for the single run of Chinook and Dolly Varden. We fitted a normal distribution to the return data to calculate daily salmon and Dolly Varden abundance throughout the run (Y_t) using the following equation:

$$Y_t = \frac{1}{\sqrt{2\pi} \times \sigma} \times \exp \left[-\frac{(t-m)^2}{2\sigma^2} \right], \quad (1)$$

where t is the counting day of the year (days from Jan. 1, DOY), m is the DOY of 50% passage, and σ is a measure of the spread of the run. Errors between the daily abundance and the normal distribution were assumed to be normally distributed, and any non-normal error would likely weight the model toward the peak of the run, which is the parameter of interest (Hodgson et al. 2006). Parameters of the model were estimated by minimizing the negative log likelihood using the equation:

$$L(X_t|Y_t, \sigma) = \prod_{t=1}^{t=N} \frac{1}{\sqrt{2\pi} \times \sigma} \times \exp \left[-\frac{(X_t - Y_t)^2}{2\sigma^2} \right], \quad (2)$$

Where t is the counting day of the year; X_t is the number of estimated individuals returning on day t , Y_t is the number predicted for each day t based on the normal distribution; N is the number of days in the counting period, and σ is the amount of daily variability between the predicted and observed counts.

From return distributions for each species, we calculated annual median return DOY as well as the difference between the 20% and 80% passage DOY as a measure of the variation in return timing. We used ANOVA and Tukey HSD post hoc comparisons to identify differences in both median return DOY and variation in timing among the semelparous species and Dolly Varden (R Development Core Team 2011).

Migration timing of Dolly Varden throughout the Eastern Pacific:

To compare Dolly Varden migration timing in Chignik with other drainages in the Eastern Pacific, we compiled records of Dolly Varden passage counts from weirs and fences throughout the range in Alaska and British Columbia (Table 1 and Figure 2). From these data we calculated the median DOY of upstream migration for each watershed-year combination (i.e., the date at which 50% of the total count for the season had passed the counting location). Stream-year combinations in which the calculated median DOY occurred in the first five days of weir operation (i.e., inadequate sampling period) and cases where < 500 fish returned as these were judged to be unreliable and excluded from the analysis. For each stream we assigned latitude as the point where the stream enters the ocean regardless of the weir's location.

We used a linear model to determine whether mean median migration DOY depended upon the latitude of stream entry to the ocean. This analysis was performed for all 18 sites as well as all sites excluding SE Alaska (n = 14), because all other sites drain directly to the open ocean, whereas sites in SE Alaska open to protected areas of the Inside Passage, potentially altering the behavior of fish in those systems.

Environmental and biological correlates with Dolly Varden run timing:

Five watersheds (Auke Creek, and the Buskin, Chignik, Goodnews and Kanektok rivers) from the larger migration timing dataset contained at least 9 years of data, and were used for correlation with environmental variables. Dolly Varden were assumed to have a coastal distribution, consequently we determined average monthly mean sea surface temperatures (SST) for a single point 5 km directly offshore of the mouth of each watershed during May, June, July, August and September for all years of weir counts using NOAA High Resolution SST database (NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, <http://www.esrl.noaa.gov/psd/>). The only exception was Auke Creek, where SST's were monthly means of daily surface water measurements made near the creek mouth (NOAA-AFSC Auke Bay Laboratories). In the Chignik River population we also included monthly mean river temperatures in May and June as environmental correlates with migration timing (ADF&G-Kodiak, unpublished data).

Multiple regressions tested the relationship between annual Dolly Varden median return day and monthly mean SST, monthly mean freshwater temperature, and median sockeye salmon return date (Chignik River), or median return day and monthly mean SST only (Auke Creek, Buskin, Goodnews and Kanektok rivers). In cases where there were strong correlations ($r \geq 0.6$) between several predictors, variables with variance inflation factors > 5 were removed from the candidate models. Forward and backward stepwise regressions were used to create a final set of candidate models for each watershed. Akaike information criterion for small sample size (AICc) (Burnham and Anderson 2004) was used to determine the models from the candidate set with the most support. All models with a delta AICc score of ≤ 2 were included in results. For watersheds with significant correlations of SST and median return day, we plotted full

season (March-October) weekly mean SST and mean median return date to illustrate when in the temperature cycle returns occur (i.e. before, during or after the peak temperature).

Results

Individual Dolly Varden migration timing in Chignik Lakes:

Of the 20 fish tagged in Chignik Lagoon each summer, 17 (2008) and 10 (2009) were detected entering freshwater, although two fish in 2008 were first detected upstream of the Chignik weir and so the detection rate there was < 100% (Table 2). First freshwater detection dates varied widely, from as early as July 17, three days after tagging, to as late as November 12. Linear models indicated no effect of fish length at tagging on arrival date in either 2008 ($p = 0.167$) or 2009 ($p = 0.386$). In 2008 the mean arrival date at Chignik River was August 20, and in 2009 it was Sept. 7, approximately one month after tagging in each year. Arrival in the Chignik River occurred during daylight hours for 25 of 30 detected individuals, with the remaining fish entering between dusk and dawn on their respective arrival date. Logistic regression correctly predicted the return during daylight hours in 75% of fish, as a function of the amount of available daylight in each return day (Day Return = $-3.271 + 8.841 * \text{Proportion Daylight}$, $r^2_D = 0.15$, $p = 0.040$, AUC = 0.765). We found no significant effect of tidal cycle (categorized as being within an hour of high, low, ebb midpoint, flood midpoint) on arrival time at the weir $X^2(3, N = 25) = 2.33$, $p = 0.506$. Upon entering the river the fish showed three distinct behaviors. Sixteen percent of individuals that entered Chignik River were never observed in or beyond Chignik Lake; those individuals were detected in the river from minutes to

weeks. Twelve percent of detected fish entered the river and remained in the lower river for at least one day before moving into Chignik Lake. The third behavior, exhibited by 72% of the fish, was rapid movement into Chignik Lake (< 1 day). In 2008 one receiver was operating at the outlet of Black Lake and it detected 9 of the 12 fish detected in Chignik Lake, and 7 of those overwintered upstream of the Black Lake receiver. In spring of 2009, 11 of 13 individuals overwintering upstream of the Chignik Lake outlet moved downstream past the weir and exited Chignik River, as did 8 of 10 fish in 2010. Those fish that did not migrate in the spring were never observed again, indicating either mortality or extended residence in freshwater.

In both years, spring downstream migration occurred near the first ice free day in the Chignik River (Table 2) for most individuals and all migrating fish exited freshwater by May 30. In 2009 and 2010, 3 and 1 individuals respectively, were detected returning after a second summer following tagging.

Movement speeds varied markedly among sections of the watershed, and whether movement was upstream or downstream (Table 3). The fastest average speeds ($1.5 \text{ km}\cdot\text{hr}^{-1}$, $1.2 \text{ BL}\cdot\text{sec}^{-1}$) were recorded during the spring migration down the Chignik River, and the slowest were upstream movements in Chignik River ($0.3 \text{ km}\cdot\text{hr}^{-1}$, $0.24 \text{ BL}\cdot\text{sec}^{-1}$) and Chignik Lake to Black Lake ($0.24 \text{ km}\cdot\text{hr}^{-1}$, $0.19 \text{ BL}\cdot\text{sec}^{-1}$) sections.

The median weir arrival DOY of Chignik Dolly Varden, sockeye and Chinook salmon differed ($F_{2,48} = 114.37$, $p < 0.001$). Post hoc comparisons using Tukey HSD indicated that there was no significant difference in mean arrival DOY between Dolly Varden ($MDOY = 192.8$, $SD = 7.01$) and Chinook ($MDOY = 195.5$, $SD = 2.43$), but both arrived significantly later than the main run of sockeye salmon ($MDOY = 174.3$, $SD =$

3.48). We also found significant differences in the spread of the run, the difference between 20% and 80% arrival DOY ($F_{2,48} = 7.56$, $p = 0.001$). In pairwise comparisons using Tukey HSD we found that Dolly Varden ($M = 22.40$ days, $SD = 9.75$) return over a significantly longer period of time than Chinook ($M = 15.76$ days, $SD = 4.68$) and sockeye ($M = 14.57$ days, $SD = 2.41$), which did not differ from one another. In addition, we identified differences in the interannual variation of return timing of Dolly Varden, Chinook, and sockeye using a Bartlett's homogeneity of variance test. Dolly Varden had more variable return timing than either Chinook ($p < 0.001$) or sockeye ($p = 0.008$) but the two salmon species did not differ from each other ($p = 0.149$).

Migration timing of Dolly Varden throughout the Eastern Pacific:

Average median upstream migration DOY across all watersheds varied by over two months (Pikmiktalik River DOY = 184, Auke Creek DOY = 246), and tended to be later at higher latitudes (Median Migration DOY = $76.02 + 2.24 * \text{Latitude}$, $F_{1,16} = 8.352$, $p = 0.010$, $r^2 = 0.302$). However, after removing the SE Alaska sites, latitude explained 53% of the variation in migration date (Median Migration DOY = $44.97 + 2.694 * \text{Latitude}$, $F_{1,12} = 15.78$, $p = 0.001$, $r^2 = 0.532$).

Environmental and biological correlates with Dolly Varden run timing:

In the Chignik Lakes watershed the median upstream migration DOY varied by 43 days over the 15 years we examined. Of the 13 models tested to explain variation in median migration DOY, June SST alone was the best predictor (Table 4; Median Migration DOY

= 245.73 -6.89*June SST, $F_{1,13} = 41.17$, $p < 0.001$, $r^2 = 0.741$). May and June freshwater temperatures were removed due to multicollinearity, and were not tested in any models. In four other watersheds we evaluated May, June, July, August, and September SST's as predictors of migration DOY. In the Buskin River both June SST (Median Migration DOY = 261.64 -7.94*June SST, $F_{1,7} = 9.755$, $p = 0.016$, $r^2 = 0.522$) and May SST ($\Delta AIC_c = 0.858$, Median Migration DOY = 247.49 -8.56*May SST, $F_{1,7} = 8.232$, $p = 0.024$, $r^2 = 0.475$) were significant predictors of migration DOY, with similar patterns to nearby Chignik River. In Auke Creek both July SST (Median Migration Date = 157.80 +6.12*July SST, $F_{1,9} = 12.53$, $p = 0.006$, $r^2 = 0.535$) and August SST ($\Delta AIC_c = 0.108$, Median Migration Date = 168.76 +5.51*July SST, $F_{1,9} = 12.53$, $p = 0.006$, $r^2 = 0.531$) explained over 50% of the variation in migration DOY. However, temperature was positively correlated with median migration DOY (warmer = later) in Auke Creek, whereas in the Chignik and Buskin rivers warmer water was associated with earlier migration. In neither the Goodnews nor Kanektok rivers was migration DOY correlated with any average monthly SST. Plots of the seasonal weekly mean SST for each watershed and its mean median return DOY revealed that the Dolly Varden return to the Chignik and Buskin systems before the peak temperatures whereas in Auke Creek they tend to return after the peak temperature (Figure 3).

Discussion

Acoustic tagging of Dolly Varden in Chignik Lagoon and subsequent monitoring of movement into freshwater habitats revealed patterns of migratory behavior not typical of the semelparous Pacific salmon sympatric at this site, nor elsewhere. Although some Dolly Varden entered freshwater soon after tagging, others remained in estuarine/marine

waters for months following tagging, likely making extensive use of the estuary for foraging, rather than a migratory corridor. The extreme delay in upstream migration observed for some individuals supports the hypothesis that some fish originating in other nearby watersheds may forage in Chignik lagoon during the summer, spawn in a natal watershed outside of Chignik in fall, and then enter Chignik Lake to overwinter post-spawning (Armstrong 1974, Bernard et al. 1995, Crane et al. 2005). Similar strategies have been observed in other salmonids, including bull trout (Brenkman and Corbett 2005), Arctic char, and brown trout (Jonsson et al. 2001, Olsen et al. 2006a, Jensen and Rikardsen 2012). Additionally, the fish detected at Chignik River in the fall that were never subsequently detected on any freshwater receiver may have left the Chignik system and overwintered or died in marine waters. Overwintering in brackish waters has been described for brown trout (Olsen et al. 2006a, Jensen and Rikardsen 2008, 2012) and Arctic char (Jensen and Rikardsen 2008, 2012) but has not been conclusively shown in Dolly Varden (Bernard et al. 1995). This contrasts markedly with coastal bull trout that may overwinter regularly in temperate Pacific Ocean waters (Brenkman and Corbett 2005). These results outline the wide diversity in migration timing of fish that were all captured in the lagoon midsummer. Nearly half returning tagged fish entered freshwater after the ADF&G weir ceased counting, indicating that a significant fraction of the large bodied individuals (≥ 300 mm FL) may not be counted by the weir. This is surprising given that the mode of Dolly Varden ascending the river occurs more than six weeks before the weir ceases counting, and may indicate alternate migratory timing among fish of different maturational status (Jonsson and Jonsson 2011).

Individuals moving from marine waters to Black Lake made rapid progress through river and Chignik Lake habitats, indicating little use of this habitat for purposes other than migration. Large bodied Dolly Varden consume eggs and tissues of spawning sockeye salmon and early migrating fish may return to do so (Denton et al. 2009, Denton et al. 2010). However, we detected no within-watershed movement demonstrating that fish were capitalizing on different salmon spawning timing to increase egg consumption, as has been shown in other consumers (Ruff et al. 2011). In addition, many fish did not enter freshwater until late fall or early winter, well after the vast majority of salmon spawning occurs, indicating those individuals may be extending their foraging opportunities in marine waters rather than returning to freshwater to consume salmon resources. It is unclear what physiological and behavioral processes drive each of the alternative migratory strategies, although size and foraging success in marine waters may determine how quickly individuals leave the marine environment for the reliability of salmon resources upstream. However, in brown trout differences in marine habitat use may result from ontogenetic shifts in habitat use (Jonsson and Jonsson 2011).

Mid-winter movements to marine habitats have been demonstrated for brown trout and Arctic char at much higher latitudes than Chignik (Jensen and Rikardsen 2008, 2012), and bull trout in more temperate systems (Brenkman and Corbett 2005). Chignik Dolly Varden, however, did not make any mid-winter downstream migrations. The earliest emigrations from the system occurred near the Chignik River's first ice free day, consistent with other Dolly Varden studies that indicate outmigration during or immediately following ice out (Lisac 2009). This contrasts with cutthroat trout, which spawn in the spring prior to outmigration (Saight et al. 2007), and some brown trout

which may exhibit extremely protracted outmigration of post-spawners, including modes in the spring and fall (Jonsson and Jonsson 2009). Movement into marine waters also preceded the large sockeye salmon smolt outmigration, which peaks in mid-to-late May (Loewen and Bradbury 2011), and Dolly Varden apparently forgo the opportunity to remain in the Chignik River and prey on smolts, in favor of an early migration to obtain marine food resources (Narver and Dahlberg 1965). This conclusion is supported by the rarity of salmon smolts in the diets of Chignik River Dolly Varden (Roos 1959), a surprising finding given the abundance of salmon smolts passing through the Chignik River on their seaward migration each spring (8.1 million and 28.1 million sockeye in 2009 and 2010 respectively; Loewen and Bradbury 2011). It is possible that despite the abundance of salmon smolts, the energetic demands of prey capture in Chignik River make extended residence in freshwater less favorable than foraging in marine habitats. Salmon smolts form an important component of cutthroat trout diets in marine waters (Duffy and Beauchamp 2008), and Dolly Varden may employ a similar strategy, feeding on salmon in marine rather than fresh waters.

The two month difference in median Dolly Varden upstream migration between the earliest and latest streams demonstrated clear variation among populations linked to local climatic regimes. Among these sites we observed a delay in upstream migration timing of Dolly Varden with increasing latitude that is more extreme than that observed in sockeye salmon over similar latitudinal ranges (Hodgson and Quinn 2002). Although the mechanisms of the delay are unclear, extreme changes in habitat and climate from south to north likely drive much of the difference in migration timing. In contrast, Atlantic salmon mature, migrate, and spawn earlier at higher latitudes (Hansen and

Jonsson 1991, Jonsson et al. 2007). Although the tendency for marine waters to be more productive than freshwater habitats is more pronounced in northern compared to southern waters (Gross et al. 1988), the timing of spring melt restricts northern fish from entering marine waters until later in the spring than in southern streams. In addition, Dolly Varden in southern streams may re-enter freshwater habitats to make use of salmon subsidies mid-summer, but such subsidies are less available in northern latitude streams where semelparous salmon are less abundant or absent (DeCicco and Reist 1999, Quinn 2005). In northern streams, therefore, Dolly Varden may maximize their time in marine waters before falling temperatures prevent stream re-entry. The four Southeast Alaska streams evaluated have very different migration patterns, including the latest median migration date we observed (Auke Creek). The more protected environment of the SE Alaskan inside passage compared to more northerly sites may promote later movement among streams that is detected at the Eva Creek and Auke Creek weirs. Additionally, other studies have found that char have poor osmoregulation in marine waters at low temperatures, possibly driving fish out of the marine environment in northern latitudes while permitting extended residence at lower ones (Finstad et al. 1989, Jensen and Rikardsen 2008).

Patterns of interannual variation in median return date differed among the five watersheds we evaluated in greater detail, indicating that Dolly Varden exhibit flexibility in upstream ascent that is comparable to semelparous species with long distance ocean migrations such as sockeye salmon (Hodgson et al. 2006), although Chignik Dolly Varden had a more protracted migration than either Chinook or sockeye. In the Chignik and Buskin rivers, where Dolly Varden tend to return prior to peak annual temperatures,

we observed similar responses of earlier returns with increasing June SST. Warm June temperatures may reflect conditions when fish entered the ocean earlier and acquired resources more rapidly, returning to the relative safety of freshwater earlier than in years with cool springs. Dolly Varden may adopt a strategy of foraging in marine waters for the minimal amount of time required to store energy for spawning and overwintering, because they spread their reproductive effort over multiple seasons, similar to other iteroparous salmonids with brief periods of marine residency (Saiget et al. 2007, Jonsson and Jonsson 2011). In Southeast Alaska, the trend was for later returns with increasing temperature and the migration tended to follow the annual temperature maximum. Maximum SST's near SE Alaskan streams are generally much higher than in the Gulf of Alaska, and Dolly Varden may be delaying their return in warm years until cooler water allows for return to the stream. Annual nearshore SST profiles for the Buskin and Chignik Rivers, as well as Auke Creek, indicate that Dolly Varden return either before or after peak temperatures, concordant with the preference for cool water observed in closely related Arctic char (Larsson 2005). In the two streams north of the Alaska Peninsula that we evaluated, we found no relationship between SST and variation in migration timing. However, the location near the stream mouth that we chose for measuring SST may not represent the water occupied by Dolly Varden north of the Alaska Peninsula, where they migrate extensively (DeCicco 1992, Morita et al. 2009). In addition, if maximum temperatures in northern latitudes do not exceed stressful thresholds, other environmental processes (e.g. ice formation, minimum flows) may play a larger role in shaping migration timing (Jonsson et al. 2007). Similar to other populations in Alaska (Denton et al. 2010, Jaecks 2010), Dolly Varden in Chignik may

rely heavily on sockeye salmon subsidies. However, we observed only a weak correlation between Dolly Varden and sockeye return timing. Most of the salmon subsidy may come weeks after peak salmon entry as they spawn and begin to senesce, reducing the necessity of coincident migration timing between the two species.

Although a number of studies have addressed migration timing of adult Atlantic salmon (Jonsson et al. 1990, Stewart et al. 2002, Vaha et al. 2011), brown trout (Jonsson and Jonsson 2002, Jensen and Rikardsen 2012) and Arctic charr (Jensen and Rikardsen 2012), much less information has been published on iteroparous Pacific species including bull trout (Hayes et al. 2011), cutthroat trout (Saiget et al. 2007) and Dolly Varden (Armstrong 1974). This is an important area of research from a management perspective and from the standpoint of our understanding of the factors that lead to the life history diversity in iteroparous trout and char. Our results contrast Dolly Varden markedly with semelparous species in the variability of return timing within and among populations, as well as the breadth of the return window. Dolly Varden, like many of the iteroparous species, must optimize their occupancy in multiple environments, trading off growth opportunities in marine or estuarine environments for growth and spawning in freshwater environments and the relative mortality risk in each. Unlike iteroparous *Oncorhynchus* species, which are spring spawners, Dolly Varden are fall spawners and must balance fall foraging opportunities with spawning immediately prior to protracted conditions of cold water and limited foraging opportunities in ice-covered systems. While attempting to maximize spawning in any given season, iteroparous species must also provide for their own survival and future breeding opportunities. On the other hand, semelparous species need only time their upstream migration to maximize reproductive opportunities. As

such, migration in semelparous species is timed to allow arrival at spawning locations at an appropriate time for egg survival and fry emergence. More effort is needed to characterize the complex anadromous migrations of iteroparous salmonids because their diverse life histories may affect their role in aquatic ecosystems and interactions with semelparous salmonids (as competitors, predators and scavengers). The shifts in phenology seen in salmonid communities as climate warms in northern areas suggest especially complicated patterns in the future (Kovach et al. 2013).

Table 1.1: Rivers and streams with published upstream Dolly Varden passage counts.

Site #	Site	Latitude (°N)	Longitude (°W)	Count Type	Years of operation	Mean total count*	Mean # counting days	mean median migration date	Average start DOY	Average end DOY
1	Eva Ck.	57.402	-135.100	Weir	1962-1964	77286	220	214	97	324
2	Taku R.	58.548	-133.676	Fish Wheel	1987-1988	818	115	198	149	263
3	Auke Ck.	58.382	-134.636	Weir	1997-2007	3716	130	246	179	308
4	Windfall Ck.	58.526	-134.779	Weir	1997	3901	130	202	100	229
5	Anchor R.	59.780	-151.838	Weir	1995	10994	43	200	185	227
6	Buskin R.	57.756	-152.483	Weir	2001-2009	9923	124	194	146	272
7	Chignik R.	56.339	-158.574	Weir	1996-1999, 2001-2011	17610	95	193	149	243
8	Frosty Ck.	55.195	-162.854	Weir	2000-2002	2550	116	217	180	295
9	Big Ck.	58.515	-156.569	Weir	2003	4901	99	201	177	275
10	Goodnews R.	59.121	-161.586	Weir	1996-2011	2662	78	204	178	255
11	Kanektok R.	59.746	-161.931	Weir	2001-2011	16854	62	206	186	247
12	Pikmiktalik R.	63.238	-162.589	Weir	2006	897	72	184	184	243
13	Kwiniuk R.	64.697	-162.016	Weir	2004-2007	5880	86	225	171	256
14	Niukluk R.	64.596	-163.321	Weir	2004-2007	1837	72	222	179	251
15	Nome R.	64.482	-165.305	Weir	2004-2007	2490	69	226	184	252
16	Lupine R.	68.718	-147.627	Weir	1971	628	59	236	190	259
17	Hulahula R.	70.996	-143.372	Acoustic Camera	2006, 2008	13967	51	244	213	263
18	Babbage R.	69.232	-138.430	Weir	1990-1992	5573	51	230	207	257

*Counts are raw reported values and not adjusted for trap efficiency.

Table 1.2: Detection metadata for Dolly Varden tagged in Chignik Lagoon in the summers of 2008 and 2009 and later detected entering Chignik River.

Tagging year	tagging DOY	first FW detection DOY (range)	Number of days in marine until first detection	Number of Days in FW (range)	first ice free DOY in spring	Spring departure DOY (range)	second summer return DOY	Number of days in marine, second summer (range)
2008	188, 195, 198	198-315 (15)	2-127	179-317	125	112-150 (11)	183-202 (3)	71-75
2009	217	222-290 (10)	5-73	214-279	131	130-140 (8)	216 (1)	79

Table 1.3: Mean travel rates for all movements by Dolly Varden among monitored watershed sections. Rates are calculated with the minimum possible distance between points, and number of body lengths for each individual \pm 1 SD. Number of individual movements for each segment included parenthetically.

	Upstream	km·hr ⁻¹	BL·Sec ⁻¹	Downstream	km·hr ⁻¹	BL·Sec ⁻¹
Weir-Chignik Lake Outlet		0.3 \pm 0.25 (9)	0.24 \pm 0.20 (9)	CLO-W	1.50 \pm 0.94 (8)	1.20 \pm 0.76 (8)
Weir-Mid Chignik Lake		0.77 \pm 0.51 (10)	0.66 \pm 0.45 (10)	MCL-W	0.59 \pm 0.35 (5)	0.47 \pm 0.28 (5)
Chignik Lake Outlet-Mid Chignik lake		1.32 \pm 0.78 (7)	1.03 \pm 0.60 (7)	MCL-O	0.73 \pm 0.83 (5)	0.64 \pm 0.81 (5)
Chignik lake Outlet-Black Lake Outlet		0.24 \pm 0.02 (2)	0.19 \pm 0.03 (2)			
Mid Chignik Lake- Black Lake Outlet		0.71 \pm 0.33 (3)	0.48 \pm 0.19 (3)	BLO-MCL	0.91 \pm 0.73 (5)	0.74 \pm 0.59 (5)
Weir-Black lake Outlet		0.30 (1)	0.21 (1)	BLO-W	0.62 (1)	0.40 (1)

Table 1.4: All tested models predicting median Dolly Varden migration date in the Chignik Lakes watershed. Lower AICc scores indicate a better fit of the data to the model.

Model	K	AICc	Δ AICc	AICc Wt.	Cum. Wt.	LL
June SST	3	86.7216	0	0.5564	0.5564	-39.2699
June SST + median sockeye migration	4	88.7235	2.0019	0.2045	0.7609	-38.3617
June SST + September SST	4	89.9731	3.2515	0.1095	0.8703	-38.9865
June SST + May SST + September SST	4	90.2744	3.5528	0.0942	0.9645	-39.1372
June SST * median sockeye migration	5	93.3614	6.6398	0.0201	0.9846	-38.3473
June SST + May SST + September SST	5	94.5711	7.8495	0.011	0.9956	-38.9522
June SST + May SST + September SST + median sockeye migration	6	97.855	11.1334	0.0021	0.9977	-37.6775
May SST + September SST	4	99.0175	12.2959	0.0012	0.9989	-43.5088
September SST	3	101.2488	14.5272	0.0004	0.9993	-46.5335
May SST	3	101.5912	14.8696	0.0003	0.9996	-46.7047
September SST + median sockeye migration	4	103.0193	16.2977	0.0002	0.9998	-45.5096
May SST + September SST + median sockeye migration	5	103.024	16.3024	0.0002	1	-43.1787
median sockeye migration	3	106.3191	19.5975	0	1	-49.0686

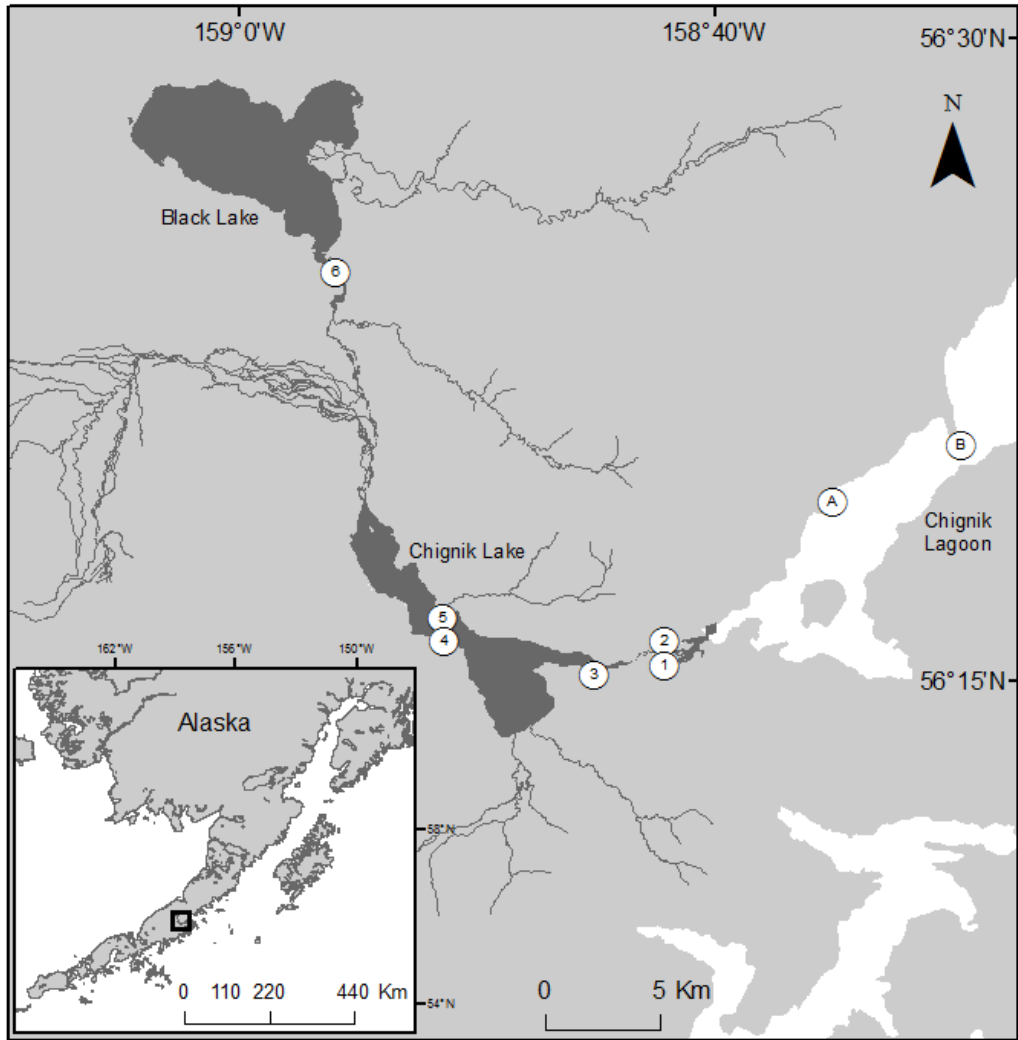


Figure 1.1: Locations of acoustic tagging and receiver placement. Tagging locations in 2008 (A and B) and 2009 (B). Monitoring receivers are points enumerated: 1 and 2 (Lower Chignik River, at Chignik Weir), 3 (Chignik Lake outlet), 4 and 5 (central Chignik Lake), and 6 (Black Lake outlet). Receivers 3 and 6 were recovered in 2008-09 only. Dark grey indicates freshwater portions of the system; white indicates marine areas.

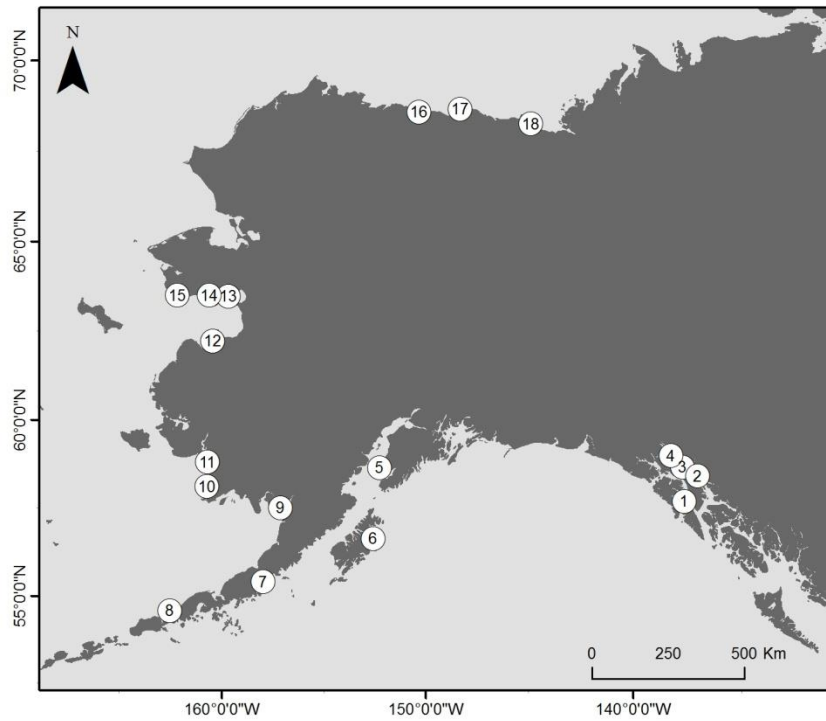


Figure 1.2: Map of Alaska and Canada where Dolly Varden were counted ascending rivers and streams. Symbol numbers correspond to Site # in table 1.

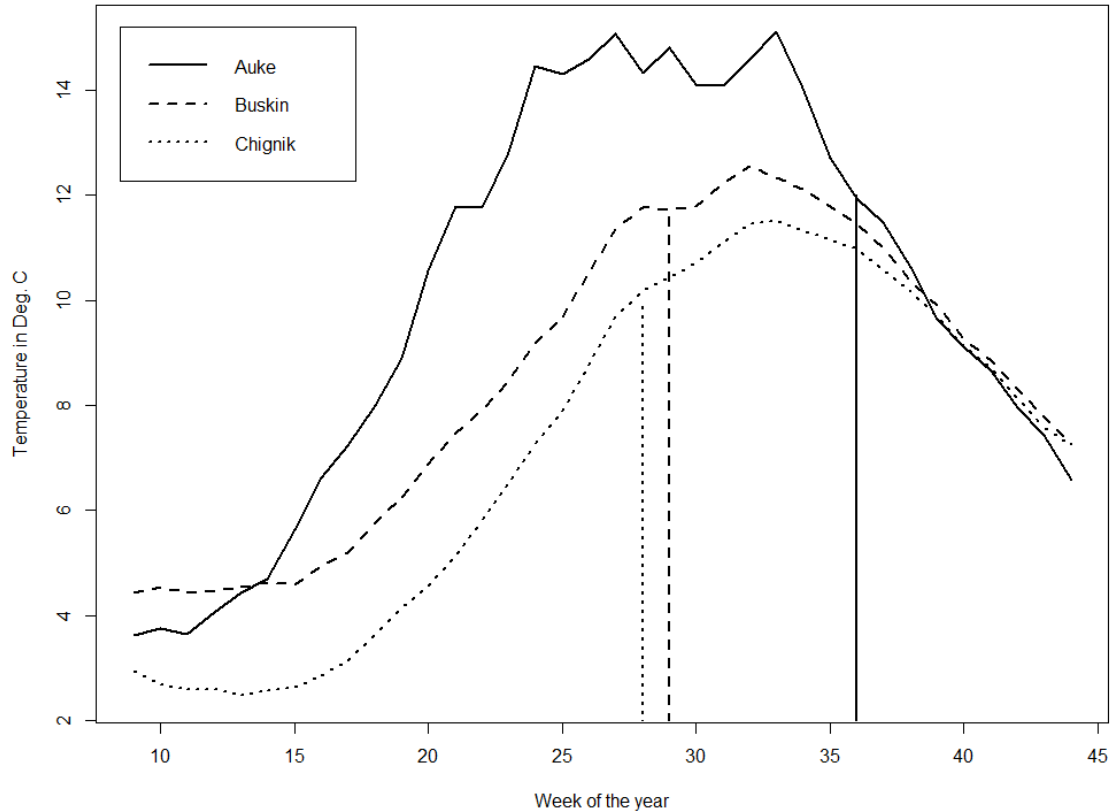


Figure 1.3: Sea surface temperature and ascent of freshwater streams. Average weekly sea surface temperature for adjacent ocean waters of Auke Creek (solid line, 1997-2007), Buskin River (dashed line, 2001-2009) and Chignik River (dotted line, 1996-2011). Vertical lines indicate the average median day of upstream migration for each population. Auke Creek SST temperature data courtesy NOAA-AFSC Auke Bay Laboratories. Chignik and Buskin Rivers SST courtesy NOAA/OAR/ESRL PSD, Boulder, Colorado, USA.

Chapter 2: Differential growth in estuarine and freshwater habitats indicated by plasma IGF1 concentrations and otolith chemistry in Dolly Varden char

Introduction

The use of both marine and freshwater habitats by migratory individuals (i.e., diadromy) is a strategy adopted by many different groups of fishes to exploit the different rates of growth and probabilities of survival in each habitat (Northcote 1978, Gross 1987, McDowall 1988). Anadromous species (those breeding in freshwater and migrating to sea to feed) are proportionally more common than catadromous species (breeding in the sea and feeding in freshwater) in high latitude watersheds that are nutrient-poor compared to adjacent marine waters (Gross et al. 1988). However, the same watersheds may have simple communities with fewer predators of juvenile fishes. In contrast, size dependent mortality in marine waters (Sogard 1997) often favors growth in freshwater environments prior to ocean entry (Rounsefell 1958, Quinn and Myers 2004). The advantages of inhabiting multiple habitats at various life stages are balanced by the energetic cost of flexible osmoregulatory ability and the arduousness of migration required to reach each habitat (Northcote 1978). Although many salmonid fishes are commonly described as anadromous, considerable variation in the scale of anadromy exists within and among species (Quinn and Myers 2004). For example, all pink salmon (*Oncorhynchus gorbuscha*) are anadromous, spending little time in freshwater habitats, maximizing growth potential at sea, and maturing at a young age (Quinn 2005). In contrast, sockeye salmon (*O. nerka*) often rear for one or two years in freshwater lakes, trading off relatively poor growth there for higher survival at sea at a somewhat larger size than the juvenile pink salmon. In some freshwater habitats, fully resident sockeye salmon forms (i.e., kokanee) have developed, trading smaller body size at maturation for increased

survival (Wood 1995, Quinn 2005). In comparison to the semelparous salmon, however, facultatively anadromous species such as *Salmo trutta*, *Salvelinus alpinus*, *S. confluentus*, *S. malma*, *O. clarkii*, and *O. mykiss* add additional complexity by varying widely in their age at migration, length of time spent at sea, and habitats used (Armstrong 1974, Armstrong and Morrow 1980, McDowall 1988, Thorpe 1994, Klemetsen et al. 2003). Consequently, individuals from a given cohort may be spread among habitats, experiencing markedly different environmental conditions affecting growth, survival, and ultimately fitness. Despite the diversity in movement patterns for facultatively anadromous individuals, few studies have attempted to evaluate the growth tradeoffs involved in movement to alternative habitats, particularly for populations that may simultaneously inhabit marine and freshwater environments.

Although growth rates of fishes are often used as a proxy for habitat quality, in semelparous anadromous species direct comparisons between marine and freshwater growth are difficult because movement often results from an ontogenetic shift and individuals in each habitat may be of different sizes or life stages. In facultatively anadromous species, however, individuals of a similar size and age may simultaneously occupy marine, estuarine, and freshwater habitats, facilitating comparisons of growth among habitats. Many studies have shown rapid growth of salmonids in estuarine environments (Reimers 1973, Healey 1979, Tschaplinski 1987). However, few studies have compared growth in estuaries to growth of conspecifics at an equivalent life stage in freshwater environments ; a comparison that is necessary to understand the relative benefit of migratory and resident behavioral strategies (Kjelson et al. 1982, Cunjak 1992, Hayes et al. 2008). In addition, large differences in habitat type, size, and fish movement

and density among estuarine, marine, and freshwater environments may present logistical challenges to making comparable measurements. As a consequence, growth comparisons are usually attempted with small sections of habitat or with caging studies, leading to difficulties in scaling results to larger portions of the habitat and population (Macdonald et al. 1988, Miller and Simenstad 1997).

There are myriad techniques to evaluate growth, from individual mark-and-recapture, to changes in the population's size modes through time. However, each of these techniques is challenging to apply to wild fish, where a large population size and habitat volume may be coupled with extensive movements that reduce the effectiveness or confidence in methods that require multiple sampling events. Low statistical power can limit the ability to confidently assess differences in growth between habitats, even when the mean change in size is indicative of growth (e.g. Cunjak 1992). To make habitat-growth comparisons more effective, a single-capture growth measure is required. Few techniques have proven effective in indicating growth in wild fishes in a single capture event, but laboratory research in multiple species indicates that plasma insulin-like growth factor 1 (IGF1) concentration can be a quantitative metric for recent somatic growth (Beckman 2011). IGF1 is a hormone produced by the liver in response to changes in growth hormone, consumption rate, and diet quality (Beckman 2011). IGF1 directly stimulates cell division and growth; therefore, IGF1 concentration may directly reflect growth and is not merely a growth correlate. Several studies in salmonids, including *Salvelinus alpinus* (Cameron et al. 2007), have indicated strong correlations between plasma IGF1 concentration and changes in fish length (Beckman et al. 2004a, Beckman et al. 2004b).

In free-ranging fish, knowledge of the movement history of an individual is important to place the observed growth rates in a spatial context. However, identifying the movement history of individuals using traditional methods (e.g., tagging and serial sampling) requires repeated sampling of all possible habitats, a challenging task in large-scale natural environments. Otolith microchemistry has repeatedly been used to determine habitat use within and among habitats in a variety of species (Brown 2006, Miller 2007, Bradbury et al. 2008, Macdonald and Crook 2010). Otoliths are calcium carbonate components of the fish inner ear, used for balance and orientation (Campana 1999). During otolith construction, fish regularly accrete calcium carbonate in a protein matrix, enlarging otoliths with age (Campana 1999). Other elements may replace calcium in proportion to their concentration in the saccule fluid, which in turn reflects the concentration of those elements in the aqueous environment (Elsdon et al. 2008). Several elements, in particular strontium (Sr) and barium (Ba) vary widely in concentration between marine and freshwater environments (Kraus and Secor 2004). The movements of diadromous fishes are therefore detectable by analyzing the concentration of elements at discrete regions in the otolith that correspond to life events (e.g., age, migration) (Elsdon and Gillanders 2003, Zimmerman 2005).

Here, we pair an analysis of plasma IGF1 concentrations from free-ranging Dolly Varden captured in a range of freshwater and estuarine environments, with chemical analysis of regions of the otolith formed in the weeks preceding capture. Together, these analyses allow for comparisons of growth and habitat use in both freshwater and estuarine habitats throughout the summer months. In addition, we use these analyses to infer the extent of movement among habitats within the estuary, as well as movement

between the estuary and lake habitat. We hypothesized that growth in estuarine environments would be higher than that in lake habitats. However, because Dolly Varden are abundant throughout the Chignik Lagoon (Narver and Dahlberg 1965), individuals may make regular movements throughout the estuary as the tidal cycle allows, weakening any site specific signals of growth unless the fish's recent movement history was considered. Therefore, IGF1 may indicate either average growth of the estuarine environment, or site specific growth depending upon the scale and timing of Dolly Varden movement.

Methods

Field collections

Dolly Varden are a facultatively anadromous species, ideally suited to comparisons of growth among habitats. In many populations Dolly Varden make their first marine migration at age 3 or 4, although where appropriate habitat exists, individuals of a range of size/age classes may be found in both marine and fresh waters simultaneously (Armstrong and Morrow 1980, Morrow 1980). In addition, Dolly Varden likely make extensive use of estuarine waters and remain in nearshore coastal waters, as they generally remain in marine environments for the summer months, returning to freshwater in late summer or fall for reproduction and overwintering (Armstrong 1974, Bernard et al. 1995, Bond and Quinn 2013).

The Chignik Lakes watershed in southwestern Alaska drains a 1536 km² basin and includes 25 km² Chignik Lake and a 33 km² semi-enclosed lagoon (Figure 1)(Narver and Dahlberg 1965, Simmons et al. in press). Chignik Lagoon loses approximately 50% of its available surface area during extreme tidal exchanges (~4 m) (Narver and Dahlberg

1965, Simmons et al. in press) and varies in salinity by tidal height, river flow and distance from the sand spit, ranging from 0‰ to 34‰ (Simmons et al. in press).

Dolly Varden were collected with a 35 m beach seine (3 mm mesh, 4 m bag tapering to 1 m wings) used to encircle a standard portion of the nearshore habitat (~ 190 m²) at six sites in Chignik Lake and five sites in Chignik Lagoon (Fig 1.) every 10 - 14 d from June through August in 2009 and 2010. Lagoon sites are names according to long term sampling convention: Peahi: Chignik River/ estuary ecotone, Alpha and Pillar Rock: inner-lagoon, Hume Point, mid-lagoon, Spit: outer-lagoon. At each site, all Dolly Varden were counted, and a subset was measured for fork length and mass. For IGF1 analysis, target sample sizes were 10 randomly selected individuals, however to ensure enough plasma for hormone analysis, individuals > 120 mm fork length were sampled from each site at each interval. Each fish was sacrificed in MS-222 anesthetic, and following measurement of length and mass, immediately bled from the caudal vein with a heparinized syringe. Whole blood was stored in individually labeled microcentrifuge tubes on ice. Within 6 h of collection, blood tubes were centrifuged at 3000 g for 5 min. Plasma was removed and stored at -20°C until the end of each field season and -80°C thereafter. Each fish was examined for gonadal development and visually categorized as immature or maturing at the time of capture by the developmental stage of the gonads; mature males and females had enlarged testes and ovaries compared to immature individuals. We also removed sagittal otoliths from each sampled individual, rinsed them in de-ionized water and stored them dry in microcentrifuge tubes.

Blood Plasma Lab analyses:

Blood plasma samples were analyzed at the National Marine Fisheries Service, Northwest Fisheries Science Center using an immunoassay to measure the concentration of IGF1 (as described in Shimizu et al. 2000). Briefly, IGF1 was isolated from plasma with an acid-ethanol extraction, and measured by TRF immunoassay using a modification of methods described by Small and Peterson (2005). Each sample was analyzed in duplicate, and samples with low (<30%) or high (> 85%) average binding, as well as those with a coefficient of variation exceeding 10% were reanalyzed or excluded. The interpretation of IGF1 concentration depends upon the maturational state of each individual as gonadal steroids may either stimulate or inhibit IGF1 independently of growth rate (Beckman 2011). IGF1 is therefore most reliable as a growth index for juvenile fish. Two methods were used to discriminate whether fish had initiated the maturation process. Gonad mass was measured for each individual; however, early in the summer gonad mass did not provide distinct discriminatory power as clear gonad development may not occur until closer to the fall spawning period (Blackett 1968). To further identify individuals preparing to mature in the year of capture we also measured plasma concentrations of 11-keto testosterone (11-KT, male), and 17 β -estradiol (E2, female) steroids in all individuals sampled in 2009. Plasma 11-KT concentrations were measured by an enzyme-linked immunosorbent assay following Cuisset et al. (1994). Plasma E2 was analyzed with a double ether extraction followed by radioimmunoassay using the methods of Sower and Schreck (1982). We used size and maturation relationships established in the 2009 collection determine which fish to include in IGF1 analyses from the 2009 and 2010 collection.

Otolith lab analyses:

Otoliths were cleaned by triple rinsing in nanopure water and sonicating in an ultrasonic bath for 10 min during the final rinse to remove any residual biological material. To create saggital sections, otoliths were glued sulcus side up, to standard biological slides with crystalbond 409 thermoplastic resin. The sulcus side was polished with successively finer polishing film until the otolith core could be resolved. Each slide was then re-heated to soften the resin and the otoliths was inverted. The remaining side was ground until the core was exposed and polished with 0.3 μm film. We then cut each slide so that the otolith remained on as small a piece of slide as possible. We adhered 14-18 pieces of slide glass, each containing an otolith, to new biological slides until all otoliths were mounted on a master slide. Each master slide was triple rinsed, sonicated for 15 min, and dried in a class 100 clean room. Edge chemistry for each otolith was analyzed with laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) at the Keck Collaboratory, Oregon State University. A VG PQ ExCell ICPMS with a New Wave DUV193 excimer laser was used for all analyses of 2009 otoliths and a Thermo X-Series II ICPMS and Photon Machines Analyte G2 193 nm laser was used to analyze 2010 otoliths. The laser was set at a pulse rate of 7 Hz with a 20- μm ablation spot and traveled at 5 $\mu\text{m sec}^{-1}$. We measured Sr, Ba, Mn, Mg, Cu, Ca, Pb, Ca and used NIST-612 glass to transform ion ratios to elemental ratios. These were converted to molar ratios using the molar mass of each element. Final analyses were computed on the element:Ca in $\text{mmol} \cdot \text{mol}^{-1}$. A calcium carbonate standard with known concentration (USGS MACS-2) was used to determine the accuracy of the element:Ca ratio and correct final element:Ca values.

Data Analyses:

We evaluated the relationship between sex steroid concentration and fork length for each sex graphically to determine a size threshold for maturing individuals. We compared fish length and either 11-KT (male) or E2 (female) concentrations to identify a size threshold for maturation in each sex that was used for both 2009 and 2010 samples. All fish above the size thresholds for maturation were removed from further analyses. In addition, some precocious males had elevated gonadosomatic index values (GSI) at very small sizes, indicating maturation below the size threshold derived in 2009. Therefore all males with a $GSI > 3\%$ were also removed from further analyses. We then tested the resulting dataset for year and sex effects and performed ANOVA as well as Tukey HSD post-hoc tests on fish length and blood plasma IGF1 concentration to identify monthly differences among sites.

Edge otolith chemistry evaluates the portion of the otolith formed over some period of time prior to capture. Because the width of annual bands generally decreases with age as the percent change in fish size decreases each year, the amount of time incorporated into a given distance of otolith transect varies among individuals. However, measurements on a finer scale than the width of the ablation trough (20 μm) are too small to overcome the coarse averaging of the laser. To balance the time of otolith formation with the analytical constraints of LA-ICP-MS we evaluated the otolith width from the last annulus to the edge using fork length, age, and capture day of the year (DOY) as predictors in a series of linear models. To determine residency at each collection site, discriminant function analysis (DFA) was performed to classify individuals from each site with the average edge ratios of Sr:Ca, Ba:Ca, Mn:Ca, Mg:Ca, Cu:Ca and Pb:Ca at four different edge distances (10 μm , 20 μm , 30 μm and 40 μm). This technique allowed

us to use all elements simultaneously to test whether fish collected at a site would assign back to the capture location. Strong assignment to the capture location would indicate extended residence at a site with similar chemistry, whereas poor assignment would indicate little difference in chemistry among sites, or high rates of movement throughout the estuary. Because data were collected with different LA-ICPMS instruments in each sampling year, and element:Ca ratios vary greatly among elements, data for each year and element were rescaled by subtracting the mean and dividing by the standard deviation.

Permutational multivariate analysis of variance (perMANOVA) was performed to determine the effects of year, site, and sampling month on the resulting groupings. For multivariate analyses, individuals from Peahi were not used due to low sample size. We assumed that fish captured in the Chignik River may have been migratory, and assigned those individuals to recent habitat with the DFA created from otoliths collected in marine and fresh waters. Additionally, all fish captured at Chignik Lake sites were grouped into a single freshwater category for otolith analyses. IGF1 and otolith chemistry data were normally distributed and did not violate the assumptions of parametric tests, which were performed with the R statistical software (R Development Core Team 2011).

Results:

Across all samples there was no difference in IGF1 concentration between 2009 ($M = 27.22$, $SD = 17.43$, $N = 213$) and 2010 ($M = 28.5$, $SD = 19.39$, $N = 428$, $t(465) = -0.8505$, $p = 0.39$) so the data from both years were combined for all further analyses. We used a visual estimation of gonadal development as an indicator of maturation in the season of capture for both males and females. For each visually estimated individual we evaluated

blood plasma 11-KT and E2 concentrations for males and females respectively. In agreement with previous research (Narver and Dahlberg 1965), in males ≥ 275 mm FL and females ≥ 300 mm FL we observed marked evidence of maturation in some but not all individuals. Males as small as 130 mm FL displayed increased gonad mass consistent with maturation, but females did not (Figure 2). We found no site effect on IGF1 concentration within Chignik Lake $F(6,133) = 1.385$, $p = 0.225$, and in subsequent analyses all six Chignik Lake sites were pooled. We found significant effects of site $F(5,378) = 15.81$, $p < 0.001$, month $F(2,378) = 4.36$, $p = 0.013$, and a site by month interaction $F(7,378) = 5.07$, $p < 0.001$ on the fork length of individuals included in final IGF1 analyses. We used Tukey-HSD post-hoc tests to determine which sites differed in mean fork length each month (Figure 3a).

There was no significant difference in IGF1 concentration between sexes in the immature individuals ($t(394.3) = 0.227$, $p=0.82$) but there were significant effects of site ($F(16,378) = 11.43$, $p < 0.001$), month ($F(2,378) = 4.661$, $p = 0.031$), and a site by month interaction ($F(10,378) = 4.12$, $p < 0.001$) on IGF1 concentration. That is, there were significant differences in growth rates among sites, but those differences varied by month. Post-hoc comparisons among all sites using the Tukey HSD test for differences in means among sites within each month indicated significant differences among sites in each month (Figure 3b). In June, only fish at mid and outer lagoon sites had growth rates significantly higher than Chignik Lake. However, by July, inner, mid and outer lagoon fish all showed higher growth than Chignik Lake. Additionally, during the same time period the mid-lagoon had a higher concentration than either the inner or outer lagoon sites. Finally, by August fish from the Chignik River site as well as all lagoon sites were

significantly higher in IGF1 concentration than Chignik Lake, although there was no difference among the lagoon or river sites.

In a series of linear models, the additive effects of fish age and DOY best predicted log transformed edge otolith band width (μm) (Table 1) with the equation:

$$O_w = e^{(1.83 - 0.152 \times \text{Age} + 0.0157 \times \text{DOY})} (1)$$

Where O_w is the otolith width in microns. Using this equation, we determine that some older fish sampled in June may have insufficient otolith growth at the time of capture to accurately reflect summer habitat residence; therefore only July and August samples were used in DFA analyses. Assignment of individuals to their collection sites with DFA of margin otolith chemistry was driven almost entirely by differences in Sr:Ca, and the effect of other elements was minimal (Table 2). There was a high degree of variability in correct assignment (26%-96%: Table 3) among sites, but overall assignment was highest with 30 μm averaging width (correct assignment: 10 μm , 77.55%; 20 μm , 77.55%; 30 μm , 78.57%; 40 μm , 77.55%), and 30 μm is used for all further assignments. Comparison of plasma IGF1 concentrations for individuals correctly assigned to their capture location and those misclassified (Table 4), indicates that IGF1 is more similar among fish from a given capture location than from assigned locations. Percentage correct assignment to Freshwater, inner, mid, and outer lagoon sites were 96%, 29%, 73% and 54%, respectively. PerMANOVA indicated significant differences in group placement in space in all but one pairwise comparison (inner lagoon-outer lagoon), while homogeneity of dispersion tests indicated no significant differences in dispersion in all cases but one (Alpha-Spit; Table 5). We were unable to test for the significance of a month effect due to insufficient sample size at each sampling station in each month. Assignment of Dolly

Varden collected in the Chignik River to Freshwater, inner, mid, or outer lagoon sites indicated that in June most individuals were of recent freshwater origin, but that proportion decreased in each month thereafter (Table 6). By August, the vast majority Chignik River fish were unassigned, indicating recent habitat use for those fish is outside of the sampled lagoon habitats.

Discussion

Plasma IGF1 concentrations allowed us to compare growth of Dolly Varden within and among freshwater and marine habitats simultaneously. We observed comparatively low growth of Dolly Varden in Chignik Lake in all months, with no differences among collection sites. However, growth rates in estuarine habitats varied widely by site and month, and otolith chemistry indicated significant seasonal differences in habitat use within estuarine waters. Our finding of the apparent spatial segregation of individuals only a few kilometers apart was unexpected given both the long-range migration potential of Dolly Varden (DeCicco 1992), and the necessary daily movement that accompanies tidal fluctuations in the estuary. In addition, some Dolly Varden remained in mid-lagoon habitats throughout the summer growing season, and achieved similar or higher growth rates compared to individuals in more marine influenced outer lagoon site, opposing what has been observed for estuary rearing cutthroat (Krentz 2007). In contrast, fish captured at the outer lagoon may have been using the lagoon as a migratory corridor between freshwater and marine habitats. DFA often assigned fish from the outer lagoon to freshwater sites rather than mid-lagoon habitats, indicating recent arrival at the outer lagoon from Chignik Lake. This suggests the possibility of at least two distinctly different behaviors; some individuals move to mid-lagoon habitats for the duration of the summer

growing season, while others move rapidly to outer lagoon or coastal waters, a strategy that has been suggested in anadromous brown trout (Jonsson and Jonsson 2011). However, in brown trout (Jonsson and Jonsson 2011), Chinook (Levings et al. 1986) and coho salmon (Miller and Sadro 2003) the migratory strategy adopted may be the result of an ontogenetic shift, possibly from increased seawater tolerance and marine reliance with increasing size. In the Chignik Lagoon, however, there is little difference in length of fish from mid and outer lagoon sites in our collection. This may result from rapidly growing individuals achieving a size threshold at which individuals leave the lagoon to return to freshwater for feeding, reproduction and overwintering. In this scenario the modal size in each habitat may not change despite different growth rates. Although no length measurement of migratory individuals has been made, Dolly Varden are observed ascending Chignik River in all months of the summer (Bond and Quinn 2013). Small scale ($\leq 10 \text{ km}^2$) estuarine site fidelity has been reported for other char, including bull trout (Hayes et al. 2011), and cutthroat trout (Johnston 1982, Krentz 2007). However, in Chignik Lagoon a distinct otolith chemical signature of the mid-lagoon habitat is surprising, as the large tidal exchange forces fish into a central channel with each tidal cycle, facilitating mixing among sites. It would seem that fish returned repeatedly to shallow feeding sites as they became inundated by rising tides.

Growth rates of Dolly Varden were lower in freshwater habitats in all months, despite late summer warming of Chignik Lake and low densities of conspecific competitors. It is likely, therefore, that the lake resident fish are trading lower growth for increased survival in the lake habitat. While there are avian predators in Chignik Lake (e.g. Pacific loon, *Gavia pacifica*), we have observed none of the large bodied predatory

fishes commonly found in other Alaskan lake systems (e.g. northern pike, *Esox lucius*; Arctic char, *Salvelinus alpinus*; lake trout, *S. namaycush*; rainbow trout, *Oncorhynchus mykiss*). Survival of lake resident fish may, therefore, be relatively high. In contrast, lagoon resident fish displayed higher growth rates despite contending with the energetic demands of osmoregulation in marine waters, higher densities of conspecifics, and the need to avoid a suite of predatory fishes (e.g., Pacific halibut, *Hippoglossus stenolepis*; fourhorn sculpin, *Myoxocephalus quadricornis*; starry flounder, *Platichthys stellatus*; Pacific cod, *Gadus macrocephalus*), and marine mammals (e.g., harbor seal, *Phoca vitulina*) which may lower foraging efficiency (Werner and Hall 1988).

We observed significant differences in growth among Dolly Varden from freshwater and lagoon sites throughout the summer months. However, in early summer sampling there was little difference between freshwater and inner estuary and ecotone sites. This may be due to either lower growth of fish at the river-estuary ecotone and inner-lagoon sites, or recent entry by fish into the lagoon environment from lake habitats. Peak Dolly Varden downstream migration occurs at least one month prior to our earliest sampling event (Bond and Quinn 2013), therefore individuals captured at ecotone and inner lagoon sites are likely resident at those sites. The differences in growth among lagoon habitats may be attributable to differences in marine residence time or foraging opportunities that each habitat affords. In previous work in Chignik Lagoon, Narver and Dahlberg (1965) found distinct suites of prey items in Dolly Varden at the mid and outer lagoon sites; in all months the diet of mid-lagoon fish was dominated by invertebrate prey, particularly amphipods. Diets of fish at the outer-lagoon, however, were more variable but composed mainly of fish including sand lance and capelin. The mid-lagoon

site may therefore afford a more optimal mix of intermediate salinities, lower competition, and fewer marine predators, allowing fish to achieve the highest measured growth in the study in two of three months, despite a less energy dense prey base. In addition, the invertebrate prey available in the mid-lagoon may be more readily available, while the distribution of capelin, herring and sand lance at the outer lagoon may be more episodic. In Atlantic salmon populations, downstream migrating individuals move rapidly to sea, making little use of the estuary (Thorstad et al. 2004, Finstad et al. 2005, Gudjonsson et al. 2005). However, in some cases a portion of the population remains resident in estuarine waters, and may experience higher growth and lower mortality rates than those in marine waters (Thorpe 1994), similar to what we observe for Dolly Varden in the Chignik system.

There was a marked increase in growth of fish in the Chignik River during August but only a small percentage were assigned to freshwater. While few of the remaining individuals assigned to lagoon sites, variability in the duration of residence in freshwater after migration from marine or lagoon habitats, or prior residence outside of the lagoon likely caused otolith chemical signals not indicative of any group included in the DFA. Therefore it is likely that Dolly Varden moving upstream in August months were returning from more coastal waters not well represented by our lagoon otolith chemistry baseline. These data are consistent with the large numbers of Dolly Varden returning to freshwater in midsummer after ca. 70 days in marine waters, based on sonic tracking and counts at a weir on the Chignik River (Bond and Quinn 2013). Therefore, the large increase in growth rates in Chignik River fish between June and August likely resulted

from movement of fish from high-growth marine to low-growth freshwater habitats in the late summer, rather than changes in the growth rate of freshwater resident individuals.

Growth of Dolly Varden was more similar among individuals at a capture location than among individuals assigned to the same location with otolith chemistry and DFA, indicating the temporal differences between the formation of otolith structure and changes in plasma IGF1 concentration. Detection of otolith chemistry among sites requires that an individual remain resident in waters of differing chemistry long enough to incorporate that chemistry into their otolith, and create enough structure that is detectable with analytical techniques. In other species, the minimum time for detection of habitat is ca. two weeks, although this is dependent upon the age and growth rate of the fish as well as the difference in water chemistry among habitats. In other fishes, IGF1 concentrations indicate growth as a seven day moving average (Beckman 2011). Even a near complete cessation of feeding, as in the case of Dolly Varden ascending Chignik River in August, will not show a significant decrease in IGF1 for at least several days (Pierce et al. 2005). Likewise, IGF1 is indicative of the long term nutritional status of the individual, and single bouts of consumption are unlikely to induce an increase in IGF1 and growth (Shimizu et al. 2009). Therefore, dissimilarity in IGF1 among habitats reflects the state of individuals at that site and their capacity for growth, and is robust to recent differences in short-term foraging success.

Differences in growth throughout the Chignik system were apparently the result of high site fidelity by some individuals, and regular seasonal movement patterns by others. While studies of fish growth in estuarine habitats have traditionally been constrained by the inherent difficulties in mark-and-recapture studies (e.g., poor recapture

rates reducing statistical power), the combined use of two independent single-capture techniques in the present study revealed differences in growth and habitat use. Published studies of the use of estuarine (Narver and Dahlberg 1965) and marine habitats (Morita et al. 2009) by Dolly Varden are rare; nearly all studies infer the use of marine environments through migration timing at weirs (Armstrong 1974, Bernard et al. 1995), and recapture of tagged fish in distant locations (DeCicco 1992). Indeed, for most facultatively anadromous fishes the growth effects of migration and residency are often inferred or assumed, but rarely demonstrated (Thorpe 1994, Northcote 1997).

This study provided strong evidence that Dolly Varden were not only using estuarine and marine waters that afforded higher growth rates than freshwater habitats, but they were spatially segregated in their use of those estuarine and marine habitats. Some individuals appeared to reside in mid-estuarine waters while others used more marine habitats. Questions remain about what factors determine whether an individual remains in freshwater, moves to estuarine habitats, or to coastal ocean habitats. Tagging and tracking of Dolly Varden in estuarine and near shore ocean habitats would allow for determination of the scale of residence and home range during the summer growing season. Although the estuary provided superior growth opportunities throughout the summer months compared to freshwater sites, the benefits of smaller scale habitat units within the estuary may vary widely. Within anadromous populations of Dolly Varden, fully resident phenotypes have been demonstrated, and the different growth and residence patterns of Dolly Varden within lagoon waters may indicate that additional migratory ecotypes exist.

Table 2.1: List of models evaluated for success in predicting the log transformed width of the otolith from the last annulus to the edge of the otolith in Chignik Lakes Dolly Varden. Lower AICc scores indicate a better fit of the data to the model.

Parameter	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Age + DOY	4	111.5852	0	0.506	0.506	-51.5148
Age x DOY	5	113.4215	1.8362	0.202	0.708	-51.2882
FL + DOY	4	114.4182	2.833	0.1227	0.8307	-52.9313
Age x FL + DOY	6	115.113	3.5277	0.0867	0.9174	-50.9565
DOY	3	115.2109	3.6256	0.0826	1	-54.441
Age x FL	5	138.0356	26.4504	0	1	-63.5953
Age	3	140.4466	28.8614	0	1	-67.0589

Table 2.2: Coefficients of linear discriminants for all elements included in DFA.
 Variance explained is the proportion of variance explained by each discriminant function.

Element	LD1	LD2	LD3
Sr:Ca	1.672852	0.105192	-0.18925
Ba:Ca	0.023995	0.115471	-0.64811
Mg:Ca	0.097359	-0.22298	-0.2365
Mn:Ca	0.087022	0.029258	-0.52635
Cu:Ca	-0.11958	-0.2295	0.026268
Pb:Ca	-0.03213	1.512145	0.28403
Variance Explained	0.966	0.0257	0.008

Table 2.3: Percentages of individuals assigned to each site by discriminant function analysis. Analyses include the element:Ca ratios of: Sr:Ca, Ba:Ca, Mn:Ca, Mg:Ca, Cu:Ca and Pb:Ca in the outer 30 μm of each otolith from fish collected in July and August of 2009 and 2010. Site names along the vertical axis indicate capture location; sites on the horizontal axis indicate assigned location with DFA. Bold numbers indicate the percentage of individuals correctly assigned to their collection site.

Capture location	Assignment %			
	Freshwater	Inner-lagoon	Mid-lagoon	Outer-lagoon
Freshwater	96	2	1	1
Inner-lagoon	29	29	8	33
Mid-lagoon	0	5	73	23
Outer-lagoon	27	4	15	54

Table 2.4: Plasma IGF1 concentrations (ng/ml) of Dolly Varden. Mean values are arranged by capture location (vertical), and otolith chemistry DFA assignment location (horizontal). IGF1 values for fish assigned to the capture location are shown in bold.

Capture location	Assignment Location			
	Freshwater	Inner-lagoon	Mid-lagoon	Outer-lagoon
Freshwater	25.8	21.0	18.0	21.9
Inner-lagoon	33.0	25.3	15.0	20.5
Mid-lagoon	N/A	38.9	44.0	41.6
Outer-lagoon	21.3	57.7	28.0	31.4

Table 2.5: F-statistic and test of homogeneity of variance for otolith chemistry. F-statistics for pairwise permutational multivariate analysis of variance (above diagonal) and test of homogeneity of multivariate dispersion (below diagonal) of otolith chemistry between Dolly Varden collection locations. Significance: *p < 0.05, **p < 0.01, Bonferroni corrected.

	Freshwater	Inner-lagoon	Mid-lagoon	Outer-lagoon
Freshwater		8.98**	36.21**	19.44**
Inner-lagoon	1.47		6.63**	2.8
Mid-lagoon	0.0008	0.7		9.7**
Outer-lagoon	1.46	4.72*	1.27	

Table 2.6: Assignment of Dolly Varden captured in the Chignik River to each reporting region with edge (30 μm) otolith microchemistry. Discriminant function analysis was created with all individuals captured at each reporting region. Only those individuals with an assignment confidence of > 90% are displayed.

Capture month	Assignment Percentage				
	Freshwater	Inner-lagoon	Mid-lagoon	Outer-lagoon	Unassigned
June	80	0	0	0	20
July	28	40	0	0	68
August	6	0	11	0	83

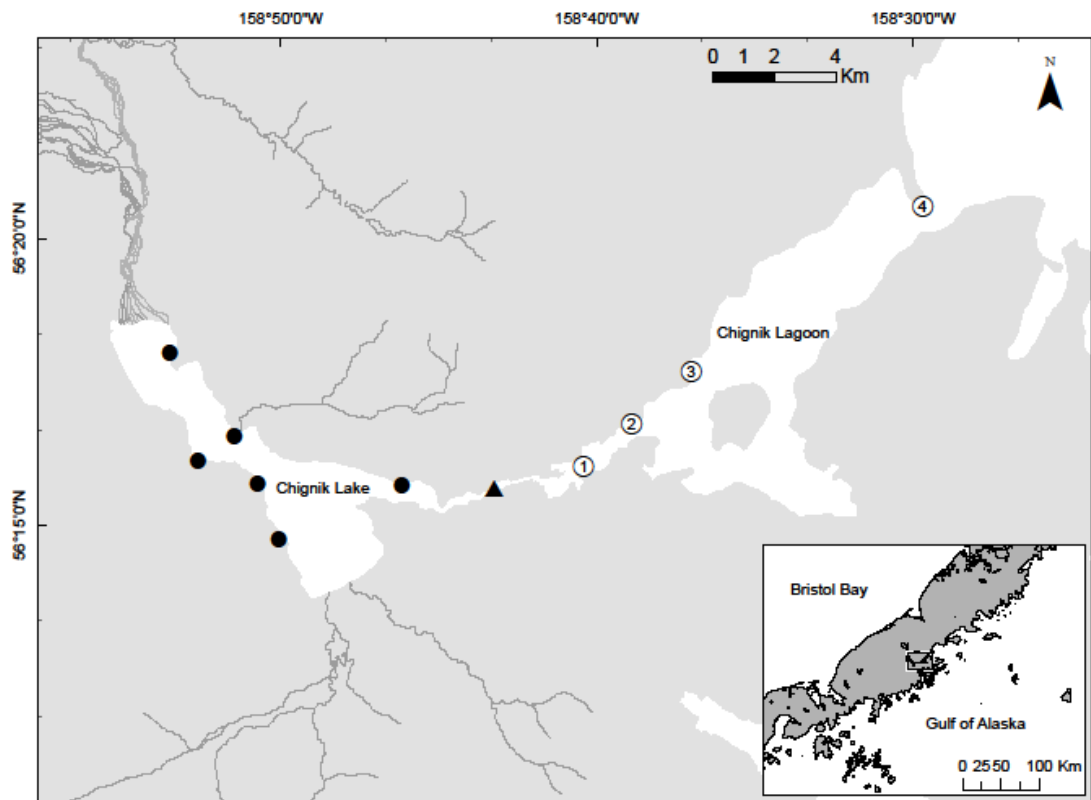


Figure 2.1: Map of Chignik Lake and Chignik Lagoon with major tributaries. Filled circles indicate sampling sites in Chignik Lake, Filled triangle indicates Chignik River sampling site. Numbered circles indicate Chignik Lagoon sampling sites from those with the least to most marine influence: 1. Peahi (river/estuary ecotone), 2. Alpha (inner-lagoon), 3. Hume (mid-lagoon), 4. Spit (outer-lagoon).

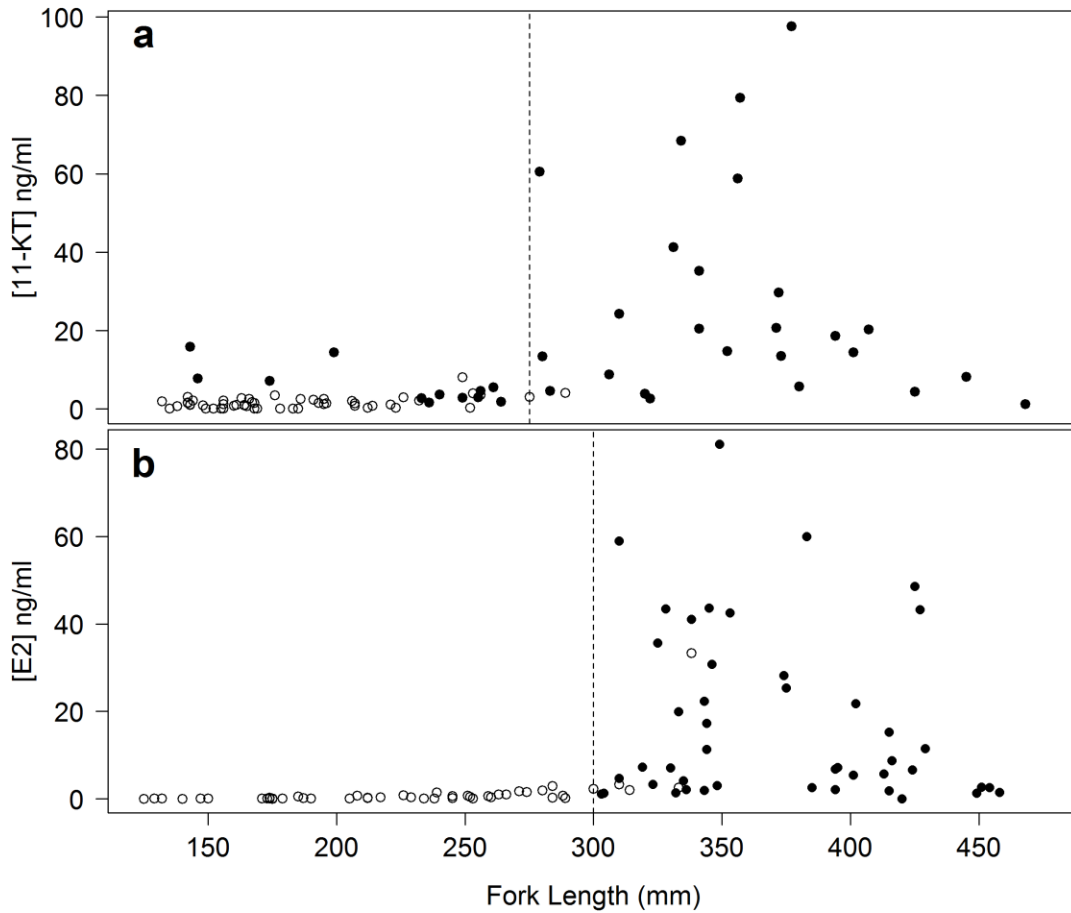


Figure 2.2: Male and female maturation hormone concentrations by fish length. Panel a) Male plasma 11-KT concentration as a function of fork length. In both panels, individuals visually assessed as mature are shown with filled circles and immature individuals are shown with open circles. Panel b) Plasma E2 concentration as a function of fork length. In both panels, individuals visually estimated to be mature (low gonadal development) are shown as filled circles and immature individuals are shown as open circles.

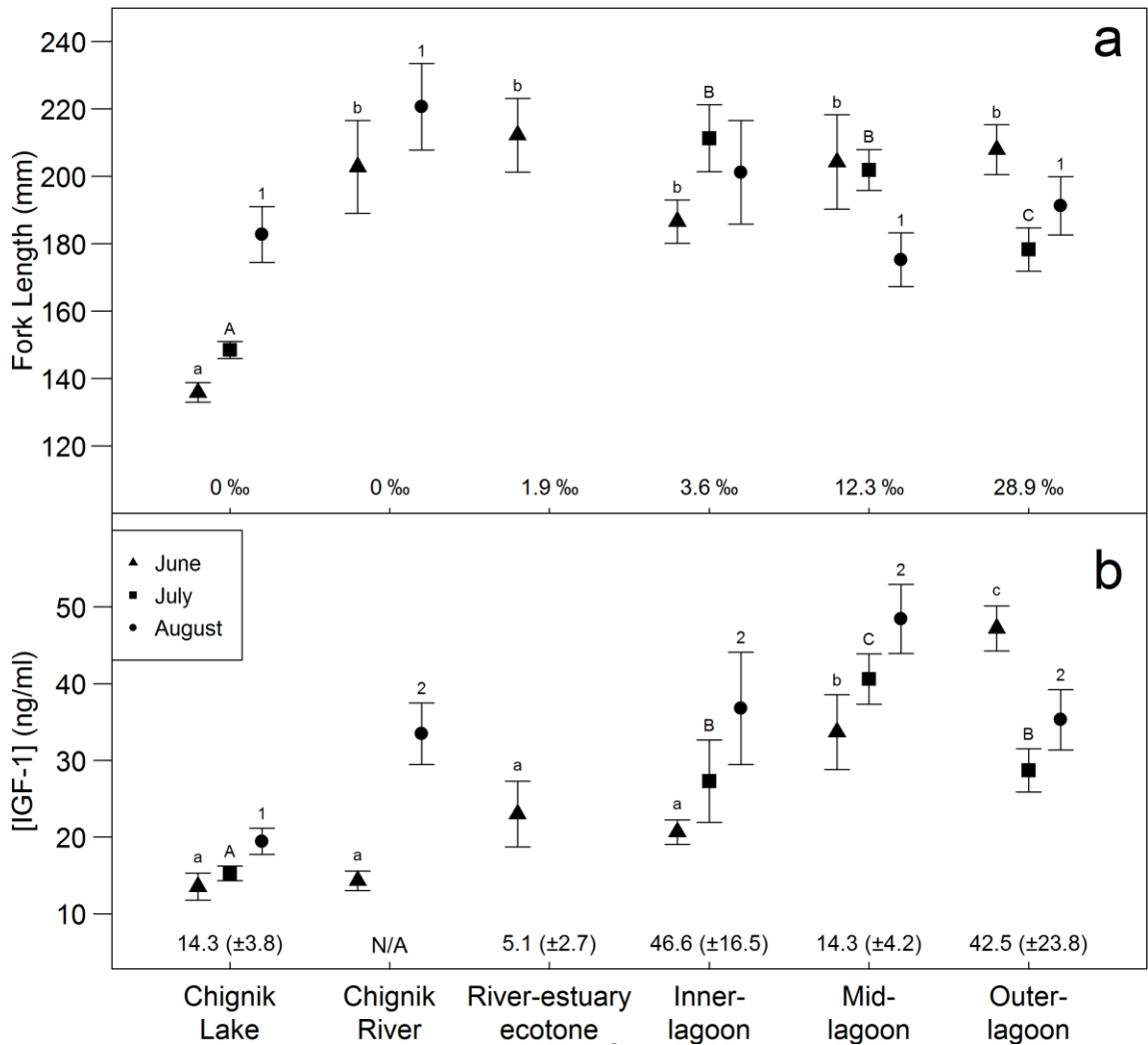


Figure 2.3: Dolly Varden length and plasma IGF1 concentrations by site and month. Panel a) Average (\pm SE) fork length of individual Dolly Varden included in the IGF1 analysis at each sampling location, arranged from uppermost in the watershed to outermost in the estuary. Lowercase letters (June), uppercase letters (July) and numbers (August) indicate significant differences among sites within each month (Tukey HSD pairwise comparisons, $\alpha < 0.05$). Average surface salinity (‰) measured at each sampling event (2008-2010) provided along the x-axis. Panel b) Average (\pm SE) plasma IGF1 concentration of fish sampled at each site. Lowercase letters (June), uppercase letters (July) and numbers (August) indicate significant differences among sites within each month (Tukey HSD pairwise comparisons, $\alpha < 0.05$). Average (\pm SE) Dolly Varden catch per net set (2008-2010) provided along the x-axis.

Chapter 3: Evidence for ontogenetic shifts in diet and habitat specialization by partially anadromous Dolly Varden

Introduction

Across a broad taxonomic range, migrations are often driven by the benefit of acquiring locally unavailable resources, decreasing of energetic costs, or entering habitats of more favorable survival (Dingle 1996, Alexander 1998). In many cases migration accompanies an ontogenetic shift, and increases in body size allow individuals to secure previously unobtainable food items (Renones et al. 2002, Post 2003, Graham et al. 2007) or be released from the effects of size dependent mortality (Sogard 1997). Movement can therefore drastically alter the realized niche of an individual as the available resources, competition, and environmental conditions will change among habitats.

Niches are often described broadly as the set of environmental conditions in which a species needs to live (Grinnell 1917, Hutchinson 1957, Roughgarden 1972, Vandermeer 1972). This concept has been explored in ecology for decades, and niche theory has evolved to describe discrete biotic (e.g. prey resources) and abiotic (e.g. breeding habitat, foraging habitat) parameters that a species has evolved to use. Recently, there has been a resurgence of interest in understanding the trophic niche of taxonomic or functional groups within a community as new tools such as analysis of stable isotopes and fatty acids permit finer resolution among groups with similar niches (Budge et al. 2007, Williams et al. 2008, Layman and Allgeier 2012). There is compelling evidence in a range of taxa for intraspecific niche partitioning (Bolnick et al. 2003, Svanback and Bolnick 2005, Araujo et al. 2008, Newsome et al. 2009), but documentation of the tradeoffs and associated evolutionary and ecological implications of such partitioning is much rarer, especially in fishes. Those studies that have been conducted generally assess

differences among distinct morphs; however, fewer studies have adequately addressed niche partitioning within morphologically indistinct individuals occurring in sympatry (Newsome et al. 2009). Thus, understanding resource partitioning among groups with different migratory behaviors and ontogenetic states remains poorly understood.

The feeding ecology of fishes has long been of interest to fish biologists, and such studies have matured over time from descriptions of the average diet of a population (e.g. Johnson and Ringler 1980) to analyses of feeding specialization in sub-groups or individuals (Schindler et al. 1997, Bolnick et al. 2003, Svanback and Bolnick 2005). In some populations the average individual may be rare and extensive variation among individuals is common, although the mechanisms that lead to this diversity are elusive. In fishes, many of these studies have focused on morphologically distinct sub-groups of fishes (e.g., threespine sticklebacks (*Gasterosteus aculeatus*) (Bentzen and McPhail 1984), Arctic charr (*Salvelinus alpinus*) (Rikardsen et al. 2000)), bluegill sunfish (*Lepomis macrochirus*) (Ehlinger and Wilson 1988). Differences in resource use among morphs coupled with disruptive selection regimes may drive phenotypic divergence, reproductive isolation and ultimately speciation (e.g., Elmer et al. 2010). However, individuals within some species or populations may differ greatly in resource use but not be morphologically or genetically divergent. In migratory fishes, the resources available where the fish is found at any given time may contribute little to the nutrition and growth of an individual if it has recently moved, or does not forage there. This is true of many anadromous fishes that may acquire the majority of their growth at sea before returning to fresh water environments where they consume little food (Schindler et al. 2003). Further, iteroparous anadromous species (e.g., brown trout, *Salmo trutta*; Arctic char, cutthroat

trout, *Oncorhynchus clarki*; Dolly Varden, *Salvelinus malma*; bull trout, *Salvelinus confluentus*) may make extensive use freshwater habitats throughout their life, while seasonally entering marine waters to acquire much of their annual energy budget and somatic growth. For some species the use of marine habitats may be relatively brief (e.g., bull trout, Hayes et al. 2011) whereas for others it might be extended for months or years (e.g., brown trout, Jonsson and Jonsson 2011).

The development of stable isotope techniques has allowed for a proliferation of diet studies in recent years that go beyond the limitations of stomach contents analysis to provide more integrative information on trophic position or movement (Cunjak et al. 2005). As organisms consume prey, the isotopic composition of the prey determines the isotopic composition of the predator with a predictable isotopic fractionation. Analysis of the isotopic ratio (commonly $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$) of all possible prey items, coupled with analysis of predator tissues allows for the characterization of the percentage of each prey type consumed (Fry et al. 1978). Several tissues integrate over different temporal scales (e.g., blood plasma: days, bone: months to years); however, in many cases integration time is driven largely by the growth rate of the fish (Trueman et al. 2005, Heady and Moore 2012). Often, statistical mixing models are used to characterize the contribution of various prey items to the diet by partitioning the isotopic signature of the consumer (Layman et al. 2012). However, these models become less useful in systems where there are many potential prey items, prey items are not well separated isotopically (Layman et al. 2012), or where poor knowledge of individual movement patterns does not allow for characterization of potential diet sources. In these cases, rather than assessing the differences in prey consumed, we can identify differences in the isotopic

niche; the area in ordination space of tissue isotope values occupied by a group of individuals (Newsome et al. 2007). Differences in isotopic niche among individuals may result from differences in diet, consumption of similar diet items from different locations, or different proportions of similar diet items. Additional measures (e.g., telemetry, gut contents) can be used to identify which process is likely driving the differences among isotopic clusters for different grouping of individuals (Cunjak et al. 2005).

Dolly Varden char are the only large bodied fish found throughout the Chignik Lakes watershed in Southwestern Alaska, and in summer months, Dolly Varden are abundant in both freshwater lake and brackish to fully marine lagoon habitats. Movement between freshwater and marine habitats generally begins at age 2-3, and occurs throughout summer months; peak downstream migration occurs in spring shortly after ice-out (i.e., late April or early May), upstream migration occurs primarily in mid to late summer (i.e., late July through August), and individuals may migrate several times throughout their life (Bond and Quinn 2013). Although multiple morphs of Dolly Varden have not been identified in the Chignik watershed, the low resident fish species diversity allows for the exploration of isotopic niche separation of sub-groups of different size and habitat use groups without the intense intraspecific competition that may exist elsewhere. Previous work on Chignik Dolly Varden provided some evidence for diet specialization in this system. In both lagoon and freshwater habitats Dolly Varden collected at a single location may each only contain one diet type, but that type may vary among individuals (Roos 1959, Narver and Dahlberg 1965)). In contrast, juvenile coho salmon (*Oncorhynchus kisutch*) collected in the same habitats have often each consumed many prey types (Jennifer Griffiths, personal communication). However, gut samples only

provide a snapshot of diet at a single time, and captured fish may be moving from areas of differing prey availability and evacuation rates of different prey types will vary. To date, all studies of char dietary differentiation rest on differences between morphologically distinct ecotypes (Bolnick et al. 2003, Fraser et al. 2008). In contrast, Dolly Varden in the Chignik system are composed of a single morph of recent post-glacial colonization (ca. 10000 yrs.). Despite their apparent physical similarity there may be significant behavioral and life history differences among habitats and size groups that have implications for the ecology of the species (Parker et al. 2001). Accordingly, the goal of this study was to determine how both fish size and movement patterns interact to shape trophic niches at multiple spatial scales. We use a combination of tissue stable isotopes and otolith microchemistry to identify the spatial scale of isotopic trophic niches throughout the watershed during the summer growing season, and investigate the relative contribution of fish size, capture location, and season determine the isotopic niche. In addition, we evaluate how additional knowledge of recent migratory history (e.g. residency, anadromy) reshapes our interpretation of stable isotope data and resource acquisition.

Methods

We collected Dolly Varden across a range of size classes and several representative habitats in the Chignik Lakes watershed (Figure 1): Chignik Lagoon, Chignik River, Chignik Lake, and the Alec River. Fish were collected twice per month, with a target sample size of 20 individuals across the available size range (> 120 mm fork length) in both 2009 and 2010. In the Alec and Chignik rivers, fish were sampled with hook and

line. In all other habitats fish were sampled with a 30 m beach seine. Upon capture each fish was euthanized in MS-222 and stored on ice.

After collection, each fish was returned to the laboratory for further analysis. First, stomachs were removed and the wet mass was separated by coarse taxonomic groups: larval trichopteran, adult trichopteran, larval ephemeropteran, adult ephemeropteran, larval diptera, adult diptera, larval chironomid, adult chironomid, *Mesidotea* isopod, gammarid amphipod, *Corophium* amphipod, salmon fry, salmon smolt, sculpin, sand lance, larval crab, unidentified fish, salmon egg, snail, unidentified larval marine invertebrate, maggot, and annelid. Prey item groups were weighed separately, and a percent of total diet mass was calculated for each type. Representative prey items in intact, undigested condition were rinsed and frozen for stable isotope analysis. Following diet analysis, a 1 g plug of dorsal muscle was removed from each individual and frozen at -20 °C. In addition, we removed the saggital otoliths from each individual and stored them dry in individual vials for chemical analysis.

Stable isotope analysis

To perform stable isotope analyses, fish muscle and prey items were freeze-dried in a lyophilizer for 24 h, then ground to a fine homogeneous powder and loaded (60 µg) into tin capsules. Stable isotope analyses were conducted at the University of Washington Isolab with a Costech elemental analyzer (Analytical Technologies Inc., Valencia, CA) coupled to a Finnigan MAT-253 stable isotope-ratio mass spectrometer (Thermal Electron Corporation, Bremen, Germany). The isotopic ratios of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) were expressed in standard notation of per mil differences from the standard atmospheric nitrogen gas and Vienna Pee Dee Belemnite, respectively (Fry

2006). In-house calibrated standards were included in each run to insure a precision of $\pm 0.3\%$. Dolly Varden muscle and prey $\delta^{13}\text{C}$ sample values were adjusted for lipid content based on the C:N ratio as described by Post et al. (2007).

Determination of recent anadromy

To determine whether individuals collected in each location had recently emigrated to or from marine habitats, we performed otolith micro-chemical analysis on a subset of fish that were analyzed for muscle stable isotopes (Campana 1999). Saggital sections of otoliths were prepared to expose the most recently deposited edge material (Bond, Chapter 2), which was analyzed with laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) at the Keck Collaboratory, Oregon State University. A VG PQ ExCell ICPMS with a New Wave DUV193 excimer laser was used for all analyses of 2009 samples and a Thermo X-Series II ICPMS and Photon Machines Analyte G2 193 nm laser was used to analyze otoliths collected in 2010. The laser was set at a pulse rate of 7 Hz with a 20- μm ablation spot and traveled at 5 $\mu\text{m sec}^{-1}$. We used NIST-612 glass to transform ion ratios to elemental ratios. These were converted to molar ratios using the molar mass of Sr and Ca. Final analyses were computed on the Sr:Ca ($\text{mmol} \cdot \text{mol}^{-1}$), and Ba:Ca ($\mu\text{mol} \cdot \text{mol}^{-1}$). A calcium carbonate standard with known concentration (USGS MACS-2) was used to determine the accuracy of the element:Ca ratio and correct final element:Ca values. Following laser ablation, photomicrographs were taken of each otolith, and distances from the core of the otolith to each annulus were calculated with ImageJ image analysis software (Abramoff et al. 2004). We paired measured annuli with transects of both Sr:Ca and Ba:Ca to identify whether a chemical signature of saline waters existed following the last annulus prior to capture. Otolith

formation in marine waters is often characterized by low concentrations of Ba and relatively high concentrations of Sr (Kraus and Secor 2004). A subset of 20 individuals captured in lagoon waters in late summer were used to validate this assumption. In each of these cases, edge chemistry indicated Sr:Ca $>3 \text{ mmol} \cdot \text{mol}^{-1}$, and Ba:Ca $<6 \text{ } \mu\text{mol} \cdot \text{mol}^{-1}$. We established these threshold concentrations as criteria for assignment of the remaining fish to either saline (anadromous) or fresh waters (resident) at any point following the last annulus prior to capture.

Calculation and comparison of isotopic ellipses

To quantitatively compare the isotopic niche space occupied by individuals of different migratory history (anadromous, resident), collection site, or size class ($>300 \text{ mm FL}$, $\leq 300 \text{ mm FL}$, Kline et al. 1998), we compared the isotopic area and amount of overlap in isotope space (Layman et al. 2007) of a standard ellipse for each group using the SIBER (Stable Isotope Bayesian Ellipses in R, Jackson et al. (2011)) routine within the R (R Development Core Team 2011) package SIAR (4.1.3). With SIBER we created a Bayesian estimate of standard isotopic ellipses using 10^5 posterior draws, a process that is robust to different sample sizes among groups. We then compared both the average size of the calculated ellipses (per mil^2) from all draws, and percentage of overlap among all ellipses. Ellipse size indicates the isotopic niche size occupied by each group (site x size class) to identify how niches change across space and time for several size classes. Ellipse overlap indicates the relative positions of the ellipses in isotope space. For example, a small ellipse may be wholly encompassed within a larger ellipse, indicating individuals comprising the smaller group use only a portion of the resources of the larger group, or have lower variation among individuals. Separation in ellipses indicated by low

or no overlap in ellipse areas indicates a separation in resource use or space occupied among groups. Although the calculated ellipses are corrected for small sample sizes, to prevent bias in estimation only site by size-class combinations with at least 10 individuals were included in the comparisons among groups.

Smaller niches indicate that individuals consume the same prey in the same proportions, that all prey have the same signatures, or that individuals in the group consume a limited number of prey types. Consequently, larger ellipses indicate more variable diets among individuals within the group, or that the isotopic signatures of similar prey are variable in space. To test these hypotheses, we evaluated the amount of variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ among similar prey items at different locations throughout the lagoon habitat, and compared those signatures to diets of individuals captured at each location to determine whether differences in isotopic signatures in Dolly Varden are due to different consumption of different prey taxa among sites, or differences in the isotopic composition of similar prey among sites.

Partitioning variance in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of lagoon Dolly Varden

In the lagoon, differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ may be due to: a seasonal shift as tissue derived in freshwater is replaced with tissue from marine sources, differences in the isotopic signature of prey available in different regions of the lagoon, ontogenetic shifts in prey selection that accompany changes in fish size, or differences among the two sampling years. In this case it is appropriate to evaluate several predictors to simultaneously explain variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ using the constrained ordination technique, redundancy analysis (RDA), (Reum and Essington 2013). RDA is the canonical form of principal components analysis that is a multivariate analog of linear

regression where ordination of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ maximizes the variance explained by the set of predictor variables (Legendre and Legendre 1998). In our analysis the predictor variables are: Location of fish capture, fork length, month of capture and year of capture. To test for the significance of each term included in our model, we performed a permutation procedure to test how often the observed result is better than random with 500 permutations. Partial RDA, therefore, is the multivariate analog of partial regression, and can be used to isolate the amount of variance in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ that is uniquely explained by each predictor, as well as the shared variance among two or more predictors (Legendre and Legendre 1998). We performed partial RDA analyses with each predictor that was significant in the full RDA model at the $P \leq 0.05$ level and report both the unique and shared components. All RDA analyses were performed with the R package ‘vegan’ (Oksanen et al. 2012)

Results

Diet composition

We found broad differences in diet composition of Dolly Varden by site and season (Table 1). However, fish with empty stomachs were prevalent at all sites, ranging from 14% of the Alec River collection to almost 70% of the Chignik River collection (Table 1). Despite finding 35 categories of prey items in all Dolly Varden throughout the watershed, 79% of all fish with non-empty stomachs contained only one diet type at the time of capture (Chignik Lagoon 73%, Chignik Lake, 76%, Chignik River, 61% and Alec River 81%). Among individuals with stomach contents, sand lance were the most common diet items by mass, followed by gammarid amphipods at the most marine site (Spit), while gammarid amphipods comprised the vast majority of diets at both mid-

lagoon (Hume) and upper-lagoon (Alpha) sites (Table 1). Although there is only minimal difference in percent mass of various prey items among the mid and upper-lagoon sites, the isotopic signatures of those items varied widely among collection sites (Table 2). For example, gammarid amphipods at the Spit site are far more enriched in both $\delta^{13}\text{C}$ (-9.60 ‰) and $\delta^{15}\text{N}$ (12.96 ‰) than the upper-lagoon site, Alpha ($\delta^{13}\text{C}$ -12.08 ‰ and $\delta^{15}\text{N}$ 7.01 ‰). Corophium also shifted, particularly in $\delta^{13}\text{C}$ between mid-lagoon Hume (-12.69 ‰) and upper-lagoon sites (-21.18 ‰), indicating broadly different carbon sources for the same organism among lagoon sites. Tricoptera larvae were the most common diet item in Chignik Lake fish, while Alec River fish consumed primarily sockeye salmon eggs. Although most Chignik River fish had empty stomachs at the time of capture, of those with food, salmon eggs were the most prominent by mass.

Otolith chemistry

Of the fish captured in fresh water (Chignik Lake, Black Lake, Alec River, Chignik River) 237 were analyzed for otolith microchemistry and 73 (30.8%) exhibited otolith signatures consistent with anadromous movements since the last annulus prior to capture (i.e., anadromous migration between the previous winter and the time of capture). In the Alec River 8 of 116 fish (6.8%) were recently anadromous, and fork length did not predict recent anadromy (logistic regression, $p = 0.992$). In contrast, in Chignik Lake and Chignik River, 22 of 55 (40%) and 43 of 58 (74.1%) were recently anadromous, respectively. For individuals captured in Chignik Lake, length was positively related to the probability of anadromy (Proportion anadromous = $-6.41 + 0.027 * \text{fork length}$, $p < 0.001$), and all but one fish > 230 mm FL were recently anadromous. In Chignik River

length was also a predictor of recent anadromy ($\text{Proportion anadromous} = -5.75 + 0.024 \times \text{fork length}$, $p = 0.001$).

Stable isotope analyses

Muscle tissue samples from 419 Dolly Varden collected throughout fresh and marine waters in the Chignik Lakes watershed revealed a broad range of isotopic signatures among and within collection sites (Table 3). However, otolith microchemistry data allowed us to identify individuals that had recently moved between marine and fresh waters, reducing the isotopic range for each migratory status (Table 3, Figure 2).

Freshwater resident Chignik Lake fish showed a broad overlap in isotopic ellipse size and overlap (Table 4, Figure 3) among collection sites, indicating that smaller Dolly Varden (≤ 230 mm) in Chignik Lake occupy a similar isotopic niche regardless of where in the lake they are found, indicative of the similar diets at each site.

We found differences in average isotopic ellipse area and overlap in ellipses by comparing each lagoon sampling location binned by size class, to binned size classes of freshwater captured fish whose otoliths indicated recent anadromy (Table 5, Figure 4). Overall we saw little difference between anadromous Chignik River and Chignik Lake fish, irrespective of length. However, fish from Chignik River and Chignik Lake had much smaller ellipses than fish of either size class at any lagoon site, and only share isotopic ellipse space with individuals from one inner-lagoon site (Pillar Rock), and the small fish from the outer lagoon (Spit). Among lagoon sites, the smaller size class of fish has a larger isotopic area than the large class in all comparisons. Alpha was the only site in which there was no overlap between small and large size classes, at Pillar and Spit sites, there was 5.2% and 11.3% overlap respectively. The small size class from the Spit

site had the largest isotopic ellipse size and overlapped with all other site-size combinations from 6.2-58.1%.

Dolly Varden collected in the Alec River displayed a relatively small isotopic ellipse, similar in location to anadromous Dolly Varden collected in Chignik River and Chignik Lake. However, despite their similarity Alec River fish had a non-overlapping standard ellipses with the river and lake sites (Figure 5), reflective of a relatively high trophic level marine diet source for each group. Alec River fish consumed primarily eggs from sockeye salmon (Table 1). The marine diet of anadromous Chignik River and Chignik Lake fish at sea is unknown, as in all cases the stomachs of captured individuals were either empty, or they had switched to freshwater prey by the time of capture.

RDA analysis indicated that together, 47.3% of the variation in muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was explained with our full model, including fish length ($F = 68.08$, $df = 1$, $P = 0.01$), capture location ($F = 13.63$, $df = 4$, $P = 0.01$) and month of capture ($F = 10.71$, $df = 2$, $P = 0.01$). Capture year was not a significant predictor ($F = 0.27$, $df = 1$, $P = 0.75$), and was not included in partial RDA analyses. The most important predictor of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was fish length, explaining 30%, although only 24% was due to fish length alone, while the remaining 5% and 1% were combined effects of length and location, and length, location and month, respectively (Figure 6). Location predicted 20% of the variation, although only 11% was unique, with 3% from a combined effect of location and month, 5% from location and length, and 1% from all three. Finally, month of capture was the least important predictor, explaining only 6% in total, and only 2% uniquely.

Discussion

By analyzing diets, tissue stable isotopes, and recent otolith microchemistry, we found evidence for trophic niche separation among sites and size classes of Dolly Varden in the Chignik Lakes watershed. Dolly Varden collections from throughout Chignik Lagoon indicated wide trophic diversity among individuals. However, on a smaller, site specific spatial scale, isotopic space occupied was far more limited. In addition, there was often little or no overlap in isotopic ellipses between smaller and larger individuals within a site, and in all comparisons we observed a smaller isotopic niche size in larger fish than smaller ones, contrary to what has been found in other studies of Dolly Varden diets (Kline et al. 1998). The smaller isotopic niche for large fish opposes the increase in prey type availability with increasing size (Craig 1984, Keeley and Grant 2001), and may signal a shift toward higher value prey (e.g. fishes) that are more similar in isotopic signatures. Although the turnover rate of muscle tissue may vary widely, even individuals experiencing rapid mid-summer growth are likely exhibiting a signal that is integrated over at least several weeks. We cannot attribute differences in isotopic ellipse size and location in ordination space to diet alone however, as even similar prey items from different sites vary in their isotopic signature. Therefore, broadly similar diets of Dolly Varden among several lagoon sites, coupled with different isotopic signatures of prey at those sites indicate the segregation in Dolly Varden isotopes may be more representative of strong site fidelity in discrete regions of the lagoon, than differences in diet among sites. The Chignik Lagoon habitat has not been mapped, so it is unknown how representative our collection sites are of the overall habitats available throughout lagoon. Likewise, no previous work has attempted to quantify the abundance of potential prey items throughout the lagoon for Dolly Varden, therefore prey selectivity remains

unknown. However, the high incidence of Dolly Varden stomachs containing only one diet type indicated either individual specialization, or prey that are patchy in time or space and individuals maximize their encounters with groups of prey. Similar results of single diet type stomach contents have been previously reported for Dolly Varden in the Chignik Lagoon (Narver and Dahlberg 1965), and other estuarine Dolly Varden that have reduced diet species richness compared to competitor species (Wolf et al. 1983). Diets at the Spit largely reflected the influence of marine waters proximate to that site (sand lance, crab larvae) rather than items produced within the confines of the lagoon. In contrast, invertebrate prey items that may be produced near the capture location dominated the inner lagoon sites. Juvenile salmon were more prevalent as prey in our collections than in previous work in Chignik lagoon (Narver and Dahlberg 1965), and may reflect differences in juvenile salmon abundance among years. High rates of empty stomachs appear to be common in Dolly Varden in both fresh (Roos 1959, McCart 1980) and marine waters (Narver and Dahlberg 1965, Craig 1975), although the rates may vary markedly by season. In some studies, empty stomachs are far less common among sympatric Dolly Varden competitor species (e.g. fourhorn sculpin, *Myoxocephalus quadricornis*; Arctic cisco, *Coregonus autumnalis*) (Craig 1975), and similar results have been found in closely related Arctic char (Rikardsen et al. 2007). In contrast, brown trout and cutthroat trout, occupying a similar niches in estuarine and marine waters, have comparative low rates of empty stomachs, suggesting a more risk-averse marine feeding strategy in char (Rikardsen et al. 2007, Duffy and Beauchamp 2008, Jones et al. 2008).

Differences in isotopic ellipse area and overlap among fish of different lengths and regions of the lagoon indicates both differential habitat use and ontogenetic shifts in

diet. Variance partitioning suggests that size is the best predictor of the isotopic signature, but capture location in the lagoon was also a large contributor, indicating that the use of specific regions was not exclusively an ontogenetic shift as has been suggested in other Dolly Varden populations (Kline et al. 1998) and species with similar life histories (e.g., brown trout, Jonsson and Jonsson 2011). Small Dolly Varden from inner (Pillar) and outer (Spit) sites overlapped broadly with many of the other size-location combinations, indicating some fish may have low site fidelity and range widely throughout the lagoon, while others have extended residence at specific sites (e.g. mid-lagoon, Hume Point). Previous otolith chemical analyses of Chignik Lagoon Dolly Varden indicated high assignment to Hume Point, a further indication of discretion in habitat use (Bond, Chapter 2). Previous work on discrete habitat use in char has focused on differences among morphs (e.g. littoral and limnetic), and little work has focused on the ontogenetic shifts in habitat use within a morph (Skulason et al. 1989a, Jonsson and Jonsson 2001, Fraser et al. 2008). Chignik contains only one known morph of Dolly Varden, therefore differences in lagoon habitat use may be best explained by size dependent differences in physiological limitations (e.g., salinity tolerance, Jensen and Rikardsen 2008), predation risk (Ehlinger and Wilson 1988, Werner and Hall 1988), or gape limitation in foraging (Keeley and Grant 2001) indicative of an ontogenetic shift in habitat use (Zimmerman et al. 2009b). Although much of the variation in isotopic position is explained by fish size, capture location uniquely accounts for nearly all of the remaining difference, suggesting that in addition to ontogeny, some fish remain in specific habitats independent of size. Although the mechanism behind such residence is unclear, salmonids certainly have the navigational capacity to return to the same habitat after each tidal cycle, and may do so

after repeated successful foraging in a location (Ruff et al. 2011), a strategy repeatedly demonstrated in other taxa (Chilvers 2008, Hillen et al. 2009, Thomson et al. 2012). It is also possible that different strategies of habitat use and movement are adopted by sub-populations of Dolly Varden within the Chignik system, however, the genetic structuring of these populations remains unclear.

In freshwater habitats, we observed broad overlap in isotopic niche among collection sites for smaller lake resident fish, indicating similar resource use in different areas of Chignik Lake. In general the isotopic niche of freshwater resident Chignik Lakes Dolly Varden is much larger than littoral or pelagic Arctic char in Norwegian lakes (Eloranta et al. 2013), or lacustrine brown trout (Grey 2001), owing to the strong addition of salmon derived nutrients in Chignik, or a lack of competitors for littoral resources (e.g. trout) common in other systems. The large niche area of freshwater Dolly Varden may result from stronger intraspecific competition driving niche separation among individuals (Bolnick et al. 2003, Svanback and Bolnick 2005). However, our results in the freshwater contrast strongly with the marine foraging patterns, as there is no evidence for size or site dependent segregation in isotopic niches within pre-smolt Dolly Varden in Chignik Lake.

Nearly all of the large bodied individuals in the Chignik Lake habitat had recently arrived from marine waters. Likewise, nearly all fish in Chignik River had recently been anadromous. The isotopic niches of anadromous Chignik Lake and Chignik River fish almost completely overlapped, and were much smaller than any of the lagoon collections. In fact, few of the lagoon fish overlapped with the anadromous lake and river fish. Although we do not have marine diet data from these fish, they occupied an isotopic space that indicated use of higher trophic resources in marine waters (Johnson and

Schindler 2009). Therefore, it may be that Dolly Varden ascending the Chignik River make use of coastal marine waters rather than the lagoon, as many fish captured in the lagoon appear to do. Therefore, these data indicated at least two distinct anadromous life-history types: lagoon resident and fully marine forms. In contrast to these two forms, Dolly Varden captured in the Alec River occupied an isotope niche similar, although non-overlapping with anadromous Chignik Lake and Chignik River fish. However, few of these individuals were anadromous during the previous year. This revealed a resident life-history that would not be identifiable from tissue stable isotopes alone, as the isotopes indicated marine origins of their food source. Alec River fish diets, by mass, were heavily dominated by sockeye salmon eggs, and they acquire the majority of their annual energy budget from returning sockeye salmon (Armstrong and Bond 2013). Therefore, although neither the Alec River nor the small Chignik Lake Dolly Varden were recently anadromous, their reliance on marine resources differed markedly. Large Dolly Varden in the Alec River seem to persist without additional energy besides salmon eggs for their maintenance and reproductive needs, whereas smaller, younger, Chignik Lake fish may not be able to survive on a single bout of eggs while investing in significant somatic growth (Armstrong and Bond 2013). In addition, egg foraging in the presence of spawning sockeye salmon may be risky for smaller fish, and less so for the large individuals found in the Alec River. Likewise, small fish may avoid competitive interactions with large Dolly Varden in salmon spawning areas, instead choosing to remain in safer small stream and lake habitats.

This study highlights the need for a combined approach in evaluating the migratory strategies of facultatively anadromous salmonids (Cunjak et al. 2005). In

Chignik Lakes Dolly Varden, otolith chemistry indicated the presence of recently anadromous individuals throughout freshwater habitats, while stable isotopes indicate extended residence in distinctly different habitats throughout the growing season, including estuarine and fully marine waters. Although the mechanisms that determine whether an anadromous individual uses the coastal ocean, lagoon habitat, or some combination are unclear, the presence of individuals of various sizes in each habitat indicate that ontogeny only explains part of the shift in habitat use. More work is needed to determine whether distinct populations of Dolly Varden have distinct life histories, whether environmental conditions among diverse rearing habitats determine future movement patterns, or some combination thereof (e.g. variable norms of reaction) (Hutchings 2011). In addition, although the costs and benefits of anadromy have been explored (Jonsson and Jonsson 1993, Northcote 1997, Aubin-Horth et al. 2006), the fitness consequences of considerable variation in movement patterns within anadromous behaviors (e.g., use of estuaries versus coastal ocean habitats) remains unquantified, yet important to understanding the fitness implications of alternate migratory strategies.

Table 3.1: Dolly Varden diet by sample location. Percentage of diet items, expressed as a percent of the total diet mass from all individuals at each capture location. The percentage of fish from each collection location with no prey items in the stomach at the time of capture are indicated by % empty. Only sites with at least 10 individuals with stomach contents are displayed.

Chignik Lagoon Spit		Chignik Lagoon Hume Point		Chignik Lagoon Alpha		Chignik Lake		Chignik River (Braids)		Black Lake Alec River	
% empty		% empty		% empty		% empty		% empty		% empty	
20.3		17.7		27.69		44.73		69.14		14.2	
Item	% mass	Item	% mass	Item	% mass	Item	% mass	Item	% mass	Item	% mass
sand lance	28.7	gammarid	92.9	gammarid	70.4	Larval Caddis	39.1	salmon eggs	58.2	salmon eggs	94.5
gammarid	26.0	Juvenile salmon	2.6	Isopod	14.8	salmon eggs	31.1	Larval Caddis	17.7	Larval Caddis	1.4
larval crab	20.4	Isopod	2.3	Juvenile salmon	8.6	3 spine stickleback	7.9	Juvenile salmon	14.7	unid. invertebrate	1.1
Corophium	5.2	sculpin	1.9	Corophium	3.7	larval chironomid	4.2	Isopod	7.8	adult caddis	1.0
larval amphipods	4.3	larval amphipods	0.2	salmon eggs	2.0	sockeye fry	2.6	snails	1.5	larval mayfly	0.8

Table 3.2: Dolly Varden muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for lagoon prey items sampled from each site. Values are corrected for trophic enrichment ($\delta^{13}\text{C} +0.5 \text{‰}$, and $\delta^{15}\text{N} +3.4 \text{‰}$).

Prey	Chignik Lagoon Spit		Chignik Lagoon Hume Point		Chignik Lagoon Alpha	
	$\delta^{13}\text{C} \text{‰} (\pm\text{SD})$	$\delta^{15}\text{N} \text{‰} (\pm\text{SD})$	$\delta^{13}\text{C} \text{‰} (\pm\text{SD})$	$\delta^{15}\text{N} \text{‰} (\pm\text{SD})$	$\delta^{13}\text{C} \text{‰} (\pm\text{SD})$	$\delta^{15}\text{N} \text{‰} (\pm\text{SD})$
three-spined stickleback	-11.20 (± 0.59)	15.55 (± 0.70)				
corophium			-12.69 (± 0.01)	9.73 (± 0.07)	-21.18 (± 1.29)	9.46 (± 0.29)
gammarid	-9.60 (± 0.42)	12.96 (± 0.21)	-10.70 (± 2.03)	10.33 (± 0.27)	-12.08 (± 0.34)	7.01 (± 0.19)
isopod			-13.05 (± 4.06)	13.22 (± 1.15)	-15.19 (± 0.24)	11.54 (± 0.62)
fish larvae	-11.93	15.49				
crab larvae	-18.04	12.30				
sand lance	-18.35 (± 0.67)	15.66 (± 0.63)				

Table 3.3: Range in muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all fish collected in the study by region, compared recent resident or anadromous individuals determined from otolith chemistry. Minimum and maximum values from the otolith subset do not equal minimums and maximums in all cases due to a reduced sample size.

Site	All fish				Freshwater resident				Anadromous			
	$\delta^{13}\text{C}$ ‰		$\delta^{15}\text{N}$ ‰		$\delta^{13}\text{C}$ ‰		$\delta^{15}\text{N}$ ‰		$\delta^{13}\text{C}$ ‰		$\delta^{15}\text{N}$ ‰	
	max and min	range	max and min	range	max and min	range	max and min	range	max and min	range	max and min	range
Alec River	-18.51 to -22.05	3.54	14.06 to 11.79	2.27	-18.87 to -22.05	3.18	14.06 to 11.79	2.27	-18.52 to -19.25	0.73	13.54 to 12.83	0.71
Chignik Lagoon	-12.90 to -24.97	12.07	14.87 to 5.26	9.61	-18.12 to -20.06	1.94	10.50 to 9.50	1.00	-13.50 to -24.89	11.40	14.57 to 7.06	7.52
Chignik Lake	-16.82 to -26.49	9.67	13.96 to 3.86	10.10	-16.82 to -25.03	8.21	13.35 to 7.11	6.24	-17.19 to -18.84	1.65	13.64 to 10.61	3.03
Chignik River	-14.27 to -25.04	10.77	13.94 to 8.64	5.30	-18.90 to -24.71	5.81	13.34 to 9.49	3.85	-14.93 to -19.84	4.91	13.94 to 9.65	4.29

Table 3.4: Isotopic ellipse sizes of Dolly Varden at three freshwater collection stations. Above diagonal: Amount of overlap (per mil²) in small sample size corrected ellipses between vertical and horizontal sites in Chignik Lake. Below diagonal: Proportion of posterior draws (10⁵) that indicate the vertical site has a smaller ellipse size (per mil²) than the horizontal site.

site	Ellipse area (per mil ²)		
	Clark	Cucumber	Hatchery
Clark	11.59	6.07	4.1
Cucumber	0.34	13.19	8.61
Hatchery	0.61	0.74	10.86

Table 3.5: Isotopic ellipse sizes and overlap of Dolly Varden from freshwater and estuarine locations. Above diagonal: Amount of ellipse overlap (per mil²) in small sample size corrected ellipses between vertical and horizontal sites in the lagoon and anadromous freshwater captured Dolly Varden in two size classes, expressed as a percentage of the vertical site. Comparisons indicating no overlap are shown in bold. Below diagonal: Values indicate the proportion of posterior draws (10⁵) where the standard ellipse of the vertical site is smaller than the horizontal site. Values in bold with * indicate vertical site has a smaller ellipse size (per mil²) than the horizontal site (≤ 0.05). Comparisons in bold with # indicate the vertical site is larger than the horizontal site. Above and below axis: Comparisons indicating significant differences are shaded dark grey for emphasis.

Site	Ellipse area (per mil ² ±SD)	Chignik River (>300 mm)	Chignik Lake (<300 mm)	Chignik Lake (>300 mm)	Lagoon Alpha (<300 mm)	Lagoon Alpha (>300 mm)	Lagoon Hume (<300 mm)	Lagoon Pillar (<300 mm)	Lagoon Pillar (>300 mm)	Lagoon Spit (<300 mm)	Lagoon Spit (>300 mm)
Chignik River (>300 mm)	0.99 (±0.22)		16.2	28.3	0.00	0.00	0.00	0.00	0.00	20.7	0.00
Chignik Lake (<300 mm)	1.33 (±.42)	0.23		22.9	0.00	0.00	0.00	21.4	2.3	36.8	0.00
Chignik Lake (>300 mm)	1.33 (±.47)	0.25	0.50		0.00	0.00	0.00	0.00	2.8	19.5	0.5
Lagoon Alpha (<300 mm)	7.62 (±1.17)	0.00*	0.00*	0.00*		0.00	27.0	52.1	0.00	48.2	0.00
Lagoon Alpha (>300 mm)	4.18 (±1.58)	0.00*	0.01*	0.01*	0.95[#]		11.2	38.8	19.1	46.4	0.00
Lagoon Hume (<300 mm)	10.81 (±1.96)	0.00*	0.00*	0.00*	0.06	0.01*		57.7	0.00	6.2	0.00
Lagoon Pillar (<300 mm)	10.05 (±3.34)	0.00*	0.00*	0.00*	0.24	0.03*	0.63		5.2	58.1	0.00
Lagoon Pillar (>300 mm)	3.44 (±1.30)	0.00*	0.02*	0.02*	0.98[#]	0.65	0.99[#]	0.98[#]		53.5	0.00
Lagoon Spit (<300 mm)	10.88 (±1.62)	0.00*	0.00*	0.00*	0.05*	0.01*	0.47	0.35	0.00*		11.3
Lagoon Spit (>300 mm)	4.27 (±1.06)	0.00*	0.00*	0.00*	0.98[#]	0.44	0.99[#]	0.98[#]	0.26	0.99[#]	

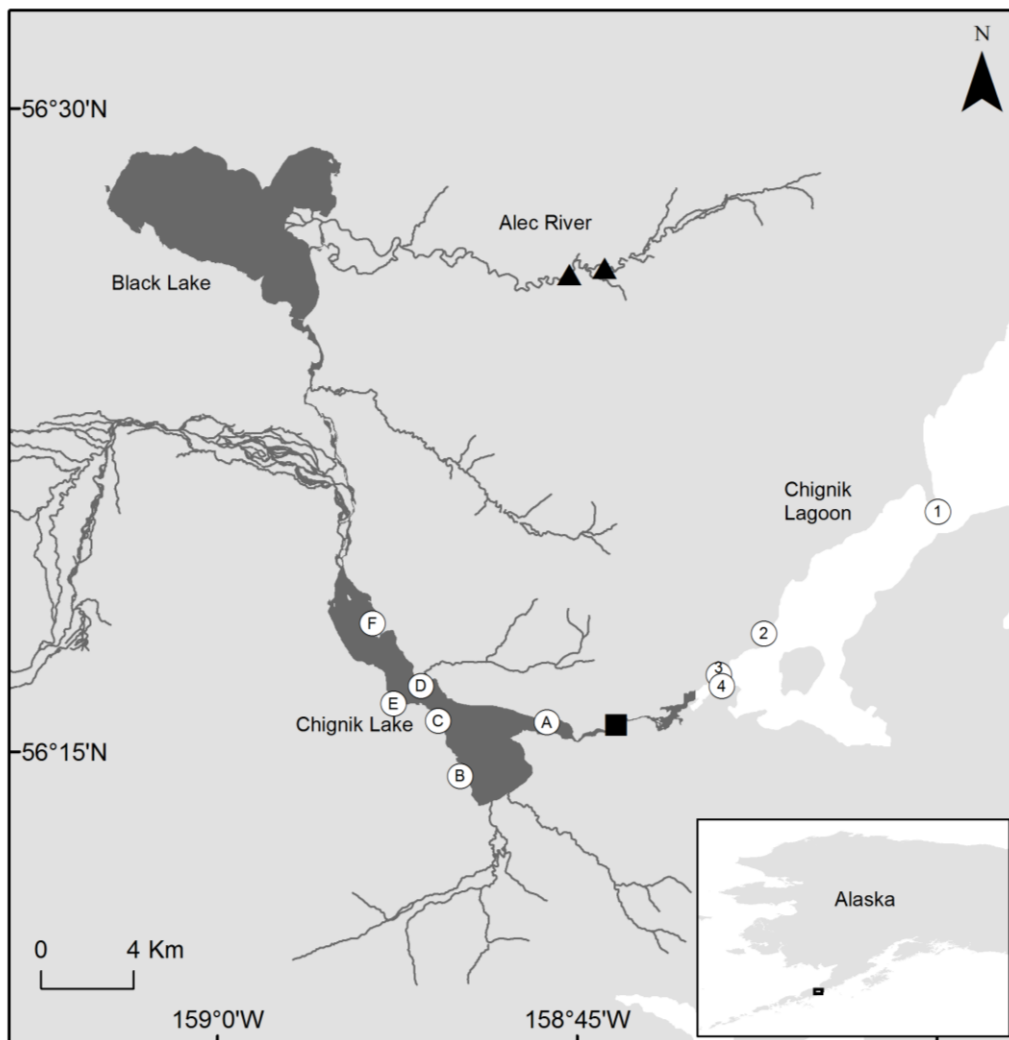


Figure 3.1: Map of the Chignik Lakes watershed depicting sampling locations. Chignik Lagoon sites are numbered from marine (1) to brackish (3-4): 1: Spit, outer lagoon, 2: Hume Point, mid-lagoon, 3: Alpha, inner-lagoon, 4: Pillar Rock, inner-lagoon. The filled square indicates the Chignik River Braids sampling site. Lettered Chignik Lake sites denote: A: Outlet, B: Clark Bay, C: South Hatchery Beach, D: Cucumber Point, E: North Hatchery Beach, F: Delta. The filled triangles indicate the Alec River sampling sites. Grey fill indicates freshwater habitats, while white fill indicates brackish to marine waters.

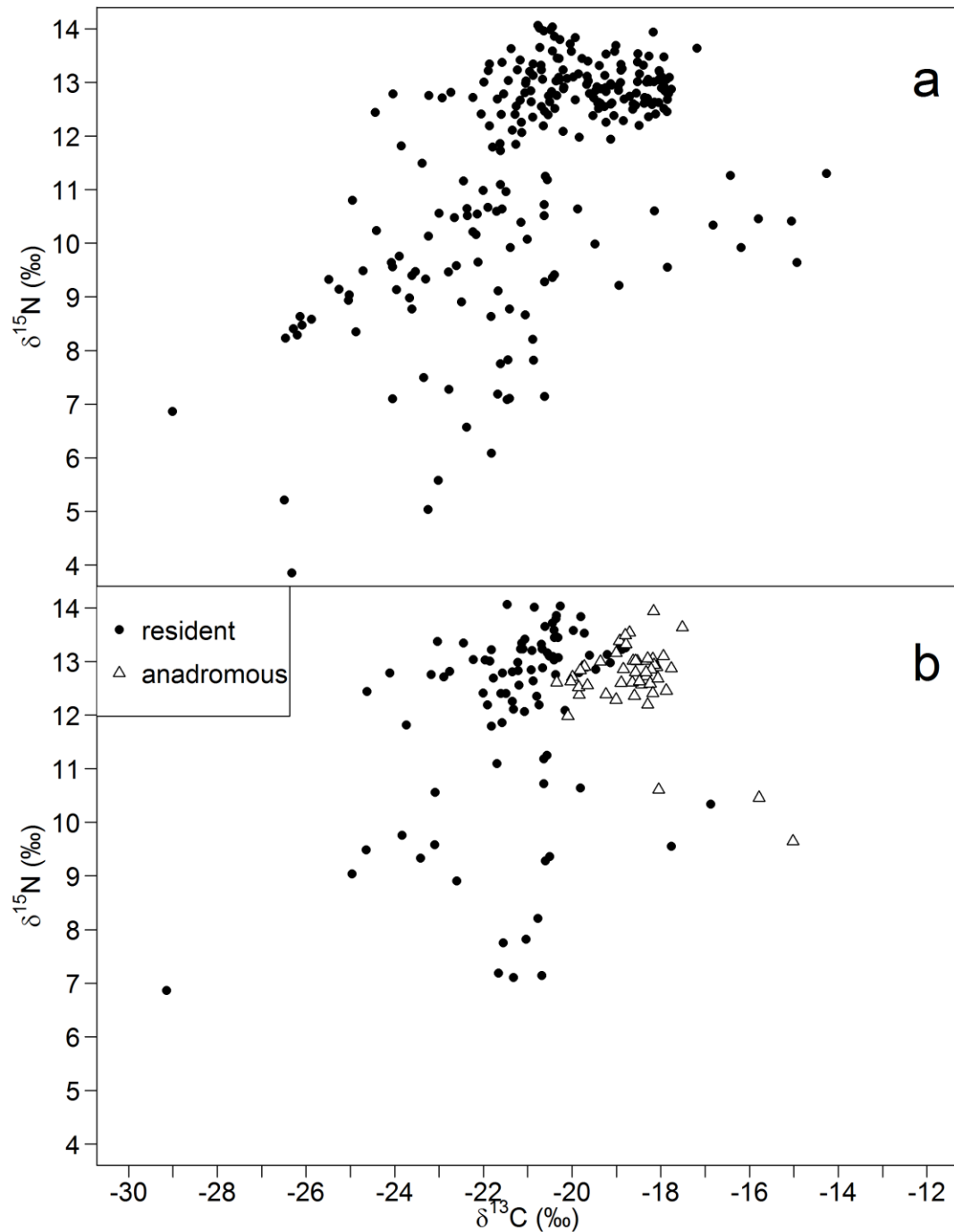


Figure 3.2: Muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Dolly Varden with and without otolith microchemistry determined migratory status. Panel a: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ bi-plot of all Dolly Varden captured in freshwater habitats. Panel b: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ bi-plot of a subset Dolly Varden captured in freshwater habitats with otolith microchemical analysis indicating recent anadromy or freshwater residency

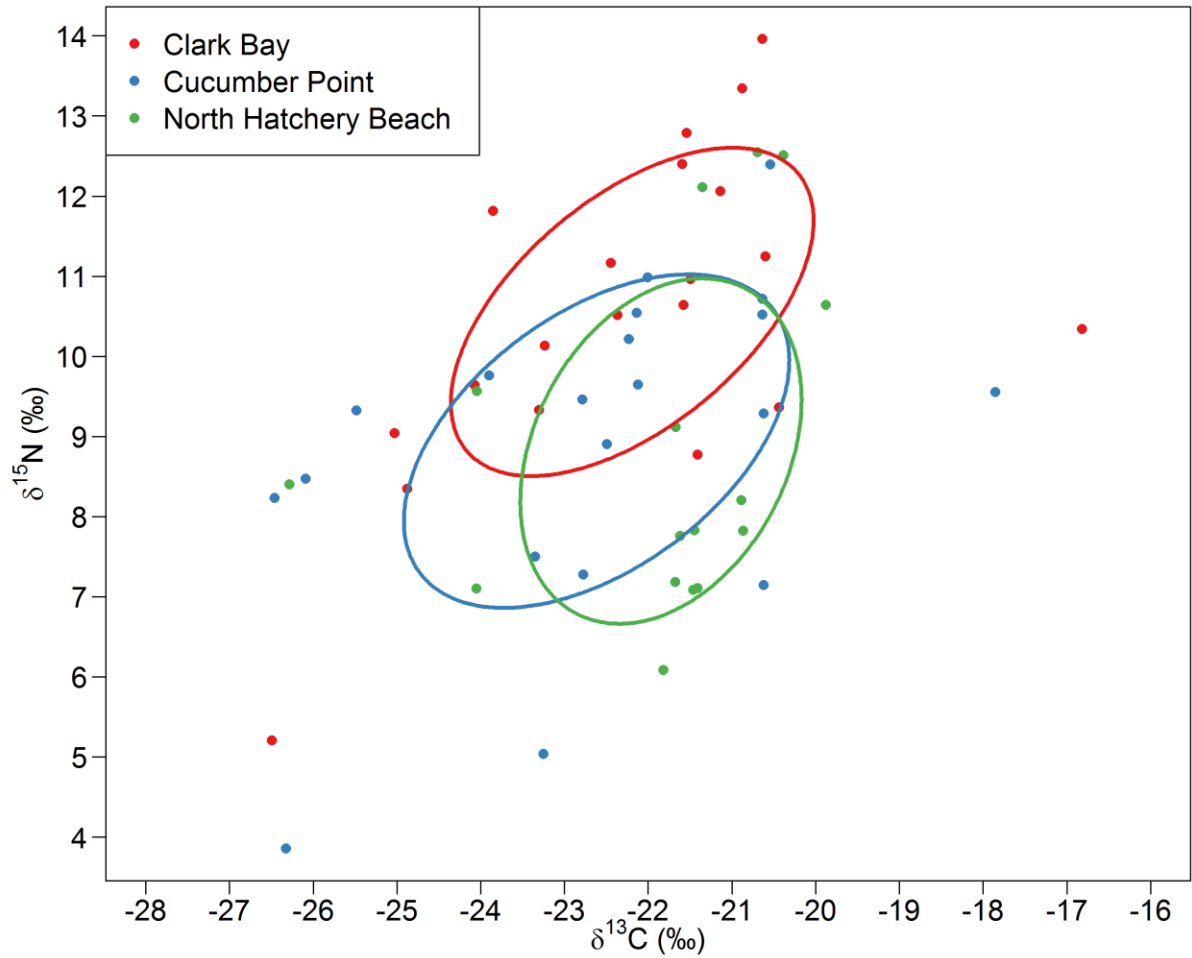


Figure 3.3: Bi-plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for Dolly Varden captured in Chignik Lake. To avoid potentially anadromous individuals, only fish smaller than 230 mm fork length are displayed. Ellipses are standard small sample size corrected ellipses depicting the overlap in isotopic niche among collection sites. These ellipses correspond to ellipse values in Table 2. Only sites with at least 10 individuals are shown.

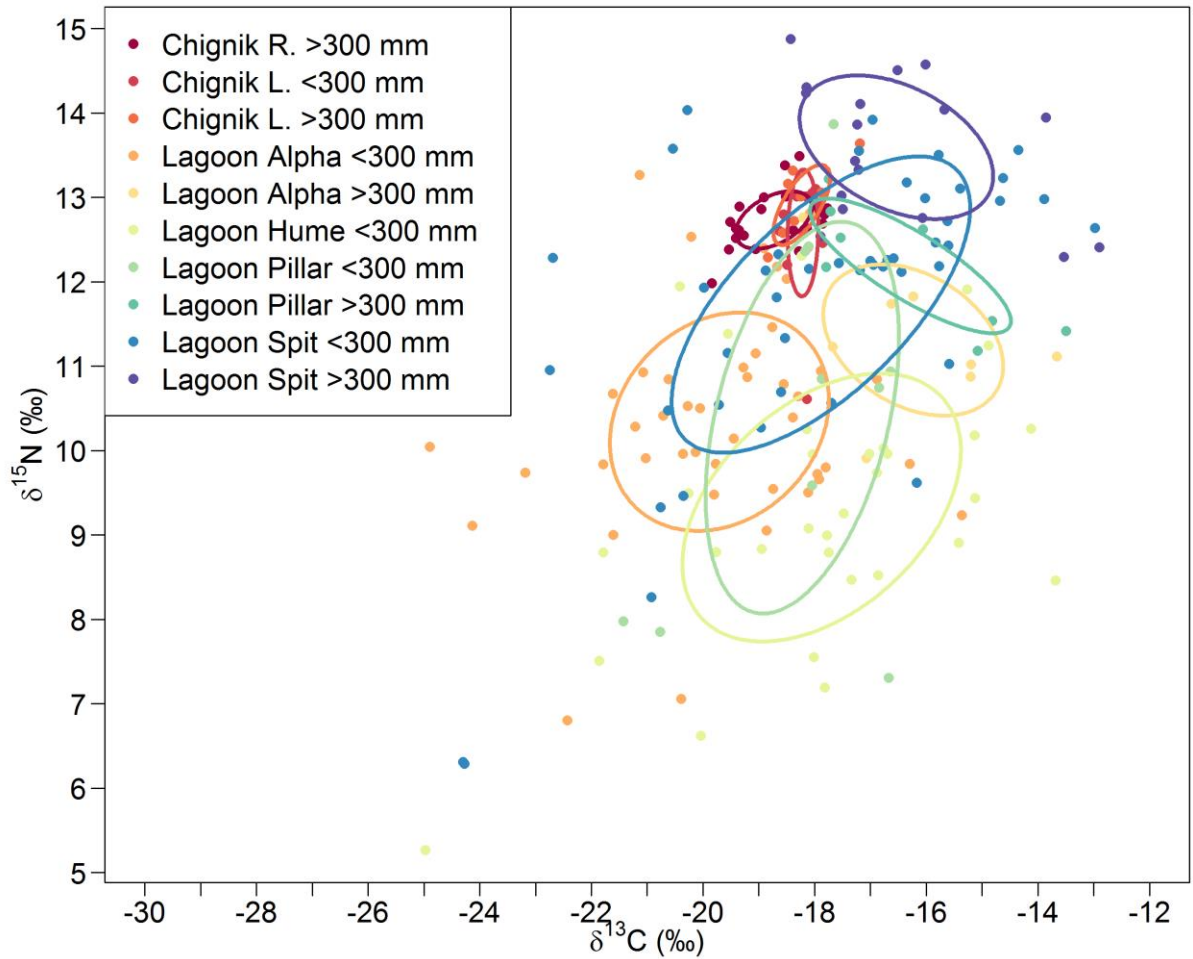


Figure 3.4: Bi-plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for Dolly Varden captured in Chignik Lagoon and freshwater. Includes individuals captured in Chignik Lake and Chignik River determined to be recently anadromous through otolith chemistry. Ellipses are standard small sample size corrected ellipses depicting the separation in isotopic niche among collection sites and size groups. These ellipses correspond to ellipse values in Table 2.

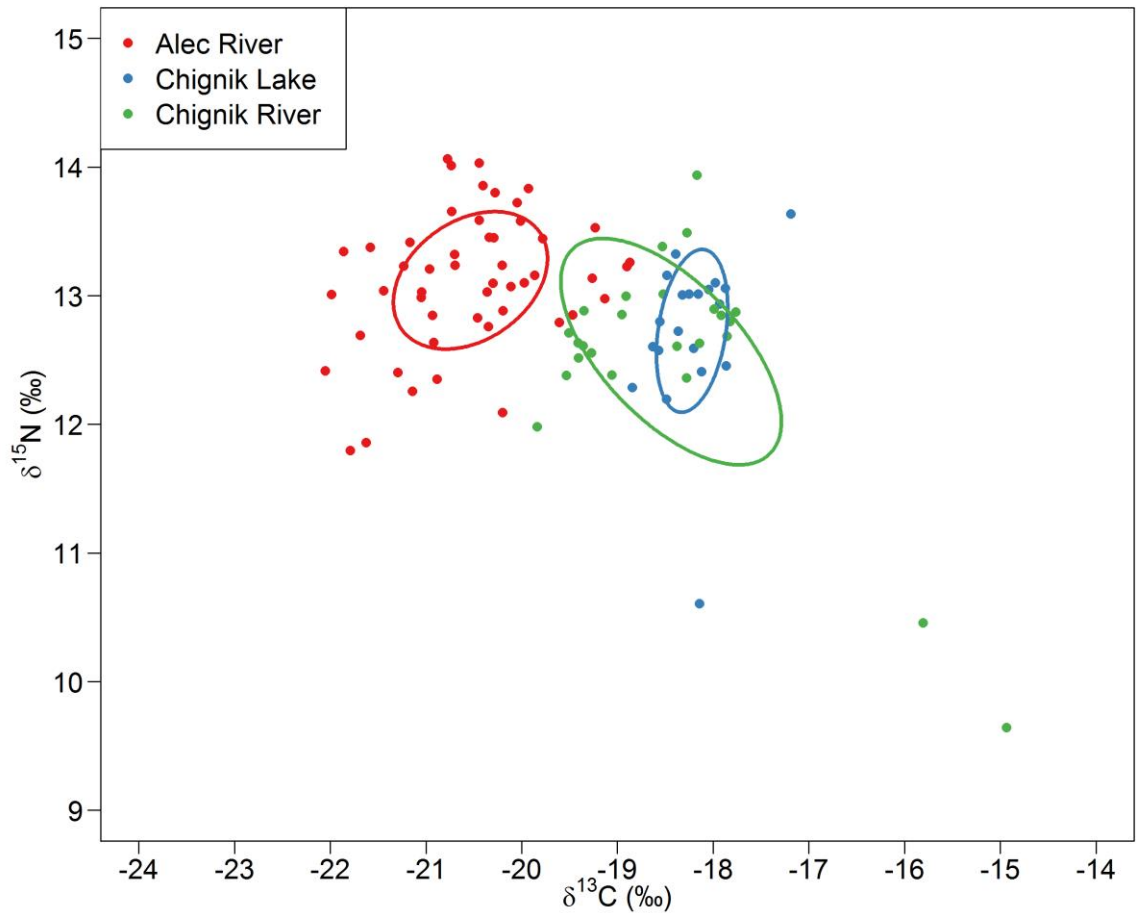


Figure 3.5: Bi-plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for Dolly Varden captured in the Alec River Chignik Lake and Chignik River. Alec River Dolly Varden (freshwater resident in year of capture) compared to recently anadromous fish from Chignik Lake and Chignik River. Determination of anadromy made from recent otolith microchemistry. Ellipses are standard small sample size corrected ellipses.

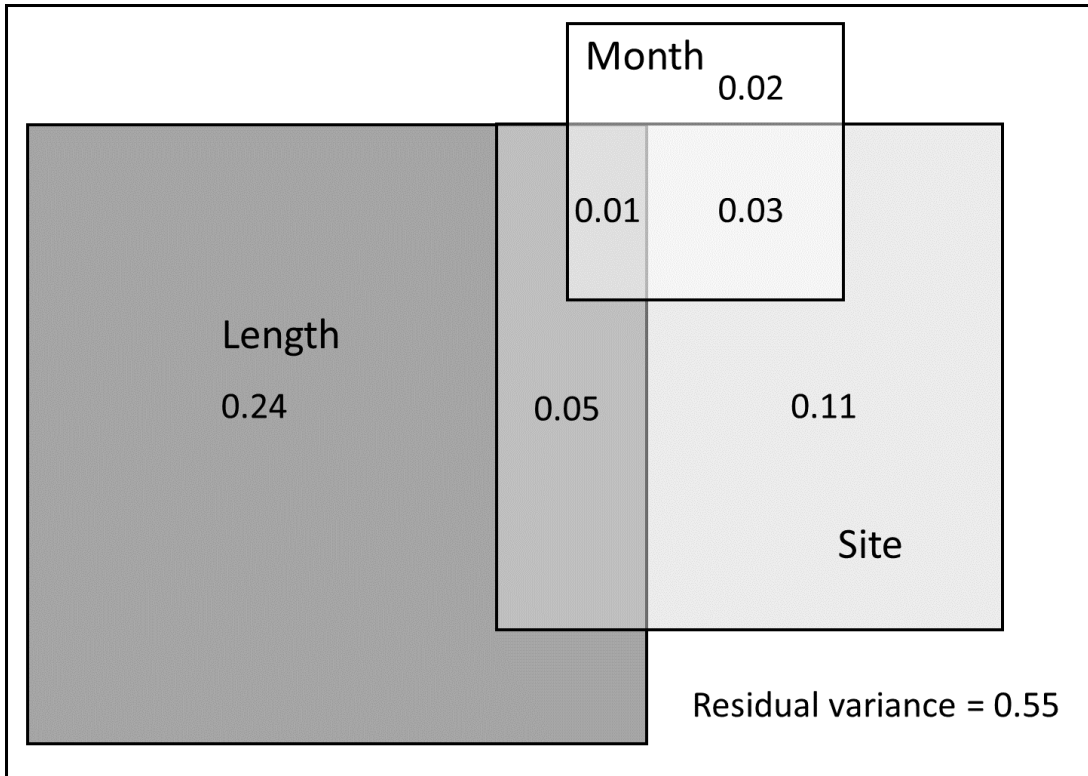


Figure 3.6: Unique and shared variance components explained by length, sample site, sample month in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with partial redundancy analysis. Year was not a significant predictor and excluded from this analysis.

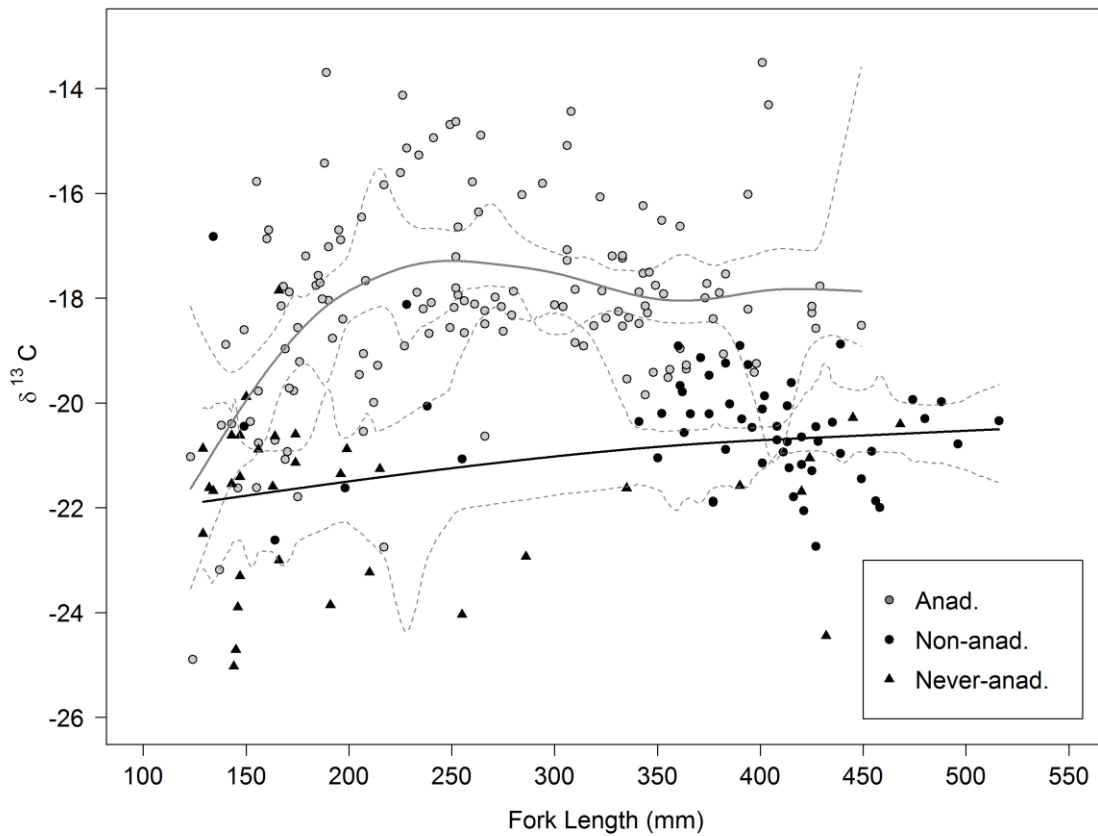


Figure 3.7: $\delta^{13}\text{C}$ values and fork length for all Dolly Varden analyzed for both stable isotope and otolith chemical signatures. Grey points indicate individuals with otolith chemistry indicative of recent anadromy. Black points indicate individuals that were non-anadromous in the year of capture, but had prior ocean residency. Black triangles indicate individuals that have never been to sea. Grey line is fitted spline for anadromous fish with 95% confidence intervals. Black line is fitted spline for individuals non-anadromous in the year of capture and individuals that have never been to sea, collectively.

Chapter 4: The initiation and cessation of migratory behavior: Retirement from anadromy by aging Dolly Varden, *Salvelinus malma*, is linked to the subsidy provided by Pacific salmon

Introduction

Variation in migratory behavior has been described for many animals, ranging from insects to mammals (Dingle and Drake 2007). In some species migration is obligate and fixed at certain life history stages because the environment is seasonally unsuitable (e.g., fledgling birds as well as adults must fly from northerly breeding areas to southerly wintering habitats, and whale calves as well as adults must depart the tropical breeding and birthing areas for northerly feeding areas in summer (Baker 1978)). In these systems, the average fitness benefits of migrating, through increased growth or survival, outweigh the costs (e.g., physiological investment, mortality) of movement. However, changes in food availability, harshness of seasonal shifts, and arduousness of migration across the landscape may favor residency in some populations and migration in others (Alerstam et al. 2003). In some cases the tradeoffs of migration are even more subtle, and populations may exhibit partial migration, where some individuals migrate whereas others do not; migration tends to be more common in the sex that experiences the largest fitness gains from increased growth (Hutchings and Morris 1985). Partial migration may therefore be a conditionally dependent trait, where population specific thresholds determine the initiation of migration (Lundberg 1988, Pulido 2011). Consequently, there may be similar thresholds that terminate migratory behavior at sizes or ages when it is no longer advantageous, although examples are sparse (but see: Näslund et al. 1993, Middleton et al. 2006).

In anadromous fishes, variation may occur in the timing of migration from freshwater to marine environments, age at migration, or whether to migrate at all. This life history variation is both interspecific, with some species being nearly fixed in their patterns of anadromy (e.g. pink salmon, *Oncorhynchus gorbuscha*), or intraspecific, with differences both among and within populations (e.g. steelhead, *Oncorhynchus mykiss*) (Hutchings and Morris 1985, Quinn and Myers 2004, Pavlov and Savvaitova 2008). As a group, char (*Salvelinus* spp.) include the almost invariably non-anadromous lake trout (*S. namaycush*), but the other species show a broad range of facultative anadromy: Dolly Varden (*S. malma*), Arctic char (*S. alpinus*), bull trout (*S. confluentus*) and brook trout (*S. fontinalis*). Variation in anadromy is often attributed to differences in the relative productivity of marine and freshwater environments, which changes broadly with latitude (Gross 1987, Gross et al. 1988) and are linked to anadromy in some salmonids such as *O. masou* and *S. salar* (Hutchings and Jones 1998, Pavlov and Savvaitova 2008, Morita and Nagasawa 2010). Despite these broad patterns, there is evidence in freshwater systems that individual fish can rapidly respond to changes in productivity among environments and migrate to maximize individual fitness (Näslund et al. 1993, Brodersen et al. 2008). However, the freshwater environment may not have adequate resources to support anadromous individuals that achieve large body sizes through increased marine growth. Therefore, iteroparous anadromous fishes are assumed to continue annual or seasonal movements to marine waters once they are initiated. Likewise, fully resident fish are often smaller at each age compared to anadromous individuals from the same populations (Pavlov and Savvaitova 2008).

Dolly Varden are facultatively anadromous in waters with ocean access (Armstrong and Morrow 1980). However, studies showing fully resident life histories in anadromous waters are more limited because of the variation in age at anadromy and small sample sizes (Scanlon 2000, Palmer and King 2005). Additionally, little is known about the diversity of migration patterns that may exist on smaller spatial scales (e.g. watershed or population level). In North America Dolly Varden are classified based on morphological and life history differences as either Northern form (North of the Alaska Peninsula to the Mackenzie River) or Southern form (South of the Alaska Peninsula to Washington State) (Armstrong and Morrow 1980). Northern Dolly Varden are commonly anadromous, may migrate to the open ocean (Morita et al. 2009) and occasionally move between Asia and North America (DeCicco 1992). Southern Dolly Varden use coastal marine habitats in summer months but may sometimes overwinter in marine waters (Bernard et al. 1995). Dolly Varden exhibit a high degree of spawning site fidelity to natal waters, but immature fish may range widely and rear extensively in watersheds other than their own (Crane et al. 2005). Closely related Arctic char are intolerant of seawater at small body sizes, and this may explain the generally large size of smolts in that species (Jensen and Rikardsen 2008). However, nothing is known of Dolly Varden salinity tolerance size thresholds that would limit marine movements of smaller individuals. Marine migrations of salmonids are often characterized by mark-recapture studies but this technique is less useful for Dolly Varden because of the lack of a targeted commercial or sport fisheries in many areas. Telemetry can provide high resolution data on a few individuals, but is not useful for characterizing the life history diversity of an entire population (Palmer and King 2005, Lisac 2006, Bond and Quinn 2013). Tagging is

often biased by capture location and sample size, such that rare or non-migratory individuals may be missed. This is especially true of Dolly Varden, where fully resident individuals may be uncommon.

Recently, there has been an increase in the use of natural variation in water chemistry and recording of that chemistry in calcified structures (e.g. teeth, bones, scales, otoliths) to characterize changes in habitat use by individual fish. Commonly, strontium and barium concentrations (Wells et al. 2003, Kraus and Secor 2004) or the isotopic ratios of sulfur (Godbout et al. 2010) or strontium (Ingram and Weber 1999, Kennedy et al. 2000) are used. These elements are not biologically regulated and their concentrations in the internal environment of the fish mimic the environment in predictable ways (Miller 2009, Phillis et al. 2011). Otoliths, a bony structure of aragonite bound in a protein matrix, are the preferred structure for measuring changes in chemistry over time. Unlike scales, from which calcium may be reabsorbed during vitellogenesis, otoliths are largely inert once the calcium carbonate structure has been deposited, leaving a more permanent record of chemical history (Campana 1999). In addition, otoliths are banded with opaque and hyaline regions corresponding to summer and winter growth, respectively. These regions allow the chemistry to be matched with specific ages of the individual. Surface chemistry can then be analyzed from the core to the edge via electron microprobe, ion microprobe, or laser ablation, depending upon the elements required. Once a concentration history is developed for each individual, it is possible to assign fish to different habitats by age (Campbell et al. 2002). In addition, in waters with low freshwater Sr concentrations ($\leq 5 \text{ mmol} \cdot \text{mol}^{-1}$), maternal anadromy in the year preceding

spawning can be assessed with Sr concentrations in the primordia because the otolith's core is essentially all maternal material (Riva-Rossi et al. 2007, Donohoe et al. 2008).

Although the use of otolith microchemistry to reconstruct migratory behavior is not new, the application of this technique to thoroughly assess the life history diversity of an entire population has rarely been demonstrated. This study used otolith chemistry and age data for Dolly Varden captured in rearing and migratory areas throughout the watershed to characterize several key life history parameters in a population complex that apparently included a wide range of life history and migration patterns. First, we calculated the incidence of maternal anadromy (i.e., what proportion of the fish had mothers that had been to sea in the summer prior to spawning?). The benefits of anadromy are more clearly outlined for females, where body size has direct consequences for fecundity and the maternal contribution is detectable in otolith primordia. Then, we calculated the age at first anadromous migration, or, for some individuals verified the existence of the resident life history. For anadromous fish, we also measured: 1) the incidence of repeat migrations, 2) the duration of freshwater residence between migrations, and 3) the number of years since the last migration. Using these data we test several hypotheses to explain the simultaneous presence of Dolly Varden in freshwater and at sea in the summer:

1. All fish go to sea and back every year but migration timing is so variable that some individuals are found in both places at all times.
2. All fish are anadromous but not every year, leading to the question: does the probability of migration vary with age?
3. If fully resident fish exist, are they predominately males?

4. At each age, anadromous fish have a size advantage over non-anadromous individuals.
5. Anadromous individuals are more likely to have anadromous mothers than non-anadromous individuals.

Despite its clear importance to both the understanding of and the conservation of fishes, assessments of migratory diversity are typically limited to assessing contemporary levels of diversity. Because of this, in systems that may have been impacted by a variety of anthropogenic influences (e.g. deforestation, fishing, dams), it is often unclear whether the current migratory diversity reflects the historic diversity of a population or region. Maintaining life history diversity is an important component of sustaining imperiled fish populations, and is included in all recovery plans for species listed under the U. S. Endangered Species Act (McElhany et al. 2000); however, historic life history diversity of imperiled species is difficult to determine. For example, bull trout were listed as Threatened in 1999 but few undisturbed populations exist, so it is difficult to determine what factors promote life history diversity. In this case, characterizing the life-history diversity that exists in a natural, unperturbed population of closely related Dolly Varden, may provide insights into not only the variability, but the natural abundance of alternate migratory phenotypes and the environmental conditions that produce and maintain those alternatives.

Methods

The Chignik Lakes watershed in southwestern Alaska drains a 1536 km² basin that includes 41 km² Black Lake, 25 km² Chignik Lake, and a 33 km² semi-enclosed lagoon (Figure 1)(Narver and Dahlberg 1965, Simmons et al. in press). Chignik Lagoon

loses approximately 50% of its available surface area during extreme tidal exchanges (~4 m) (Narver and Dahlberg 1965, Simmons et al. in press) and varies in salinity by tidal height, river flow and distance from the sand spit that separates it from the more marine Chignik Bay, ranging from 0‰ to 34‰ (Simmons et al. in press).

We collected Dolly Varden across a range of size classes and several representative habitats in Chignik Lagoon, Chignik River, Chignik Lake, and the Alec River. Fish were collected twice per month at each site, with a target sample size of 20 individuals across the available size range (> 120 mm fork length) in both 2009 and 2010. In the Alec and Chignik rivers, fish were sampled with hook and line. In all other habitats fish were sampled with a 30 m beach seine. Upon capture each fish was euthanized in MS-222, measured for length and weight, and gonads were removed and weighed. The saggital otoliths were removed from each individual, rinsed in de-ionized water to remove tissue, and stored dry in individual plastic vials.

A subset of 366 Dolly Varden that encompassed the size range captured in each habitat was evaluated for previous anadromous migrations. In the laboratory, one otolith from each individual was mounted for ageing and elemental analysis. All otoliths were bonded sulcus (ventral) side up to individual glass microscope slides with Crystalbond 509 thermoplastic cement (Aremco Products, Inc.). The sulcus side of each otolith was then ground with successively finer grades of polishing film (50-1 μm) lubricated with nanopure water until the sulcul groove was nearly removed. The anti-sulcus (dorsal) side was ground until the entire saggital plane was visible in one flat section from the core (primordial) to the edge. For large fish (ca. ≥ 500 mm FL), the otoliths were prepared in

the transverse section (posterior-anterior rather than dorsal-ventral) to expose the core to the edge in a single plane.

Edge chemistry for each otolith was analyzed with laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) at the Keck Collaboratory, Oregon State University. A VG PQ ExCell ICPMS with a New Wave DUV193 excimer laser was used for all analyses of 2009 otoliths and a Thermo X-Series II ICPMS and Photon Machines Analyte G2 193 nm laser was used to analyze 2010 otoliths. The laser was set at a pulse rate of 7 Hz with a 20- μm ablation spot and traveled at 5 $\mu\text{m sec}^{-1}$. We measured Sr, Ba, Mn, Mg, Cu, Ca, Pb, Ca and used NIST-612 glass to transform ion ratios to elemental ratios. These were converted to molar ratios using the molar mass of each element. Final analyses were computed on the element:Ca in $\text{mmol} \cdot \text{mol}^{-1}$. A calcium carbonate standard with known concentration (USGS MACS-2) was used to determine the accuracy of the element:Ca ratio and correct final element:Ca values with each laser-ICPMS system.

Following ablation, microphotographs were taken of each otolith. ImageJ software (Abramoff et al. 2004) was used to measure the distance of each annulus and the core from edge following the trough produced by laser ablation. Chemical transects were aligned with annuli and core distances from photographs to identify Sr:Ca and Ba:Ca ratios for each year of life for each fish. These data were used to determine maternal anadromy, as well as classify each year of life as anadromous or non-anadromous. Maternal anadromy was assumed when core Sr:Ca ratios were $\geq 1 \text{ mmol} \cdot \text{mol}^{-1}$ greater than the surrounding freshwater chemistry, and when the core of the otolith coincided with a nadir in Zn:Ca (Halden et al. 2000). If the core indicated no decline in Zn:Ca, we

assumed that the primordia was missed in the polishing process did not evaluate maternal anadromy. To classify anadromy, we evaluated the Sr:Ca and Ba:Ca ratios at the midpoint between each annulus; values of Sr:Ca $>3 \text{ mmol} \cdot \text{mol}^{-1}$, and Ba:Ca $<6 \text{ } \mu\text{mol} \cdot \text{mol}^{-1}$ were considered anadromous movements (Bond, Chapter 3). Values outside this range were considered to be indicative of non-anadromous behavior.

We determined the probability of anadromy for each age as the percentage of fish that entered the ocean in each year of life. Additionally, we determined the number of individuals at each age that had been to sea at least once in their life, as a cumulative probability of anadromy. To evaluate the benefits of anadromy in terms of growth, we calculated the fork length at age of capture for fish with no anadromous movements compared to individuals with 1-5 ocean migrations. We assessed maternal effects by comparing the size at age for individuals with anadromous mothers to individuals with non-anadromous mothers in the year of capture. Finally, we evaluated the incidence of fully non-anadromous individuals (i.e. individuals that had not been to sea, and were unlikely to do so.), as all fish older than the maximum age at first migration that had not been to sea. The sex ratio of non-anadromous fish could then be evaluated for deviation from 50:50.

Results

The percentage of fish sampled that had been to sea in any year increased with age, from a low of 0% for individuals in their first year of life, to a peak of 71% for individuals in their fourth year of life (Figure 2). However, after age 4 the probability of anadromy declined, such that only 6% and 5% of fish in their seventh and eighth year of life, respectively, had been to sea in that year (though nearly all fish of such an age had been to sea in earlier years). No fish in our collection made an anadromous migration after its

eighth year of life. Similarly, the percentage of Dolly Varden that had been to sea at least once increased to a peak of 88.4% for fish in their fifth year of life (Figure 2). The percentage declined to 68% by the eighth year of life, after which the sample size became too small to make useful calculations of the incidence of anadromy.

There was no significant effect of sex on length at age of Dolly Varden ($F = 1.48$, $df = 2$, $p = 0.23$). Anadromous Dolly Varden in their third and fourth years of life were larger than non-anadromous fish of the same age (Table 1, Figure 3). However, fish in the fifth, sixth and seventh years of life with one to five anadromous migrations were not larger than non-anadromous individuals of the same age (Table 1). However, for some ages, fish whose mothers had been to sea in the season prior to spawning were significantly larger for their age than those with mothers that had been in fresh water (Figure 4). The mean fork length of age 3 fish was not significantly different for those with non-anadromous ($M = 170.1$ mm) and anadromous ($M = 159.8$) mothers ($t_{(9.46)} = 0.55$, $p = 0.594$). However, fish with anadromous mothers were significantly larger at age 4 than fish whose mothers had not been to sea (257.1 vs. 197.6 mm, $t_{(19.83)} = 2.85$, $p = 0.009$), age 5 (354.3 vs. 293.2 mm, $t_{(60.93)} = 3.51$, $p < 0.001$), age 6 (396.6 vs. 362.3 mm, $t_{(57.46)} = 2.17$, $p = 0.034$), and marginally significant for age 7 (441.6 vs. 406.62 mm, $t_{(11.45)} = 2.09$, $p = 0.059$). Ages older than 7 were not evaluated due to low sample sizes.

To evaluate the sex ratio of non-anadromous individuals, we determined the distribution of ages at first migration, which did not differ between the sexes, $X^2 (3, N = 306) = 3.45$, $p = 0.33$. For all fish that had been to sea at least once, 4.2% made their initial migration in their second year, 41.1% in their third year, 47.3% in their fourth year, and 7.1% in their fifth years of life. No individuals made their first marine migration after

their fifth year, so all fish in their sixth year or older with no marine migrations were assumed non-anadromous. Of the twenty non-anadromous individuals (9 male, and 11 female) there was no significant deviation from a 50:50 sex ratio $X^2 (1, N = 20) = 0.2, p = 0.65$. Non-anadromous fish comprised 18.8% of all fish collected in freshwater that were in their sixth year, or older.

To estimate whether females spawned in every year once they first matured or skipped some years, we evaluated the gonadosomatic index (GSI) for females captured in August, the month nearest spawning. Only females of mature size (≥ 300 mm FL) were included (Bond, Chapter 2). Other research has found that skip-spawning females in August have a GSI of 1% or less (Blackett 1968). In Chignik, 4 of 34 (11%) females captured in August had a GSI of less than 1%, while the average GSI was 3.58%, indicating the presence of females likely skipping spawning in the year of capture.

Discussion

The patterns of age-specific migration indicated that Chignik Lakes Dolly Varden are partially anadromous. Although most individuals made at least one migration, some non-anadromous individuals were sampled in river, including the Chignik River, within a few km of the Chignik Lagoon. Consistent with other studies (Armstrong and Morrow 1980), anadromous fish made their first migration to sea in their third or fourth year. Other anadromous char, including Dolly Varden, smolt and migrate at similar ages (Armstrong 1970), possibly driven by poor osmoregulation in seawater for smaller char (Finstad et al. 1989). However, the decreasing incidence of anadromy after the fourth year of life, and near complete cessation of anadromy by the seventh year was unexpected. In other iteroparous anadromous fishes, age at anadromy may vary, but individuals do not revert to residency following the initiation of migratory behavior. Anadromous brown trout

(*Salmo trutta*) and Atlantic salmon (*Salmo salar*) may overwinter in freshwater following spawning, if conditions allow, but will resume migrating in the spring (Jonsson and Jonsson 2011). Arctic char also migrate annually once migration is initiated (Radtke et al. 1998), as do bull trout (Brenkman and Corbett 2005, Brenkman et al. 2007). Above the Arctic Circle, Arctic char and lake trout (*Salvelinus namaycush*) may follow a marine migration with residence in freshwater for 1 and as many as 5 years respectively, before resuming migration (Swanson et al. 2010a), however, there is no evidence that these fish become residents, abandoning migration entirely. Dolly Varden in Chignik and other watersheds with large salmon subsidies may revert to residency because they have large energetic reserves relative to their basal metabolic rate. The body size hypothesis, that larger individuals can sustain greater levels of fasting and need not migrate, has been proposed (Ketterson and Nolan 1976, Ketterson and Nolan Jr 1983) and evaluated in bird (Boyle 2008). Similar mechanisms have been proposed to explain freshwater fish movements, where larger or higher condition individuals remain in less risky, but resource poor habitats, while small individuals or those in poor condition move (Näslund et al. 1993, Brodersen et al. 2008). Similarly, Neverman and Wurtsbaugh (1994) found young cottids moving to warmer, riskier habitats for rapid digestion, while larger individuals were more sedentary. It appears that few young fish in the Chignik system acquire the resources needed for long-term residence in freshwater where resources are scarce until sockeye salmon eggs, flesh, and maggots that feed on them become available during and after spawning, mainly in August. By migrating to productive marine environments in summer months, young fish can invest in both somatic growth, energy needed for overwinter survival, and eventually reproduction. Older, fully resident, and

previously anadromous fish that have reverted to non-anadromy as they become large may shift more energy resources to reproduction and survival, requiring less for growth. Gut atrophy allows these fish to cut energetic costs enough to survive through winter and spring months on the summer subsidy of salmon eggs, thereby alleviating themselves of the energetic burden and risk of marine migration and osmoregulation (Armstrong and Bond 2013).

Growth in marine environments is often superior to freshwater habitats, and the length and mass of anadromous fish may quickly exceed freshwater residents of similar age (Hutchings and Morris 1985). However, anadromous Dolly Varden in the Chignik Lakes watershed only had a size advantage over resident individuals in their third and fourth year. In subsequent years, the number of migrations had no significant bearing on size. Over the last 20 years, the sockeye salmon (*Oncorhynchus nerka*) escapement in the Chignik Lakes watershed has averaged ca. 760,000, providing a large subsidy of eggs and tissues to resident fishes, including Dolly Varden. In the Chignik system, and other watersheds with abundant spawning salmon, resident individuals may be able to achieve similar maximum sizes as the anadromous fish, although it may take a year or two longer to do so. Therefore, the benefit of anadromy may be manifested as earlier reproduction than fully resident fish, or higher fecundity (Hutchings and Morris 1985, Fleming and Gross 1990) rather than greater maximum size. Once near-maximum size has been reached, the net benefits of continued anadromy may be weakened by the mortality risk in the marine environment. Therefore, anadromy is favored at young ages, when salmon subsidies may not be as available to small fish, allowing them to achieve reproductive size. However, once reproductive size is reached, a reversion to residency may become

avored. Large Dolly Varden (ca. 400+ mm fork length) can remain in freshwater, subsisting on little but the annual salmon subsidy, a strategy that may not be energetically feasible for smaller individuals (Armstrong and Bond 2013). Regular seaward migration has repeatedly been found in systems with far lower rates of salmon subsidy, where the resources may not exist for larger bodied fish to survive in freshwater habitats (Brenkman et al. 2007).

Increasing female fecundity with body size indicates that females have more to gain from remaining in high growth environments (Hutchings and Morris 1985, Fleming and Gross 1990). Additionally, many studies have found a strong male bias in resident fish in partially migrating salmonids populations (Jonsson and Jonsson 1993, Rundio et al. 2012), and a female bias in migratory fish (Jonsson and Jonsson 1993, Pavlov and Savvaitova 2008). However, we found no male bias in lifelong resident Dolly Varden in the Chignik Lakes system, indicating that the advantages of migration are not as pronounced as they are in other systems. This is also evident in the disappearance of a size advantage for anadromous fish after age 4. It is likely, therefore, that the large salmon subsidy in Chignik provides a similar resource to the marine environment, without the costs or risks of migration. The similarity in size between mature age anadromous and non-anadromous individuals indicates that, unlike in above-below barrier systems, the two life history strategies may have similar fecundity and fitness.

Female Dolly Varden in some systems may skip one or more years between spawning events (Blackett 1968, Palmer and King 2005). Although the processes leading to skip spawning in char are unknown (Rideout and Tomkiewicz 2011), the incidence of skip-spawning may be higher in non-anadromous populations where fish are resource

limited (Palmer and King 2005). Female Dolly Varden in Chignik Lakes become mature at 300 mm fork length, and the periodicity of their spawning is unknown (Bond, Chapter 2). However, skip-spawning is likely a strategy to reduce energetic costs in a long-lived fish where annual survival of mature individuals is high. In Chignik all four potential skip spawning females (i.e. individuals > 300 mm FL, GSI < 1% in August) were returning from their second consecutive marine migration, indicating that movement to the marine environment does not necessarily determine spawning frequency, even though it provides beneficial growth young fish (Bond, Chapter 2).

Although population estimates for Chignik Lakes Dolly Varden are not available, the large percentage of fish with mothers who were non-anadromous in the year of capture, coupled with the relatively low incidence of fully resident fish, indicate that formerly anadromous fish may comprise a substantial portion of the spawning population. The high incidence of fully resident individuals with anadromous mothers, and the high rates of switching between resident and migratory strategies indicate that anadromy is likely a conditional response in Dolly Varden, rather than a genetically determined evolutionary stable strategy (ESS) (Smith and Price 1973). In a true ESS, each strategy must produce equal fitness, and the success of each strategy is frequency dependent (Lundberg 1987). In iteroparous salmonids, many cases of genetic differentiation between resident and anadromous individuals compare allopatric fish separated by barriers, which may exert perfect selection against migrants in the above barrier population (Pearse et al. 2009). The weak or undetectable genetic differentiation between sympatric resident and anadromous individuals (Olsen et al. 2006b, Johnson et al. 2010), coupled with much stronger differentiation among spawning areas (e.g.

streams, rivers, lakes, etc.) indicates phenotypic plasticity in migratory behavior maintains both phenotypes in many species (Jonsson and Jonsson 1993). Although the threshold for migratory behavior is itself under selection, the condition-dependent migratory model allows for both rapid migration behavior response to novel environmental conditions (Jonsson and Jonsson 1993, Pascual et al. 2001, Pulido 2011), and switching between strategies as individual or environmental conditions change (Näslund et al. 1993).

Dolly Varden in Chignik Lakes are the only known population of anadromous fish where a substantial component of the population becomes sedentary after one or more marine migrations, largely owing to the easy migration (short distance, low elevation, and absence of local areas of difficult passage), and the substantial marine subsidy in the form of eggs and salmon flesh. Although this is the first documentation of such behavior, it is probably not unique to the Chignik watershed. Dolly Varden co-exist with large runs of semelparous fish throughout coastal Alaska, and in many cases putative resident fish may be formerly anadromous individuals. Without adequate assessment of the entire life-history of these fish, the fully resident population would be overestimated. Likewise, using otolith microchemistry of juvenile fish to evaluate the contribution of resident fish to the population (Zimmerman and Reeves 2000, Donohoe et al. 2008, Zimmerman et al. 2009a), would also over-emphasize the productivity of resident fish. In Chignik most fish migrate to sea at least once; the short, low elevation migration, coupled with a productive lagoon and coastal marine environment increases growth rates for young fish (Bond Chapter 2, 3). However, large bodied fish may revert to residency in Chignik because of the large subsidy of salmon eggs that are maintained

at high salmon spawner densities (Essington et al. 2000, Moore et al. 2008). In watersheds with unsuitable environmental conditions (e.g., high mid-summer temperatures), or where salmon subsidies have been reduced, Dolly Varden and other iteroparous species may not, or may no longer, display an anadromous-turned-resident phenotype. In these systems only one or both discrete migratory phenotypes may exist; large bodied anadromous fish that migrate annually, trading shorter lives for increased body size and fecundity, and small resident fish that are longer lived, but have lower annual fecundity.

Table 4.1: Fork length (mm, \pm SD) at capture of Dolly Varden from throughout the Chignik Lakes watershed by age and by number of lifetime seaward migrations.
 Bold values indicate lengths that are significantly different ($P < 0.001$) from individuals with no migrations.

Year of Life	Number of migrations					
	0	1	2	3	4	5
3	135.8 (\pm 14.3) n=12	179.9 (\pm39.0) n=14				
4	165.0 (\pm 37.2) n=22	211.4 (\pm57.2) n=64	242.4 (\pm67.1) n=26			
5	278.0 (\pm 95.9) n=5	293.7 (\pm 100.4) n=22	342.4 (\pm 60.7) n=53	337.1 (\pm 68.6) n=20		
6	363.1 (\pm 98.5) n=8	394.9 (\pm 63.0) n=19	373.9 (\pm 67.4) n=28	365.1 (\pm 54.6) n=18	386.2 (\pm 53.4) n=6	358.0 (\pm 21.2) n=2
7	429.2 (\pm 42.6) n=6	434.2 (\pm 26.4) n=6	439.3 (\pm 23.5) n=7	370.5 (\pm 13.4) n=2		392.7 (\pm 28.0) n=3

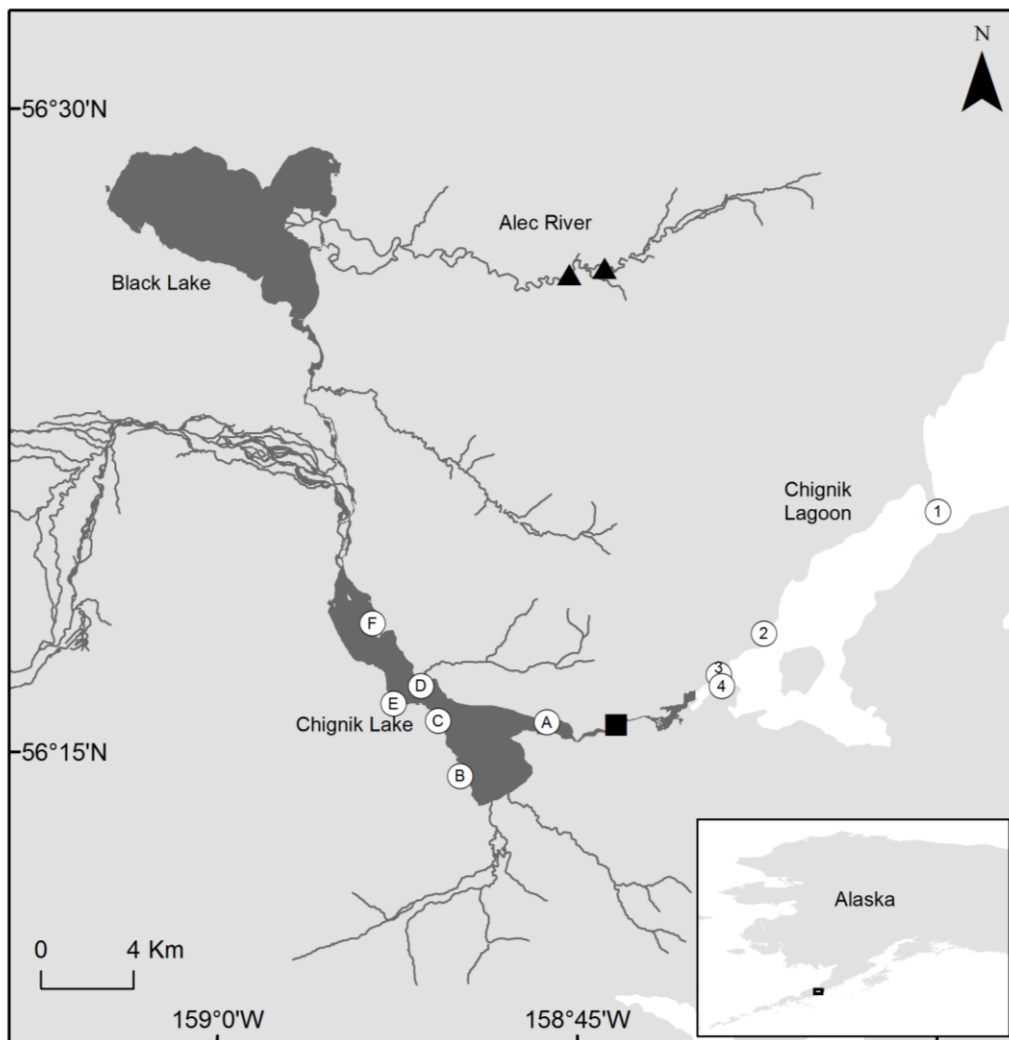


Figure 4.1: Map of the Chignik Lakes watershed depicting sampling locations. Chignik Lagoon sites are numbered from marine (1) to brackish (3-4): 1: Spit, outer lagoon, 2: Hume Point, mid-lagoon, 3: Alpha, inner-lagoon, 4: Pillar Rock, inner-lagoon. The filled square indicates the Chignik River Braids sampling site. Lettered Chignik Lake sites denote: A: Outlet, B: Clark Bay, C: South Hatchery Beach, D: Cucumber Point, E: North Hatchery Beach, F: Delta. The filled triangles indicate the Alec River sampling sites. Gray fill indicates freshwater habitats; white fill indicates brackish and marine waters.

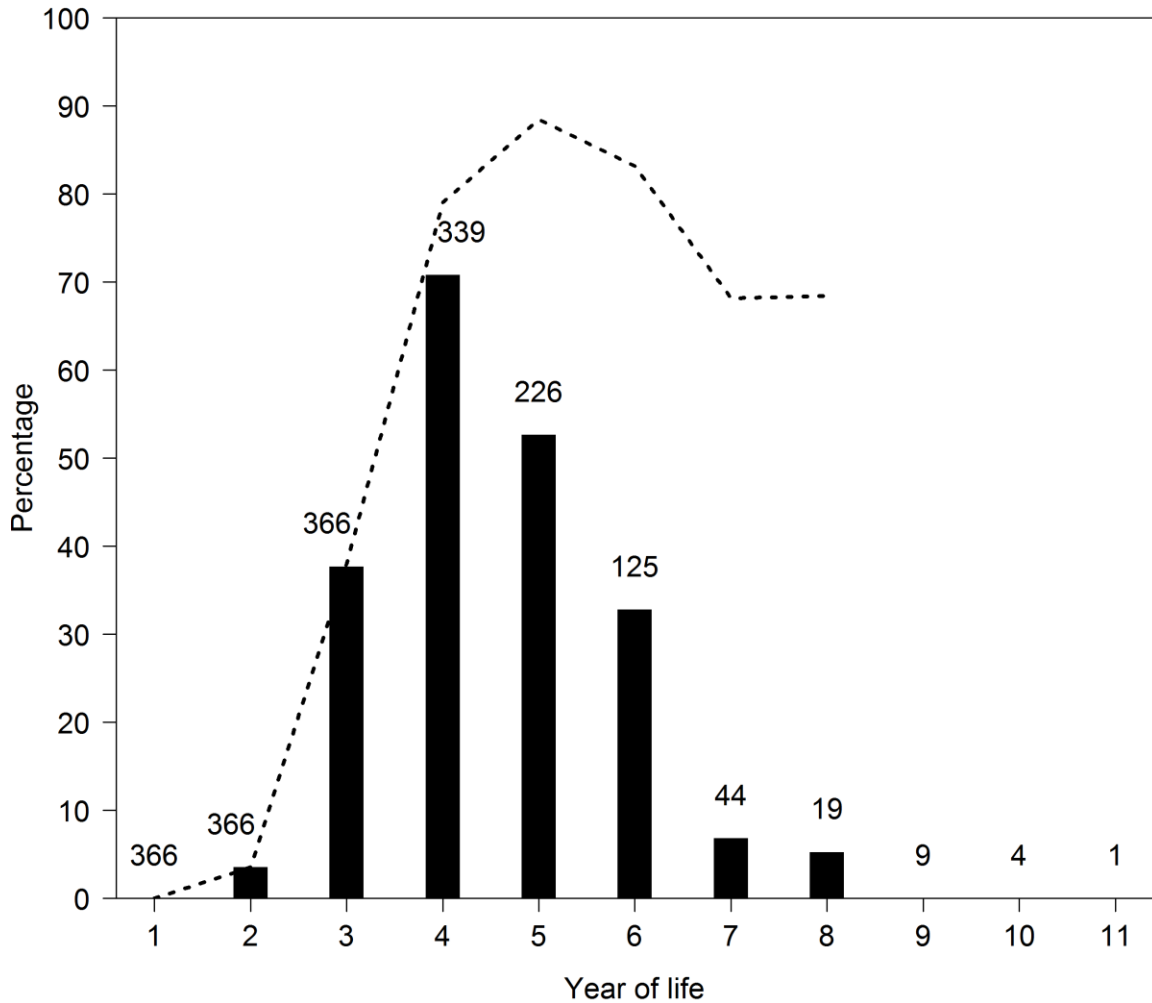


Figure 4.2: The percentage of individual Dolly Varden exhibiting anadromous behavior in each year of life, indicated by vertical bars. Numbers above each bar indicate the number of fish sampled for each age. The dotted line indicates the percentage of fish at each age that had made at least one migration to sea in their life; percentages are not shown for ages with fewer than 10 individuals.

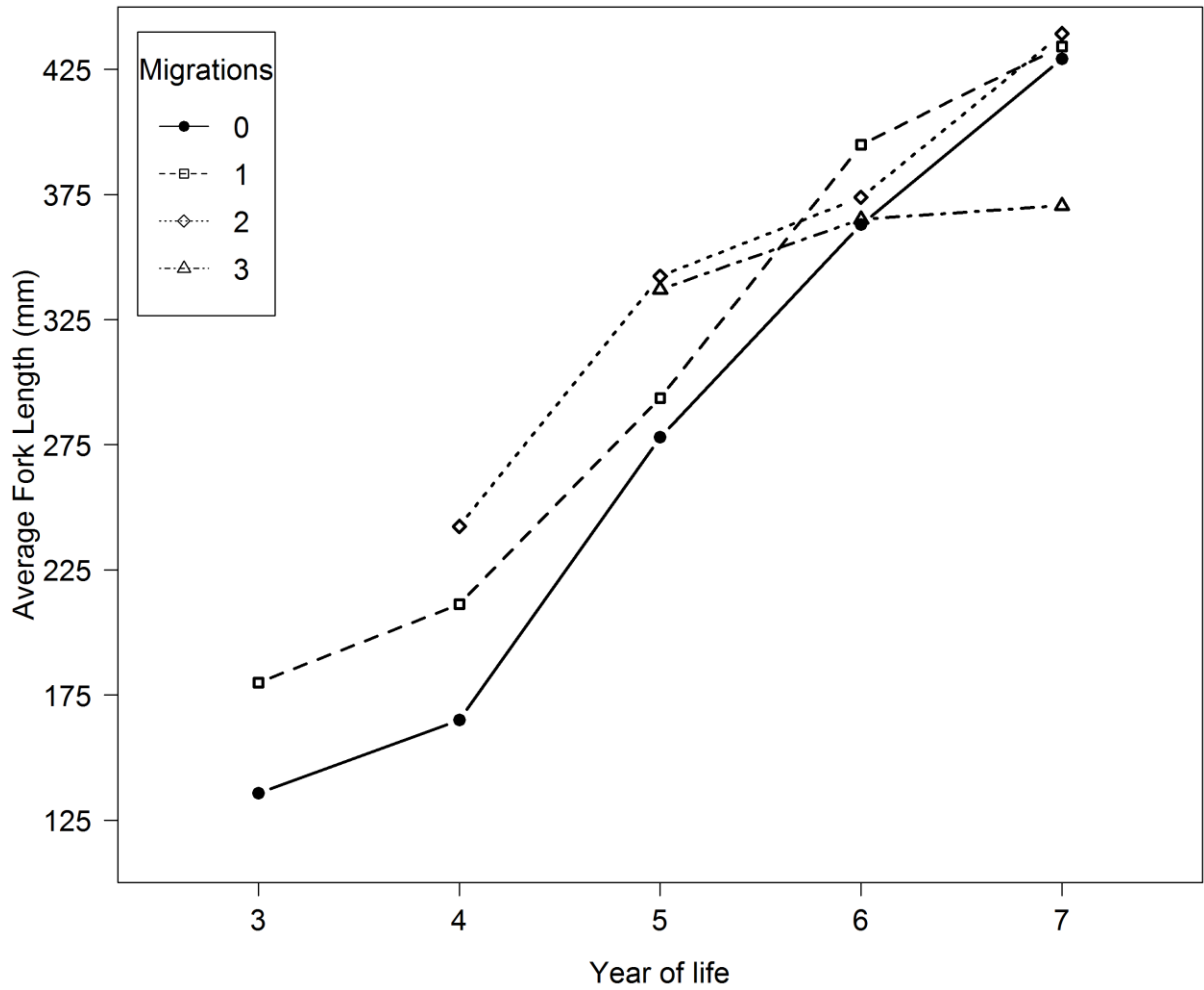


Figure 4.3: Average length at age for Chignik Lakes Dolly Varden with 0, 1, 2, or 3 lifetime migrations to marine waters. Length-age combinations with fewer than 5 individuals were omitted.

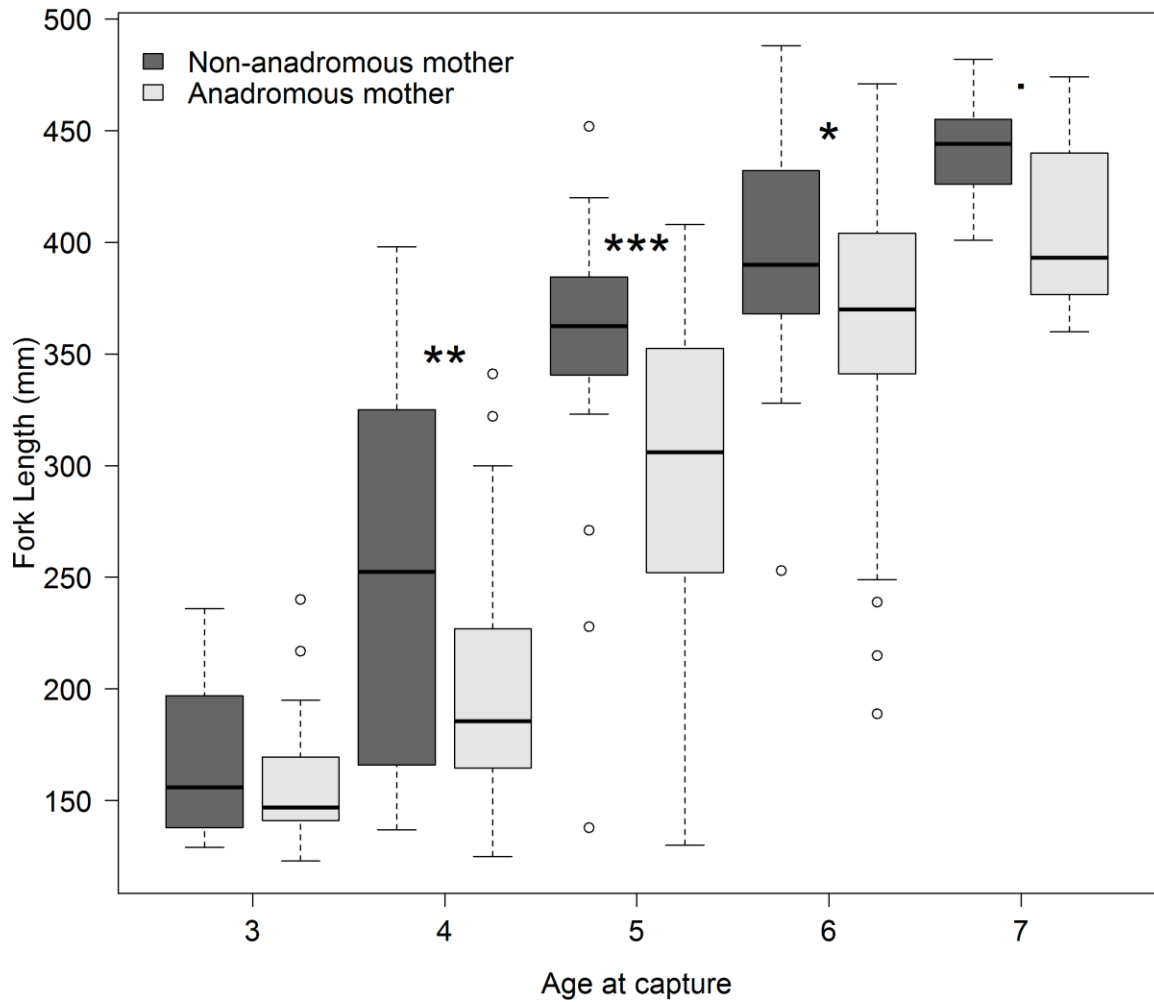


Figure 4.4: Boxplots of length at age for Dolly Varden. Individuals with mothers that migrated to sea (anadromous, in light gray) or did not migrate (non-anadromous, in dark gray) in the year of capture. Symbols indicate significance at the significance level P: . = 0.059, * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001.

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Appendix A: Data sources used for the comparison of run timing across the North American range of anadromous Dolly Varden.

Site	Latitude (°N)	Longitude (°W)	Years of operation	Data source
Anchor R.	59.780	-151.838	1995	Larson 1997
Auke Ck.	58.382	-134.636	1997-2007	Echave 2007, Hoover 2007, 2008, Lum et al. 1999, Lum et al. 2000, Lum et al. 2001, 2002, Lum et al. 1998, Lum and Taylor 2004, 2006a, b, c
Babbage R.	69.232	-138.430	1990-1992	Sandstrom et al. 1997
Big Ck.	58.515	-156.569	2003	Anderson et al. 2004
Buskin R.	57.756	-152.483	2001-2009	Alaska Department of Fish and Game, Kodiak, Alaska
Chignik R.	56.339	-158.574	1996-1999, 2001-2011	Alaska Department of Fish and Game, Kodiak, Alaska
Eva Ck.	57.402	-135.100	1962-1964	Alaska Department of Fish and Game, Division of Sport Fish, Juneau
Frosty Ck.	55.195	-162.854	2000-2002	Cornum et al. 2004
Goodnews R.	59.121	-161.586	1996-2011	U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge, Dillingham, Alaska
Hulahula R.	70.996	-143.372	2006, 2008	U.S. Fish and Wildlife Service, Fairbanks, Alaska
Kanektok R.	59.746	-161.931	2001-2011	U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge, Dillingham, Alaska
Kwiniuk R.	64.697	-162.016	2004-2007	Kent 2006, 2007, Kent et al. 2008, Menard and Kent 2005
Lupine R.	68.718	-147.627	1971	Yoshihara 1972
Niukluk R.	64.596	-163.321	2004-2007	Kent 2006, 2007, Kent et al. 2008, Menard and Kent 2005
Nome R.	64.482	-165.305	2004-2007	Kent 2006, 2007, Kent et al. 2008, Menard and Kent 2005
Pikmiktalik R.	63.238	-162.589	2006	Dunmall and Kroeker 2008, Kroeker and Dunmall 2003, 2005, 2006
Taku R.	58.548	-133.676	1987-1988	McGregor and Clark 1988, 1989
Windfall Ck.	58.526	-134.779	1997	Jones and Harding 1998

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