Beyond dichotomous life histories in partially migrating populations: cessation of anadromy in a long-lived fish

MORGAN H. BOND,[1,3] JESSICA A. MILLER,[2] AND THOMAS P. QUINN[1]

[1]*School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195 USA*
[2]*Coastal Oregon Marine Experiment Station, Hatfield Marine Science Center, Department of Fisheries and Wildlife,
Oregon State University, 2030 SE Marine Science Drive, Newport, Oregon 97365 USA*

Abstract. Across animal taxa, migration allows individuals to exploit habitats and resources that predictably vary seasonally in suitability. Theory predicts that the "decision" to migrate or not is shaped by the relative fitness costs and benefits of exhibiting a given life history. Adoption of a migratory strategy is widely thought to reflect a dichotomous outcome; individuals are either resident or migratory, and continue to exhibit this life history until death. In fishes, anadromy and freshwater residency represents a well-studied life history dichotomy. Resident individuals may adopt a migratory life history later in life, but migratory individuals are not known to abandon this pattern. Here, we investigated the fitness benefits, as measured by body size, of residency and anadromy in a salmonid fish, Dolly Varden, *Salvelinus malma*, in Alaska, and reveal a novel life history: cessation of migration by older, larger individuals. Otolith microchemical analysis of Dolly Varden showed that while most fish migrated to sea at least once in their lives, lifelong resident fish exist in streams with close proximity to the ocean. Moreover, the probability of seaward migration in any year of life decreased annually after an individual's fourth year, and no fish migrated after their eighth year, while the oldest fish were captured in their 11th year. Migration conferred a size advantage in young fish, but the size benefits of marine foraging declined in older fish, at which time fish increasingly "retired from anadromy." Additionally, measurement of both natal otolith chemistry and the gonadosomatic index indicated a continued contribution to lifetime fitness, rather than senescence, in retired individuals. We suggest that the novel life history of reversion to residency by older fish is viable because foraging opportunities are subsidized by the predictable annual supply of energy-rich eggs and carcasses of spawning Pacific salmon.

Key words: *char; charr; diadromy; fitness; life history; partial migration; salmon; subsidy.*

INTRODUCTION

Variation in migratory behavior has been described for many animals 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 (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 trade-offs of migration are even more subtle, and populations may exhibit partial migration, where some individuals migrate whereas others do not. Partial migration may therefore be condition dependent, with population-specific thresholds determining the switch between migratory and nonmigratory life histories (Lundberg 1988, Pulido 2011). The energetic, reproductive, and survival trade-offs that promote migration also favor its annual or seasonal persistence, and nearly all migratory animals continue a cycle of migration for the duration of their lives once they commence migration. Likewise, once resident animals initiate a sedentary life history, they generally do not later commence migrating (Jonsson and Jonsson 1993, Berthold 1999). These lines of evidence have resulted in a paradigm of dichotomous life history pathways in partially migratory populations. However, empirical evidence in birds suggests some thresholds promoting a return to residency after migration (Hockey et al. 2003, Middleton et al. 2006). For example, in some species individuals may develop a large enough body mass that they can fast through times of low food abundance, while smaller individuals are forced to move to less harsh climates (Ketterson and Nolan 1976, Boyle 2008, 2011).

Anadromy is one of the world's most striking migration patterns; fish move regularly between freshwater for spawning and saltwater for rearing, requiring flexible physiology and behavior. Although anadromy is uncommon among fish species (McDowall 1988),

millions of individual shad, salmon, lamprey, sturgeon, and other species make such migrations each year. Even within anadromous fishes there is considerable variation in the timing of migration from freshwater to marine environments, age at migration, or whether to migrate at all (Hendry et al. 2004, Dodson et al. 2013). Migratory diversity is both interspecific, with some species being nearly fixed in their patterns of anadromy (e.g., pink salmon, *Oncorhynchus gorbuscha*), and intraspecific, with differences both among and within populations (e.g., steelhead/rainbow trout, *O. mykiss*; Hutchings and Morris 1985, Quinn and Myers 2004, Pavlov and Savvaitova 2008). Variation in anadromy is often attributed to the magnitude of productivity between marine and freshwater environments, which changes broadly with latitude (Gross 1987, Gross et al. 1988), coupled with the relative survival rates in each habitat. In some salmonids such as *O. masou* and *Salmo salar*, anadromy appears to be determined by large-scale clines in productivity and survival (Hutchings and Jones 1998, Pavlov and Savvaitova 2008, Morita and Nagasawa 2010). In some species migration is displayed by a higher fraction of females than males (Jonsson and Jonsson 1993, Tamate and Maekawa 2004, Rundio et al. 2012), as fitness is more closely linked with increasing body size in females than males (Beacham and Murray 1993, Theriault and Dodson 2003). In contrast, male alternative mating strategies may include both large anadromous, small anadromous, and small freshwater-maturing individuals (Hutchings and Myers 1988). In both sexes, freshwater resident fish are often smaller at each age compared to anadromous individuals from the same populations, owing to the reduced growth potential that northern latitude freshwater habitats generally afford (Pavlov and Savvaitova 2008). The combination of iteroparity and anadromy presents an additional physiological challenge; the bioenergetics of long-distance migration favors large body size (Bernatchez and Dodson 1987), yet fish return from marine migrations to freshwater habitats that may not have adequate food resources to support an abundance of large-bodied individuals. Thus, in order for individuals to maintain a large body size and reproduce year after year, iteroparous anadromous fishes are assumed to continue annual or seasonal movements to marine waters once they are initiated.

In contrast to the idea that individual resource requirements drive continued migration by iteroparous anadromous fish, large individuals have lower mass-specific metabolic requirements than smaller fish (Brett and Glass 1973, Brett 1979), making them suited to long migrations but also allowing them to fast in resource-poor freshwater environments when needed (Bystrom et al. 2006). Fasting allows individuals the opportunity to ascend streams, spawn, and remain in freshwater in high densities until appropriate conditions allow return to marine waters. Fasting comes with a cost, though, as low rates of repeat spawning indicate that some

populations are functionally semelparous (Keefer et al. 2008). However, when provided with a predictable energy-rich, though ephemeral, food resource consisting of salmon eggs and flesh, some larger fish can consume and store enough energy in a few weeks to remain in freshwater until the next spawning season when eggs again become available (Armstrong and Bond 2013). Therefore, we hypothesized that younger, smaller fish may move to sea to forage and grow when water temperatures are warm and metabolic requirements are high, while paradoxically, the largest individuals in a population may binge and fast in the relative safety of freshwater. To the extent that this is true, individuals may switch from migratory to resident behaviors in habitats where reliable resource availability (food and holding habitat) and the energetic efficiencies of large body sizes allow. Here we investigate this potential alternative life history form: cessation of anadromy by formerly migratory individuals.

We reconstructed the lifetime migration histories of Dolly Varden (*Salvelinus malma*, see Plate 1), an iteroparous, facultatively anadromous salmonid in an Alaskan watershed. Previous work in this system revealed a population complex of Dolly Varden that included a wide range of life history and migration patterns, including annual migrations to sea during the summer months for anadromous individuals followed by overwintering in freshwater (Roos 1959, Narver and Dahlberg 1965, Bond and Quinn 2013). Specifically, during summer, fish of a wide and broadly overlapping range of body sizes, including immature and sexually mature individuals, are found simultaneously in both marine and freshwater habitats. Our goal here was to determine whether these patterns were the result of: (1) the presence of distinct migratory and lifelong resident life histories, (2) sex-biased migration, (3) all fish migrating, but not in every year, or (4) cessation of migration by previously anadromous individuals. In addition, we evaluated the growth trade-offs of migration and residency in a system where both modes appear to occur in sympatry.

METHODS

Study site

The Chignik basin in southwestern Alaska drains a 1536-km^2 basin that includes 41-km^2 Black Lake, 25-km^2 Chignik Lake, and a 33-km^2 semi-enclosed lagoon (Fig. 1; Narver and Dahlberg 1965, Simmons et al. 2013). Chignik Lagoon loses ~50% of its wetted area during extreme low tides (~4 m; Narver and Dahlberg 1965, Simmons et al. 2013) 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. 2013). Although all five species of Pacific salmon spawn in the Chignik basin in the late summer and fall, Dolly Varden are the only large-bodied fish species found in nearly every available marine, river, and lake habitat
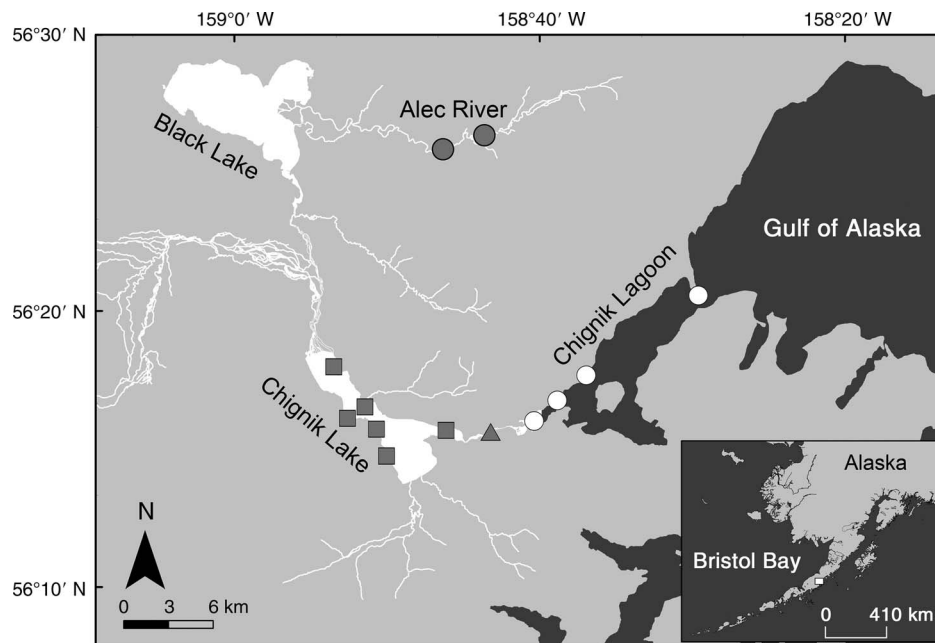
FIG. 1. Map of the Chignik basin depicting: freshwater sampling locations; Chignik River (gray triangle), Chignik Lake (gray squares), Alec River (gray circles), and brackish to marine sampling locations; Chignik Lagoon (white circles).

throughout the summer months (Roos 1959, Narver and Dahlberg 1965).

Dolly Varden collections

We collected Dolly Varden across a range of sizes and several representative habitats in Chignik Lagoon, Chignik River, Chignik Lake, and the Alec River in the summers of 2009–2011. We sampled during June, July, and August because previous work has shown that fish descend to marine waters almost exclusively during the month of May, and re-ascend to freshwater in the fall for spawning (Bond and Quinn 2013). Therefore, sampling outside of the summer months would find all fish in freshwater, regardless of anadromous behavior, further confusing residency and anadromy. Fish were collected twice per month at each site, targeting individuals across the available size range ($\geq$120 mm fork length). In the Alec and Chignik rivers (see Fig. 1), fish were sampled with hook and line. In all other habitats fish were sampled with a 30-m beach seine. Although sampling method can bias a comparison of size distributions, long-term beach seining data from the Chignik basin indicates that the full suite of Dolly Varden sizes larger than young-of-the-year (fry) are susceptible to this method, and much larger adult salmon are regularly captured. Size distribution data from angling can be biased where only some size classes are susceptible to the gear type used. However, extensive sampling throughout southwestern Alaska, including the Chignik basin, indicates that Dolly Varden of all sizes in our target range are readily captured using lures mimicking eggs during the summer salmon spawning

season (Jaecks and Quinn 2014). Upon capture all fish were measured for length, and up to 20 were euthanized in MS-222 (Argent Labs, Redmond, Washington, USA). During beach seine sampling we retained individuals representing the size distribution at each site by counting all captured fish, then removing individuals at even intervals during measurement to ensure that 20 were selected across the available range (e.g., if 60 were captured we retained every third measured fish). During some sampling events fewer than 20 fish were captured, and all were retained. Selected individuals were weighed, and gonads were removed and weighed after sex determination. The saggital otoliths were removed from each individual, rinsed in de-ionized water to remove tissue, and stored dry in individual plastic vials.

Otolith chemical analysis

To quantify the migratory life histories of individuals we used otolith microchemistry. Calcified structures (e.g., teeth, bones, scales, otoliths) that record natural variation in water chemistry are often used to characterize lifetime changes in habitat use by individual fish (Elsdon et al. 2008). Commonly, the ratios of strontium and barium to calcium in otoliths are used (Kraus and Secor 2004), as these elements mimic the environment experienced by a fish in predictable ways (Miller 2009, Phillis et al. 2011). Therefore, an element : calcium history can be created for each otolith, and when combined with age analysis, fish can be assigned to different habitats by age (Campbell et al. 2002). In addition, in waters with low freshwater Sr concentrations ($\leq$5 mmol/mol), maternal anadromy in the season

preceding spawning can be assessed because the otolith core is derived from the maternal environment experienced during vitellogenesis (Riva-Rossi et al. 2007, Donohoe et al. 2008). We employed these otolith microchemistry approaches to evaluate maternal anadromy and reconstruct migratory histories of Dolly Varden that encompassed the size range captured in each habitat.

In the laboratory, one otolith from each individual was sectioned and polished to expose otolith material from core (primordial) to edge (recent) in a single plane for chemical analysis (see Bond et al. 2014a for detailed otolith preparation methods). Life history profiles for each otolith were collected with laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) at the Keck Collaboratory, Oregon State University. A VG PQ ExCell ICPMS (Thermo Fisher Scientific, Waltham, Massachusetts, USA) with a New Wave DUV193 (ESI, Portland, Oregon, USA) excimer laser was used for all analyses of otoliths collected in 2009 and a Thermo X-Series II ICPMS (Thermo Fisher Scientific) and Photon Machines Analyte G2 (Photon Machines, Bozeman, Montana, USA) 193-nm laser was used to analyze otoliths collected in 2010 and 2011. The laser was set at a pulse rate of 7 Hz with a 20-μm ablation spot and traveled at 5 μm/s. We measured Sr, Ba, Zn, and Ca, and used NIST-612 glass to transform ion ratios to elemental ratios and measure the mean percent relative standard deviations for each element (^{43}Ca = 3.9%, ^{86}Sr = 6.9%, ^{138}Ba = 4.6%, and ^{66}Zn = 7.5%). Elemental ratios were converted to molar ratios using the molar mass of each element. Final analyses were computed on the element : Ca in millimoles per mole. A calcium carbonate standard with known concentration (USGS MACS-1) was used to determine the accuracy of the element : Ca ratio (>95% for all element : Ca) 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 from the primordia of each annulus 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 to classify each year of life as anadromous or non-anadromous. Maternal anadromy was assumed when core Sr:Ca ratios were ≥1 mmol/mol 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 primodia was missed in the polishing process, and did not evaluate maternal anadromy for that individual. To classify anadromy, we evaluated the mean Sr:Ca and Ba:Ca ratios across 30 μm spanning the midpoint between each annulus, which represents spring/summer growth. From prior analysis of fish

captured in saltwater (n = 23), and pre-smolts from freshwater (n = 22), values of Sr:Ca > 3 mmol/mol and Ba:Ca < 6 μmol/mol reliably indicated anadromous movements, and values outside this range indicated non-anadromy (Bond 2013).

Prior to identification of age- and length-specific migration patterns, we first determined whether males and females had different growth trajectories and needed to be analyzed separately. We fitted von Bertalanffy growth models (Francis 1988) to our entire data set, estimating parameters of the model: L_∞, the asymptotic average fish length, K, the growth rate coefficient, and t_0, the age at length 0. Then, we fitted separate models estimating each parameter separately for males and females, as well as a single model where all three parameters varied by sex, for a total of seven competing models. All models were fitted using nonlinear least-squares analysis in the R statistical software platform (R Development Core Team 2011) and compared using AIC.

To identify trends in migratory behavior, we determined the percentage of fish that went to the ocean in each year and compared those percentages across all ages. We evaluated the benefits of anadromy, in terms of size at age of capture, by comparing size at capture for fish that had not migrated to individuals with 1–3 previous marine migrations. The variance in length data was unequal among migration groups, so we used the nonparametric Kruskal-Wallis Analysis of Variance (ANOVA). If significant differences were identified, we employed a post hoc multiple comparison test to identify the number of migrations associated with different fish lengths at capture with the R package *pgirmess*, following the method of Seigel and Castellan (1988). By including only the migration number, total age, and capture length of each fish, we ensured that our conclusions did not rely on back-calculated fish lengths. Back-calculated results may suffer from a poor relationship between fish length and otolith size as well as issues of nonindependence. Finally, we evaluated the presence of lifelong residents as the number of fish that had not been to sea, and were also older than the maximum observed age at first migration. Younger fish may become lifelong residents, but their behavior cannot be predicted; thus younger fish were excluded from this analysis. The sex ratio of anadromous and lifelong resident fish was then evaluated for deviation from 50:50 using a proportion test in R.

Spawning activity

To estimate whether formerly migratory females became senescent or continued to breed following cessation of migration, we evaluated the gonadosomatic index (GSI: gonad mass as a percent of total body mass) for individuals captured in August, the sampling month nearest the fall spawning period, as spawning occurs in late September and October. We compared their GSI to those of known anadromous spawners captured during

TABLE 1. The capture location and number (n), length ($\pm$SD), and age ($\pm$SD) of fish analyzed for life history patterns with otolith microchemistry in the Chignik basin.

Location	n	Fork length (mm)	Average age	Retired (%)	Lifelong resident (%)
Alec River	124	401.5 ($\pm$66.0)	6.0 ($\pm$1.4)	92.7	17.9
Chignik Lake	55	215.8 ($\pm$85.0)	4.1 ($\pm$0.9)	17.3	0
Chignik River	58	336.9 ($\pm$74.9)	5.4 ($\pm$1.2)	16.3	24.0
Chignik Lagoon	129	230.2 ($\pm$74.0)	4.5 ($\pm$0.9)	N/A	N/A

Notes: Retired (%) indicates the percentage of all fish captured that had been to sea at least once, followed by a year or more of residence in freshwater. Lifelong resident (%) indicates the percentage of fish age 6 or older from each location that had never been to sea. Fish from the lagoon are captured in saltwater and cannot be retired or resident, as indicated with an N/A.

August in Hood Bay Creek, Alaska, during an extensive study of Dolly Varden reproduction (Blackett 1968). The GSI of Chignik basin Dolly Varden falling within the range of known spawners from Blackett (1968) were assumed to be preparing to spawn in the months following capture, while those with a GSI lower than those found in Hood Bay Creek were assumed to be either skip spawners or senescent.

RESULTS

A total of 2964 Dolly Varden were captured and measured in 2009–2011 (Table 1, Fig. 2). Preliminary analysis in 2009 indicated that most fish did not initiate marine migration until age 3 or older. Therefore, fish older than age 2 ($\sim$120 mm fork length) were retained for otolith chemical analysis. However, some fish ($\sim$5%) had broken or vateritic otoliths that rendered them unreadable and were removed from further analyses. Usable otoliths were analyzed from 366 fish with LA-ICP-MS to reconstruct lifetime migration histories, which were reduced to a 1 (migration) and 0 (non-migration) for each year of life (e.g., Fig. 3).

Anadromy and residency

Analysis of fitted von Bertalanffy growth models indicated that the common model, where L_∞, K, and t_0 did not vary with sex was the most likely model (Δ AIC = 0). The next most likely model indicated only a
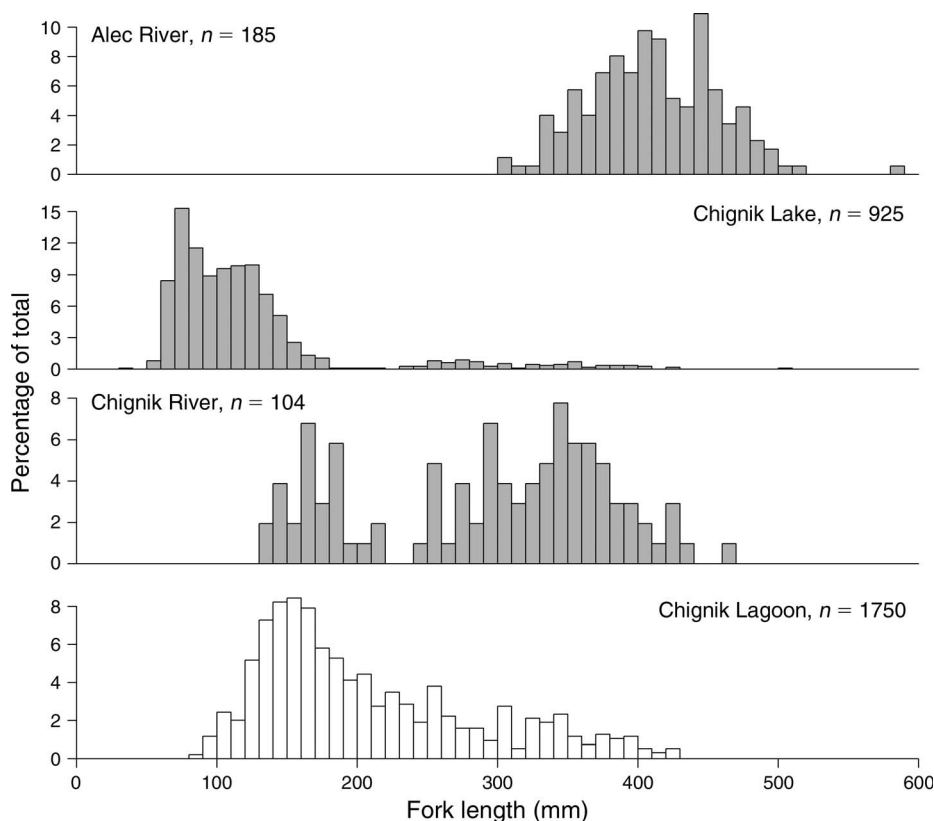

FIG. 2. Length frequency and sample size of Dolly Varden measured in freshwater (gray bars, Alec River, Chignik Lake, Chignik River), and saltwater (white bars, Chignik Lagoon) habitats from 2009 to 2011.
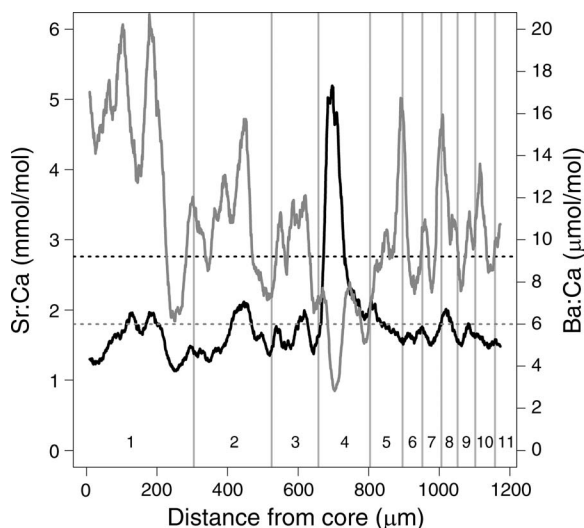
FIG. 3. An example of microchemistry plot from a 425-mm FL Dolly Varden captured in the Alec River. The running average of $Sr \cdot Ca^{-1}$ is shown in black and $Ba \cdot Ca^{-1}$ in gray. Vertical lines indicate winter annuli, and numbers between annuli indicate the year of life. A single ocean migration occurred during the fourth year of life, followed by 6+ years of residence in freshwater and capture in the 11th year. Low Sr:Ca values near the origin indicate that this fish's mother had not been to sea in the year of spawning. Sample values were required to both exceed the $Sr \cdot Ca^{-1}$ threshold and fall below $Br \cdot Ca^{-1}$ threshold (black and gray dotted horizontal lines, respectively) to be considered anadromous; this occurred only during the fourth year of life in this fish.

common t_0 (Δ AIC = 1.73), but estimated two additional parameters, so we concluded that the simpler common model best fit the data. In addition, the distribution of ages at first migration, for all migratory individuals, did not differ between the sexes, χ^2 (3, $N = 306$) = 3.45, $P = 0.33$. Accordingly, sexes were pooled for further analyses of age at migration. Of the 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 year of life. No individuals of any age made their *first* marine migration after their fifth year, so all fish six years or older with no previous marine migrations were assumed to be lifelong residents. These lifelong residents comprised 18.9% of all 6+ year-old fish collected in freshwater (20 of 106). By region, 17.9% (14 of 78) of Alec River fish and 24.0% (6 of 25) of Chignik River fish were lifelong residents. The presence of lifelong resident fish in the Chignik River indicated a nonmigratory strategy in fish only 3 km from saltwater (Fig. 1).

Sex-biased migration

Of the 20 life-long residents (9 males and 11 females) there was no significant deviation from a 50:50 sex ratio χ^2(1, $N = 20$) = 0.2, $P = 0.65$. Likewise, there was no significant sex bias of fish captured in saltwater habitats (70 female, 59 male), χ^2(1, $N = 129$) = 0.77, $P = 0.54$.

Variation in migration by age and cessation of migratory behavior

The percentage of fish sampled that had been to sea in each year of life increased with age, from 0% of individuals in their first year of life, to an overall maximum of 71% of individuals migrating in their fourth year of life (Fig. 4). However, consistent among all ages at capture, the probability of marine migration declined after the fourth year of life, such that only 6.8% migrated after their sixth year of life, even though nearly all these fish had gone to sea at least once earlier in their lives. Likewise, no fish migrated to sea after its eighth year of life. Thus, larger-bodied fish in freshwater during the summer months were a combination of lifelong resident fish, and formerly migratory individuals. Additionally, all fish making more than one migration did so in consecutive years. Pooling the number of years in freshwater over all the formerly migratory fish, we observed 480 fish-years of resident behavior following cessation of anadromy, and did not detect the resumption of migratory behavior in any fish. Therefore, there were no instances of "skipped migrations" where individuals remained in freshwater for one or more years before resuming migratory behavior.

Body size and reproduction

Anadromy conferred a size advantage for younger individuals, but the body size of anadromous and lifelong resident fish converged later in life. Anadromous Dolly Varden in their third (H(1) = 9.37, $P < 0.01$, difference = 9.21 mm) and fourth (H(2) = 25.53, $P < 0.001$, difference = 30.36 mm and 46.94 mm for one and two migrations, respectively) years of life were larger than non-anadromous fish of the same age (Fig. 5). However, anadromous fish in the fifth (H(3) = 4.52, $P = 0.21$), sixth (H(3) = 3.00, $P = 0.39$), and seventh (H(2) = 0.08, $P = 0.95$) years of life, with one to three migrations to sea, were not significantly larger than non-anadromous individuals of the same age.

Most formerly migratory females (30 of 34) had August gonad development (GSI average, 3.58; range, 1.5–6.7) consistent with other measurements of Dolly Varden spawning in the season of capture (GSI range, 1.1–7.8, from Blackett 1968), indicating the initiation of sexual maturation in formerly migratory females. The remaining 11% (4 of 34) of nonmigratory, formerly anadromous females captured in August had GSI values <1%, indicating that some females were either skipping a spawning season or were senescent. All four putative skip-spawning females were returning from their second consecutive marine migration, and were similar in length at age and mass at length, than were individuals with a larger GSI.

Otolith core material was clearly identified in 265 of 366 analyzed otoliths. In the remainder, elevated Zn, or ambiguous Sr signatures indicated possible grinding error that missed all or part of the embryonic region; these were removed from further analysis. Of those that
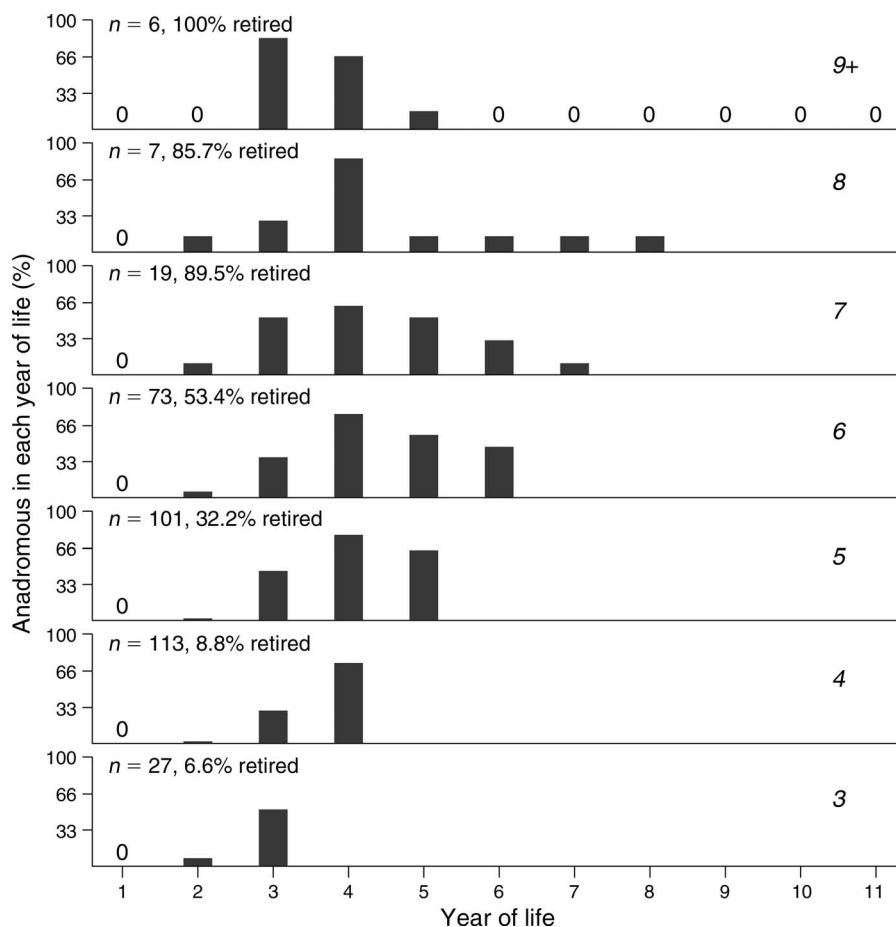
FIG. 4. The percentage of Dolly Varden exhibiting anadromous behavior in each year of life as indicated by otolith microchemistry, by total age at capture (shown as large italic numbers). Zeroes indicate years of life in which no fish of that age migrated to marine waters. "Retired" migrants indicates the percentage of previously migratory fish at each age at capture that have retired, returning to a resident life history following one or more migrations. To prevent bias, lifelong residents ($n = 20$) are excluded from this plot.

were identifiable, most (166; 62.6%) showed clear maternal anadromy, but in the remainder (99; 37.4%) their mother had apparently remained in freshwater in the season prior to spawning χ^2 (1, $N = 265$) $= 16.44$, $P \ll 0.001$. Among the 16 lifelong resident fish ($\geq$age 6 with no migrations), 6 had anadromous mothers, while 10 had mothers that had not been to sea in the year prior to spawning.

DISCUSSION

Here, we describe a novel life history for anadromous fishes; migration occurred at intermediate ages, whereas the youngest and oldest individuals were nonmigratory. Initiation of migration generally occurred after several years of residence in freshwater, and this is common in anadromous fishes (Quinn 2005). However, the return to residency in the oldest, largest individuals is the unusual pattern in this system. It is likely that the extreme caloric subsidy provided by salmon eggs and flesh during the spawning season permitted older, larger fish to remain in an otherwise low-growth environment rather than

continuing annual migrations. In addition, the size advantage of migratory fish over similarly aged lifelong resident fish was only significant at ages 3 and 4, after which their body sizes were similar, irrespective of the number of lifetime marine migrations. Similarly, the sex ratio did not differ from 50:50 among anadromous or migrant fish, indicating that there was no observed gender bias in the benefit of anadromy. We thus found evidence consistent with predictions that migration is shaped by fitness costs and benefits; individuals showed an increasing tendency to abandon migratory behavior with each passing year after the size advantage of migration declined after age 4.

Cessation of migratory behavior

The patterns of age-specific migration unequivocally confirmed that Chignik basin Dolly Varden are partially anadromous. Although most individuals made at least one migration to saltwater, some lifelong resident individuals were sampled in very close proximity to saltwater. Therefore, residency did not reflect physical
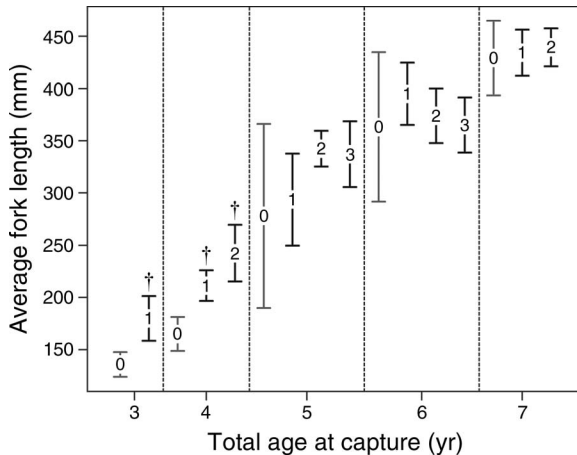
FIG. 5. Average fork length (±SD) at total age of capture for Chignik basin Dolly Varden with 0 (gray), 1, 2, or 3 lifetime migrations (black) to marine waters. Daggers (†) indicate a size at age for anadromous fish that is significantly larger than fish with no lifetime migrations at the same age, from nonparametric pairwise comparisons. Length–age–migration number combinations with fewer than five individuals were omitted from this analysis.

barriers or energetic challenges to migration. Consistent with other studies on this species (Armstrong and Morrow 1980), most anadromous fish made their first migration to sea in their third or fourth year of life, possibly a consequence of poor osmoregulation in seawater by smaller, younger char (Finstad et al. 1989) or other size-selective mortality risk (Yamamoto et al. 1999). However, the decreasing incidence of anadromy after the fourth year of life, and near complete cessation of migration by the seventh year, was unexpected and to our knowledge a novel life history in salmonids, and rare among migratory animals. In other iteroparous anadromous fishes, age at first migration may vary, but individuals do not revert to residency following the initiation of migratory behavior. The life history we describe is distinct from the observations of anadromous brown trout (*Salmo trutta*) and Atlantic salmon overwintering in freshwater following spawning if conditions allow, as these fish resume seaward migrations the following spring (Jonsson and Jonsson 2011). Arctic char also migrate annually once this life history 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 one and as many as five years respectively, before resuming migration (Swanson et al. 2010), but there is no evidence that these fish abandon migration entirely.

Benefits of switching migratory behaviors

Growth in northern marine environments is often faster than that in freshwater habitats, and the length and mass of anadromous fish may quickly exceed freshwater residents of similar age (Hutchings and Morris 1985). However, for species that make annual migrations, populations may incur high rates of marine mortality, even among larger-bodied repeat migrants (Berg and Jonsson 1990). In contrast, watersheds with abundant spawning salmon may offer foraging rates for resident fishes (Denton et al. 2010, Armstrong and Bond 2013) that temporarily equal or surpass those of similar fish in the marine environment (Brodeur et al. 2007), without incurring the higher risk of mortality associated with marine habitats. The ephemeral but extreme abundance of salmon eggs in freshwater favors residency among those that can capitalize upon it, such that marine movements are not necessary for somatic maintenance and reproduction (Armstrong and Bond 2013). Over the last 20 years, the sockeye salmon (*O. nerka*) escapement in the Chignik basin has averaged ~760 000 (Witteveen et al. 2007). However, the majority of sockeye salmon spawn in a ~15-km section of the Alec River; producing high spawner densities that make eggs freely available to the larger-bodied Dolly Varden found there (Moore et al. 2008). In fact, fish smaller than 300 mm FL were conspicuously absent from the Alec River during any sampling month, yet smaller Dolly Varden in other parts of the watershed and elsewhere (Jaecks and Quinn 2014) are readily caught by angling using lures that mimic salmon eggs, so their absence in the Alec River samples was not likely a result of sampling method bias. Both snorkel (M. H. Bond, *unpublished data*), and electrofishing surveys (Bond et al. 2014b), in the Alec River found only young-of-the-year (≤50 mm FL) and large (>300 mm FL) individuals. Therefore, intermediate-sized Dolly Varden may be using lake or marine environments during the summer months, a theory supported by another study of Dolly Varden in rivers (Jaecks 2010).

We propose that Dolly Varden in the Chignik basin and other watersheds with abundant salmon subsidies may revert to residency because they have large energetic reserves relative to their basal metabolic rate (Armstrong and Bond 2013). The body size hypothesis, that larger individuals can sustain greater levels of fasting and need not migrate, has been proposed (Ketterson and Nolan 1976, 1983) and evaluated in birds (Boyle 2008), but not anadromous fish. However, 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, Biro et al. 2003, Brodersen et al. 2008). Although we do not have comprehensive temperature data for the Chignik basin, water temperatures near 6°C are found in the Alec River for ~9 months of the year (Armstrong and Bond 2013), and the Alec River is on average 3°–4°C cooler than Black Lake, immediately downstream (Griffiths et al. 2011). As the largest source river in the system, the Alec

PLATE 1.   Dolly Varden (*Salvelinus malma*) in a southwestern Alaska stream. Photo credit: M. H. Bond.

River may provide the thermal refuge required for fasting fish.

Anadromous Dolly Varden in the Chignik basin only had a size advantage over lifelong resident individuals in their third and fourth years. In subsequent years, the size of individuals was not related to the number of migrations, indicating that lifelong resident individuals may grow as large as anadromous fish, although it may take a year or two longer to do so. Therefore, the benefit of anadromy may be manifested as younger maturity and higher lifetime fecundity (Hutchings and Morris 1985, Fleming and Gross 1990) rather than greater maximum size for migrating individuals. Once near-maximum size has been reached, the net fitness benefits of continued migration may be reduced by the mortality risk in the marine environment. This finding is in stark contrast to the patterns observed in comparisons of Dolly Varden above and below barriers, where non-anadromous fish are smaller and less fecund (Blackett 1968).

Increasing female fecundity with body size indicates that females generally have more to gain from remaining in high-growth marine environments, despite the mortality risk that such environments may entail (Hutchings and Morris 1985, Fleming and Gross 1990). Likewise, many studies have found a strong male bias in resident fish within partially migrating salmonid populations (Jonsson and Jonsson 1993, Rundio et al. 2012). The prevalence of non-anadromous males may result, in part, from alternative reproductive tactics: display and aggression favoring large males, and sneaking fertilizations favoring small males (Fleming and Reynolds 2004). Despite these predictions and evidence elsewhere, we found no male bias in lifelong resident Dolly Varden in the Chignik basin, indicating that the advantages of migration are not as pronounced as they are in other watersheds or other species. A size-selective fishery in saltwater that removes large individuals during their marine phase, could shift the cost of marine residence such that only smaller, younger individuals migrate, as we have observed. However, the commercial sockeye salmon purse-seine fishery in Chignik Lagoon removes few Dolly Varden as bycatch, and recreational or subsistence fishing for Dolly Varden is minimal. Therefore, anthropogenic influences on survival are not likely responsible for the size distributions we observe.

Implications of migration cessation and altered subsidies

Although this is the first documentation of switching migratory behavior in an anadromous fish, the conditions we describe are not unique to the Chignik basin. Putative resident fish co-exist with large runs of semelparous fish throughout the Pacific Rim, and in some cases resident fish may be formerly anadromous individuals. Although population estimates for Dolly Varden in the Chignik basin are not available, the large percentage of fish (~40%) whose mothers had not been to sea in the year of spawning, coupled with the relatively low incidence of lifelong resident fish (~18%), indicate that either formerly migratory fish comprise a substantial portion of the spawning population, or lifelong resident females are more successful at producing offspring. The latter is not likely, as lifelong residents are no larger than their anadromous or retired counterparts. In addition, considerable midsummer

gonad development indicates that most formerly migratory individuals continue to spawn annually.

In other systems resident and anadromous individuals may be afforded different levels of statutory protection (e.g., status under the U.S. Endangered Species Act) or managed separately in terms of fishing regulations. However, cessation of migration to sea by formerly migratory fish (i.e., "retirement from anadromy") confounds the use of otolith microchemistry to determine the fraction of juveniles produced by anadromous mothers (Zimmerman and Reeves 2000, Donohoe et al. 2008, Zimmerman et al. 2009). The offspring of such females could not be distinguished from the offspring of females that had never been to sea. Therefore, in cases where a reversion to residency is possible, knowledge of life-cycle migration history for adults in addition to analysis of maternal anadromy in juveniles is warranted.

The incidence of lifelong 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. In other systems, the weak or undetectable genetic differentiation between sympatric resident and anadromous individuals (Olsen et al. 2006, Johnson et al. 2010), coupled with much stronger differentiation among spawning areas (e.g., streams, rivers, lakes, etc.) indicates phenotypic plasticity likely maintains variation in migratory behavior in many species (Jonsson and Jonsson 1993), though not all (Wood and Foote 1996). Although the reaction norm for migratory behavior is itself under selection, the condition-dependent migratory model allows for both rapid behavioral 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, Hutchings 2011).

The maintenance of the migrant-turned-resident life history we describe likely requires an adequate, temporally reliable, supply of salmon eggs to persist (Armstrong and Bond 2013). However, the availability of eggs responds nonlinearly to the number of salmon in the system (Essington et al. 2000, Moore et al. 2008). In watersheds with unsuitable environmental conditions (e.g., high midsummer temperatures), or where salmon subsidies have been reduced, only discrete migratory strategies may exist: large-bodied anadromous fish that migrate annually, or small, resident fish that are longer lived, but have lower annual fecundity. Challenges arise if poor freshwater resource availability leaves anadromy as the only viable life history while habitat fragmentation precludes the expression of that life history. Therefore, the changes in the magnitude or reliability of resource pulses that have been observed in many salmon-bearing streams (Nehlsen et al. 1991, Gustafson et al. 2007) have implications for anadromy and the population dynamics of species whose life history is centered on those subsidies and connectivity between the marine and freshwater environments.

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