

Patterns and influences on Dolly Varden migratory timing in the Chignik Lakes, Alaska, and comparison of populations throughout the northeastern Pacific and Arctic oceans

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Abstract: Dolly Varden (*Salvelinus malma*) are a facultatively anadromous salmonid common around much of the North Pacific Rim, but little is known about the environmental factors affecting the timing and diversity of their migration. We combined telemetry of anadromous fish with long-term monitoring of Dolly Varden upstream migration timing and environmental data in the Chignik Lakes watershed in Alaska and then compared the timing data with that of other streams where only count data were available. Telemetry revealed two upstream migration modes: midsummer and late fall at the Chignik Lakes. Weir counts indicated that timing fluctuated markedly over the monitoring period (1996–2011) and was negatively correlated with June sea surface temperature. The relationship between sea surface temperature and migration timing in other watersheds with long-term records was as follows: negative (Buskin River), positive (Auke Creek), or nonexistent (Goodnews and Kanektok rivers). Among 18 streams and rivers throughout the eastern Pacific range of Dolly Varden, median upstream migration date increased with latitude. Overall, Dolly Varden migration timing is more variable, protracted, and more strongly influenced by local sea surface temperatures than is typical of semelparous salmonids. These results are likely indicative of other iteroparous salmonids in Pacific waters that share similar environments and life-history characteristics.

Résumé : Si le dolly varden (*Salvelinus malma*) est un salmonidé anadrome facultatif répandu dans le Pacifique Nord, les facteurs environnementaux qui influent sur le moment et la diversité de sa migration demeurent méconnus. Nous avons combiné le suivi télémétrique de poissons anadromes à la surveillance à long terme du moment de la montaison et de données environnementales dans le bassin versant des lacs Chignik, en Alaska, puis comparé les données temporelles aux données relatives à d'autres cours d'eau pour lesquels seules des données de dénombrement étaient disponibles. La télémétrie a mis au jour deux modes de montaison aux lacs Chignik, soit une montaison au milieu de l'été et une autre vers la fin de l'automne, et les dénombrements aux barrières indiquent une variabilité considérable du moment de la montaison durant la période de surveillance (1996–2011) et une corrélation négative de ce paramètre avec la température de la surface de la mer en juin. La relation entre la surface de la mer et le moment de la migration dans d'autres bassins versants pour lesquels des données à long terme sont disponibles s'établissait comme suit : négative (rivière Buskin), positive (ruisseau Auke) et non existante (rivières Goodnews et Kanektok). Pour 18 ruisseaux et rivières recensés dans l'aire de répartition du dolly varden dans le Pacifique oriental, plus la latitude est élevée, plus la date de montaison médiane était tardive. Dans l'ensemble, le moment de la migration des dolly varden est plus variable, prolongé et fortement influencé par la surface de la mer locale que celui des salmonidés semelpares typiques. Ces résultats indiquent vraisemblablement la présence d'autres salmonidés itéropares dans les eaux du Pacifique vivant dans des milieux semblables et présentant des caractéristiques du cycle biologique similaires. [Traduit par la Rédaction]

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 (*Oncorhynchus mykiss*) and Atlantic salmon (*Salmo salar*) also return almost exclusively for reproduction as their feeding in fresh water as postmigratory adults is limited (Johansen 2001). However, for other iteroparous salmonids (e.g., cutthroat trout (*Oncorhynchus clarkii*), bull trout (*Salvelinus confluentus*), Arctic char (*Salvelinus alpinus*), Dolly Varden (*Salvelinus malma*), and brown trout (*Salmo trutta*)), anadromy is often more complicated (Armstrong 1984;

Swanson et al. 2010; 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 fresh water 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

Received 23 September 2012. Accepted 27 January 2013.

Paper handled by Associate Editor Bror Jonsson.

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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 (*Oncorhynchus nerka*), Chinook (*Oncorhynchus tshawytscha*), and 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 years), 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, 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 with 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 fresh water (Armstrong and Morrow 1980), allowing them to feed on the eggs and flesh of senescent Pacific salmon, followed by spawning and overwintering in fresh water (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 (*Oncorhynchus 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 with that of passage counts of Dolly Varden and also with that of co-occurring sockeye and Chinook at a weir located in the upper limit of the 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 (approximately 56°N–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 five watersheds with long-term (≥ 10 years) weir count data.

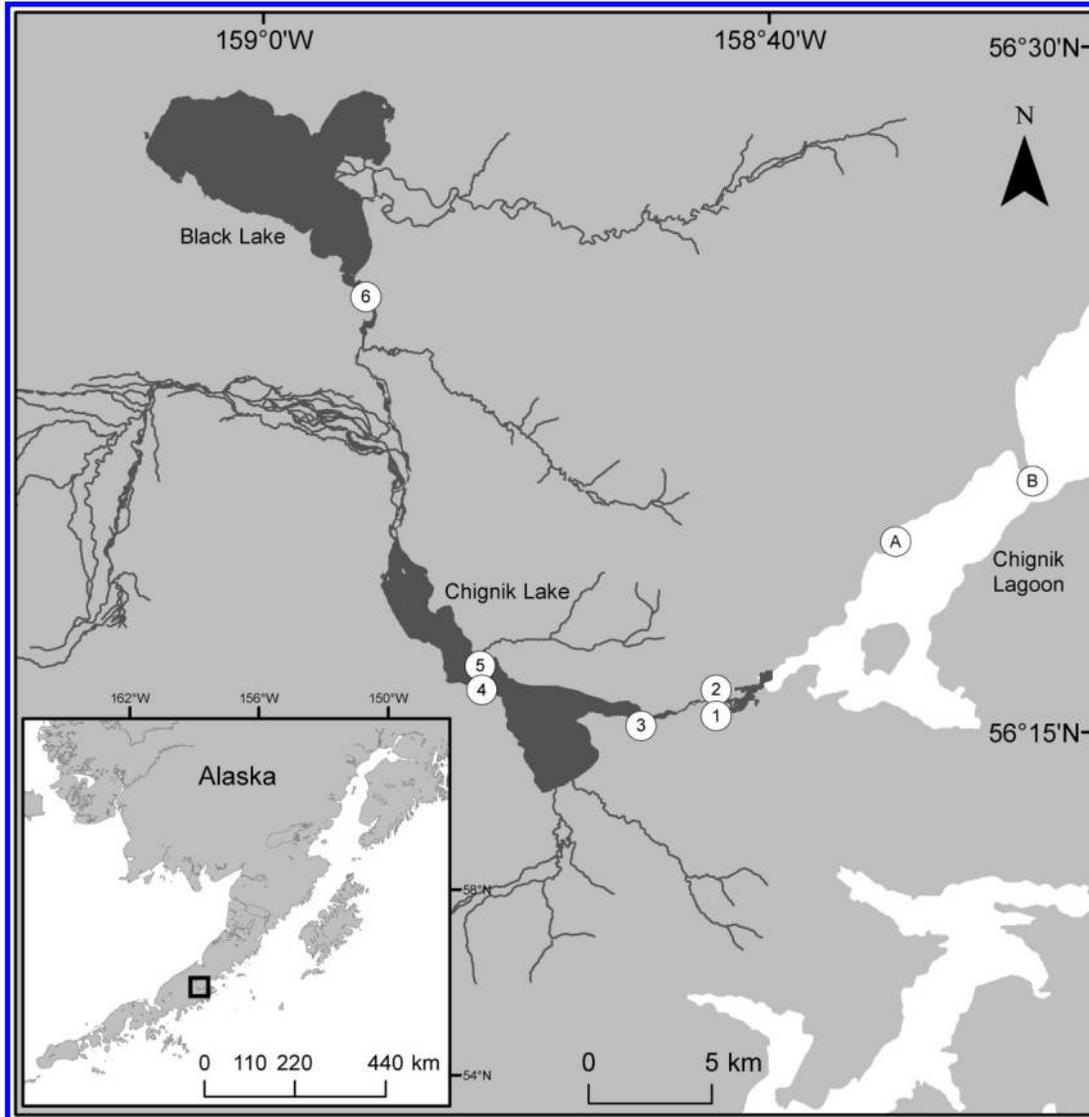
Materials and methods

Dolly Varden migration timing in the Chignik Lakes

Close examination of Dolly Varden migration was conducted in the Chignik Lakes watershed on the Alaska Peninsula (Fig. 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 has been counting adult Dolly Varden ascending Chignik River through a weir (Fig. 1) during summer months (ca. 24 May – 4 September) since 1996, concurrent with the migrations of sockeye and Chinook. 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 (~15 km), semi-enclosed estuary that varies in salinity from fresh water where the Chignik River enters to full seawater (~32‰) near its opening to the sea (Simmons et al. 2013). The lagoon is generally shallow and loses nearly half of its wetted surface area during extreme tidal exchanges (~4 m) (Narver and Dahlberg 1965; Simmons et al. 2013).

We used acoustic telemetry to identify upstream migration timing of anadromous individuals. The V9-2L transmitter (69 kHz, 60 s nominal ping rate; Vemco Inc., Shad Bay, Nova Scotia, Canada) was chosen to optimize the balance between small size and battery life. Under ideal conditions, V-9L 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, and 198) in two locations (Fig. 1) in Chignik Lagoon (salinity ~30‰) in 2008, and one date in 2009 (DOY 217). Fish with >300 mm fork length were selected to increase postsurgery survival and decrease tagging effects; fish with visible injuries or scale loss were avoided. Each selected fish was anesthetized in buffered MS-222 (tricaine methanesulphonate, 10 mg·L⁻¹) until equilibrium was lost and measured for length and mass. A small incision (~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

Fig. 1. Locations of acoustic tagging 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 2008–2009 only. Dark grey indicates freshwater portions of the system, whereas white indicates marine areas.



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 2008 to detect tagged fish (Fig. 1). Because of shallowness, extensive dewatering at low tide, and ice scour, no receivers were placed in the lagoon. Data were recovered in the 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 fresh water, overwinter freshwater duration, timing of downstream migration, and speed of migration through riverine and

lacustrine portions of the migration route in kilometres per hour ($\text{km}\cdot\text{h}^{-1}$) and body lengths per second ($\text{BL}\cdot\text{s}^{-1}$). 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 2h20min (range 2h–2h34min) after the published high and low tides for Kodiak Island, Alaska (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 the Chignik Lakes, we compared the median arrival date, as well as the spread in arrival timing, of Dolly Varden, sockeye, and Chinook over 16 years of data. The Alaska Department of Fish and Game weir operators use a video monitoring system to count all upstream moving salmonids passing through two openings in the

Table 1. Rivers and streams with published upstream Dolly Varden passage counts.

Site No.	Site	Latitude (°N)	Longitude (°W)	Count type	Years of operation	Mean total count*	Mean no. of counting days	Mean median migration DOY	Average start DOY	Average end DOY
1	Eva Creek	57.402	135.100	Weir	1962–1964	77 286	220	214	97	324
2	Taku River	58.548	133.676	Fish wheel	1987–1988	818	115	198	149	263
3	Auke Creek	58.382	134.636	Weir	1997–2007	3 716	130	246	179	308
4	Windfall Creek	58.526	134.779	Weir	1997	3 901	130	202	100	229
5	Anchor River	59.780	151.838	Weir	1995	10 994	43	200	185	227
6	Buskin River	57.756	152.483	Weir	2001–2009	9 923	124	194	146	272
7	Chignik River	56.336	158.574	Weir	1996–1999, 2001–2011	17 610	95	193	149	243
8	Frosty Creek	55.195	162.854	Weir	2000–2002	2 550	116	217	180	295
9	Big Creek	58.515	156.569	Weir	2003	4 901	99	201	177	275
10	Goodnews River	59.121	161.586	Weir	1996–2011	2 662	78	204	178	255
11	Kanektok River	59.746	161.931	Weir	2001–2011	16 854	62	206	186	247
12	Pikmiktalik River	63.238	162.589	Weir	2006	897	72	184	184	243
13	Kwiniuk River	64.697	162.016	Weir	2004–2007	5 880	86	225	171	256
14	Niukluk River	64.596	163.321	Weir	2004–2007	1 837	72	222	179	251
15	Nome River	64.482	165.305	Weir	2004–2007	2 490	69	226	184	252
16	Lupine River	68.718	147.627	Weir	1971	628	59	236	190	259
17	Hulahula River	70.996	143.372	Acoustic camera	2006, 2008	13 967	51	244	213	263
18	Babbage River	69.232	138.430	Weir	1990–1992	5 573	51	230	207	257

Note: DOY indicates day of the year from 1 January.

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

weir for the first 10 min 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, we used the daily catch in the Chignik salmon fishery and escapement estimates (Todd Anderson, Alaska Department of Fish and Game, Kodiak, Alaska, unpublished data) from the first day of weir operation until 4 July each year, which comprises the large early run of sockeye (Chasco et al. 2007). The entire annual data set 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:

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

where t is the counting DOY (from 1 January), 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 following equation:

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

where t is the counting DOY, 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

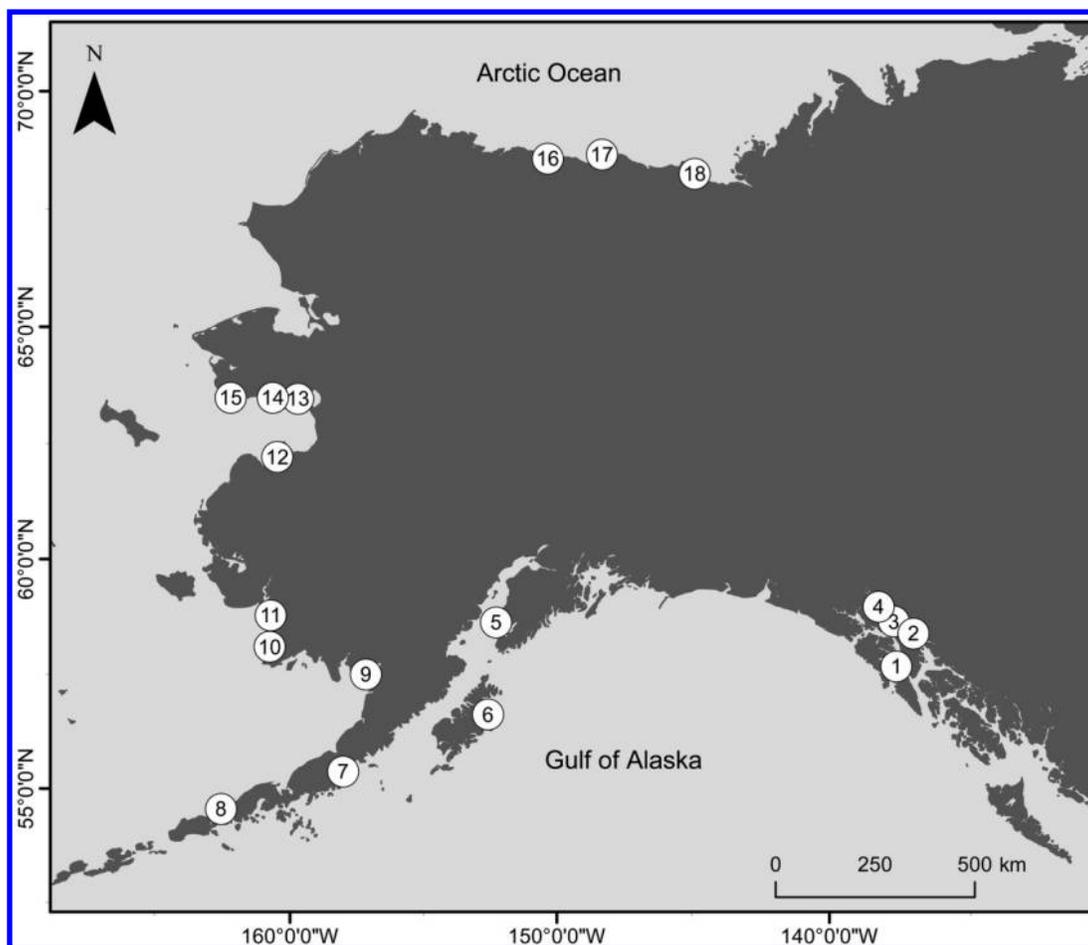
To compare Dolly Varden migration timing in the Chignik Lakes with other drainages in the eastern Pacific, we compiled records of Dolly Varden passage counts from weirs and fences throughout the range in Alaska and British Columbia (Table 1; Fig. 2). From these data, we calculated the median DOY of upstream 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 5 days of weir operation (i.e., inadequate sampling period) and cases where <500 fish returned 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 data set contained at least 9 years of data and were used for correlation with environmental variables. Dolly Varden were assumed to have a coastal distribution, so, 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; <http://www.esrl.noaa.gov/psd/>). The only exception was Auke Creek, where SSTs were monthly means of daily surface water measurements made near the creek mouth (NOAA-AFSC Auke Bay Laboratories, Juneau, Alaska). In the Chignik River population, we also included monthly mean river temperatures in May and June as environmental correlates with migration timing (Alaska Department of Fish and Game, Kodiak, Alaska, unpublished data).

Fig. 2. Locations in Alaska and Canada where Dolly Varden were counted. Symbol numbers correspond to the site numbers in Table 1.



Multiple regressions tested the relationship between annual Dolly Varden median return day and monthly mean SST, monthly mean freshwater temperature, and median sockeye 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 (AIC_c) (Burnham and Anderson 2004) was used to determine the models from the candidate set with the most support. All models with ΔAIC_c 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 DOY 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 the Chignik Lakes

Of the 20 fish tagged in Chignik Lagoon each summer, 17 (2008) and 10 (2009) were detected entering fresh water, although two fish in 2008 were first detected upstream of the Chignik weir and so the detection rate there was $<100\%$ (Table 2). Freshwater detection dates varied widely, from as early as 17 July, 3 days after tagging, to as late as 12 November. 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 in the Chignik River was 20 August, and in 2009 it was 7 September, 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 = $-3.271 + 8.841 \times \text{proportion daylight}$, $r_D^2 = 0.15$, $p = 0.040$, $AUC = 0.765$). We found no significant effect of tidal cycle (categorized as being within an hour of high, low, ebb midpoint, or flood midpoint) on arrival time at the weir ($X^2 = 2.33$ (3, $n = 25$), $p = 0.506$). Upon entering the river, the fish showed three distinct behaviors. Sixteen percent of individuals that entered the 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 1 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 detected 9 of the 12 fish detected in Chignik Lake, and 7 of those fish 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 fresh water.

Table 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 freshwater detection DOY (range)	No. of days in marine water until first detection	No. of days in fresh water (range)	First ice-free DOY in spring	Spring departure DOY (range)	Second summer return DOY	No. of days in marine water, 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

Note: DOY indicates day of the year from 1 January.

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 fresh water by 30 May. 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 km·h⁻¹, 1.2 BL·s⁻¹) were recorded during the spring migration down the Chignik River, and the slowest were upstream movements in the Chignik River (0.3 km·h⁻¹, 0.24 BL·s⁻¹) and Chignik Lake to Black Lake (0.24 km·h⁻¹, 0.19 BL·s⁻¹).

The median weir arrival DOY of Chignik Dolly Varden, sockeye, and Chinook 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 ($M_{DOY} = 192.8$, $SD = 7.01$) and Chinook ($M_{DOY} = 195.5$, $SD = 2.43$), but both arrived significantly later than the main run of sockeye ($M_{DOY} = 174.3$, $SD = 3.48$). 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 2 months (Pikmiktalik River DOY = 184, Auke Creek DOY = 246) and tended to be later at higher latitudes (median migration DOY = $76.02 + 2.24 \times \text{latitude}$, $F_{[1,16]} = 8.352$, $p = 0.010$, $r^2 = 0.302$). However, after removing the SE Alaska sites, latitude explained 53% of the variation in migration date (median migration DOY = $44.97 + 2.694 \times \text{latitude}$, $F_{[1,12]} = 15.78$, $p = 0.001$, $r^2 = 0.532$).

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 = $245.73 - 6.89 \times \text{June SST}$, $F_{[1,13]} = 41.17$, $p < 0.001$, $r^2 = 0.741$). May and June freshwater temperatures were removed because of multicollinearity, and they were not tested in any models. In four other watersheds, we evaluated the SST for May, June, July, August, and September as predictors of migration DOY. In the Buskin River, both June SST (median migration DOY = $261.64 - 7.94 \times \text{June SST}$, $F_{[1,7]} = 9.755$, $p = 0.016$, $r^2 = 0.522$) and May SST ($\Delta AIC_c = 0.858$, median migration DOY = $247.49 - 8.56 \times \text{May SST}$, $F_{[1,7]} = 8.232$, $p = 0.024$, $r^2 = 0.475$) were significant predictors of migration

Table 3. Mean travel rates for all movements by Dolly Varden among monitored watershed sections.

	Speed of migration	
	km·h ⁻¹	BL·s ⁻¹
Upstream		
Weir - Chignik Lake outlet	0.3±0.25 (9)	0.24±0.20 (9)
Weir - Mid Chignik Lake	0.77±0.51 (10)	0.66±0.45 (10)
Chignik Lake outlet - Mid Chignik Lake	1.32±0.78 (7)	1.03±0.60 (7)
Chignik Lake outlet - Black Lake outlet	0.24±0.02 (2)	0.19±0.03 (2)
Mid Chignik Lake - Black Lake outlet	0.71±0.33 (3)	0.48±0.19 (3)
Weir - Black Lake outlet	0.30 (1)	0.21 (1)
Downstream		
Chignik Lake outlet - Weir	1.50±0.94 (8)	1.20±0.76 (8)
Mid Chignik Lake - Weir	0.59±0.35 (5)	0.47±0.28 (5)
Mid Chignik Lake - Chignik Lake outlet	0.73±0.83 (5)	0.64±0.81 (5)
Black Lake outlet - Mid Chignik Lake	0.91±0.73 (5)	0.74±0.59 (5)
Black Lake outlet - Weir	0.62 (1)	0.40 (1)

Note: Rates are calculated with the minimum possible distance between points and number of body lengths (BL) for each individual ±1 SD. Number of individual movements for each segment included parenthetically.

DOY, with similar patterns to nearby Chignik River. In Auke Creek, both July SST (median migration DOY = $157.80 + 6.12 \times \text{July SST}$, $F_{[1,9]} = 12.53$, $p = 0.006$, $r^2 = 0.535$) and August SST ($\Delta AIC_c = 0.108$, median migration DOY = $168.76 + 5.51 \times \text{July SST}$, $F_{[1,9]} = 12.53$, $p = 0.006$, $r^2 = 0.531$) explained over 50% of the variation in migration DOY. However, temperature was positively correlated with median migration DOY (warmer equals 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 peak temperatures, whereas in Auke Creek they tend to return after the peak temperature (Fig. 3).

Discussion

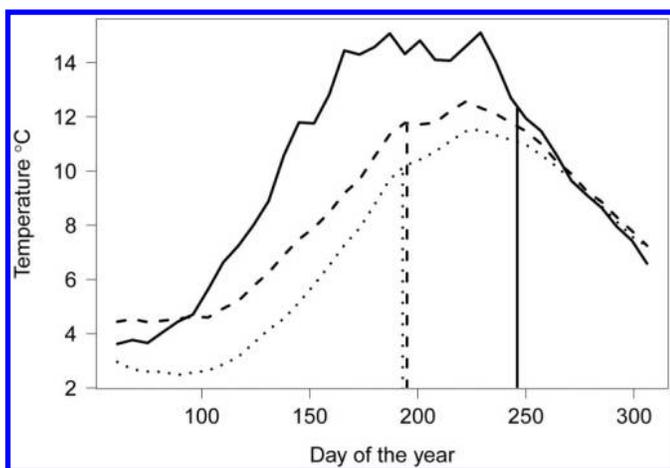
Acoustic tagging of Dolly Varden in Chignik Lagoon and subsequent monitoring of movement into freshwater habitats revealed patterns of migratory behavior not typical of the semelparous Pacific salmon sympatric at this site, nor elsewhere. Although some Dolly Varden entered fresh water soon after tagging, 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 the Chignik system in fall, and then enter Chignik Lake to overwinter postspawning (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. 2006; Jensen and Rikardsen 2012). Additionally, the fish detected at Chignik River in the fall that were never subsequently detected

Table 4. All tested models predicting median Dolly Varden migration date in the Chignik Lakes watershed.

Model	K	AIC _c	ΔAIC _c	AIC _c 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

Note: Lower AIC_c scores indicate a better fit of the data to the model. SST, sea surface temperature.

Fig. 3. Average weekly sea surface temperature (SST) 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 data courtesy of NOAA–AFSC Auke Bay Laboratories, Juneau, Alaska. Chignik and Buskin rivers SST data courtesy of NOAA–OAR–ESRL Physical Sciences Division, Boulder, Colorado.



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. 2006; 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 of the returning tagged fish entered fresh water after the Alaska Department of Fish and Game weir ceased counting, indicating that a significant fraction of the large bodied individuals (≥ 300 mm fork length) may not be counted by the weir. This is surprising given that the mode of Dolly Varden ascending the river occurs more than 6 weeks before the weir ceases counting, which 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, and early migrating fish may return to do so (Denton et al. 2009, 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 fresh water 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 fresh water 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).

Midwinter movements to marine habitats have been demonstrated for brown trout and Arctic char at much higher latitudes than the Chignik system (Jensen and Rikardsen 2008, 2012) and bull trout in more temperate systems (Brenkman and Corbett 2005). Chignik Dolly Varden, however, did not make any midwinter downstream migrations. The earliest emigrations from the system occurred around the first ice-free day in Chignik River, 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 (Saiget et al. 2007), and some brown trout, which may exhibit extremely protracted outmigration of postspawners, including modes in the spring and fall (Jonsson and Jonsson 2009). Movement into marine waters also preceded the large sockeye 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 fresh water 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 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 with 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 midsummer, 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 SE 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 with 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 (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 fresh water 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 SE Alaska, the trend was for later returns with increasing temperature and the migration tended to follow the annual temperature maximum. Maximum SSTs 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 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; Vähä 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).

Acknowledgements

We thank J. Griffiths, C. Gowell, L. Ciepiela, and R. Simmons for sampling assistance. M.H.B. received support from the Moore Foundation, NSF's BioComplexity Program, the US Army Corps of Engineers, the H. Mason Keeler Endowment, and the Institute for Food Sciences and Technology Endowment. T. Anderson, N. Nichols, A. St. Saviour, and M.-B. Loewen of The Alaska Department of Fish and Game Commercial Fish Division provided data and access to the Chignik weir site. M. Lisac of the US Fish and Wildlife Service Togiak National Wildlife Refuge and R. Harding of the Alaska Department of Fish and Game provided unpublished data. We also thank the Editor and two anonymous reviewers for suggestions that improved the manuscript.

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Appendix

Table A1. 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 River	59.780	151.838	1995	Larson 1997
Auke Creek	58.382	134.636	1997–2007	Echave 2007; Hoover 2007, 2008; Lum et al. 1998, 1999, 2000, 2001, 2002; Lum and Taylor 2004, 2006a, 2006b, 2006c
Babbage River	69.232	138.430	1990–1992	Sandstrom et al. 1997
Big Creek	58.515	156.569	2003	Anderson et al. 2004
Buskin River	57.756	152.483	2001–2009	Alaska Department of Fish and Game, Kodiak, Alaska
Chignik River	56.339	158.574	1996–1999, 2001–2011	Alaska Department of Fish and Game, Kodiak, Alaska
Eva Creek	57.402	135.100	1962–1964	Alaska Department of Fish and Game, Division of Sport Fish, Juneau, Alaska
Frosty Creek	55.195	162.854	2000–2002	Cornum et al. 2004
Goodnews River	59.121	161.586	1996–2011	US Fish and Wildlife Service, Togiak National Wildlife Refuge, Dillingham, Alaska
Hulahula River	70.996	143.372	2006, 2008	US Fish and Wildlife Service, Fairbanks, Alaska
Kanektok River	59.746	161.931	2001–2011	US Fish and Wildlife Service, Togiak National Wildlife Refuge, Dillingham, Alaska
Kwiniuk River	64.697	162.016	2004–2007	Kent 2006, 2007; Kent et al. 2008; Menard and Kent 2005
Lupine River	68.718	147.627	1971	Yoshihara 1972
Niukluk River	64.596	163.321	2004–2007	Kent 2006, 2007; Kent et al. 2008; Menard and Kent 2005
Nome River	64.482	165.305	2004–2007	Kent 2006, 2007; Kent et al. 2008; Menard and Kent 2005
Pikmiktalik River	63.238	162.589	2006	Dunmall and Kroeker 2008; Kroeker and Dunmall 2003, 2005, 2006
Taku River	58.548	133.676	1987–1988	McGregor and Clark 1988, 1989
Windfall Creek	58.526	134.779	1997	Jones and Harding 1998

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