Population Dynamics and Trophic Ecology of Dolly Varden in the Iliamna River, Alaska: Life History of Freshwater Fish Relying on Marine Food Subsidies

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General Introduction

Ecosystems are comprised of not only the habitats and populations of organisms within them, but also the interactions of populations with each other and their environments. A full understanding of these interactions is crucial to sustain healthy ecosystems and for successful management with human influence. However, with the expanding footprint of human populations, undisturbed areas are increasingly rare, making it difficult to parse out natural dynamics of ecosystems. Studying populations in undisturbed settings can provide important perspectives on how natural ecosystems function that can assist in the restoration of other systems that have suffered habitat degradation or population losses

Understanding population dynamics and interactions in undisturbed settings is especially important for resident salmonids in cold-water streams. These fishes require diverse habitats throughout their lives including spawning and rearing areas, seasonal refuges, and access to functioning migration corridors. In areas where resident salmonids receive subsidies from semelparous Pacific salmon (*Oncorhynchus* spp.), their life history is often inextricably tied to the input of salmon indirectly through nutrient deposition, but also directly as a food source.

This thesis examines the population dynamics and trophic ecology of resident Dolly Varden (*Salvelinus malma*) from 2005-2009 in the unaltered setting of the Iliamna River, flowing into the southeast portion of Iliamna Lake in southwest Alaska (Figure 1). Dolly Varden are an iteroparous, fall spawning, and facultatively anadromous salmonid. This species, like many within the genus, are a challenge to managers in that they display diverse life histories across their range which extends from the northwest United States north to the Arctic Ocean and west to eastern Russia and south to Hokkaido, Japan. The Iliamna River is a largely unaltered setting that receives minimal fishing pressure and is regulated for catch and release. Like many of the rivers in the region, it receives large runs of sockeye salmon (*O. nerka*) each year after a well-managed fishery that provide large marine subsidy for resident fishes.

This thesis examines the population dynamics and trophic ecology of this Dolly Varden population. In the first chapter, we quantify vital rates of growth, maturity and abundance in this population from 2005-2009 through mark and recapture techniques and discuss implications of management for not only remote populations that display similar population dynamics, but also implications for other populations that are in decline or suffer from habitat degradation and overexploitation. In the second chapter, we examine the trophic ecology of this population using diet and stable-isotope analysis with emphasis on direct connection to Pacific salmon and discuss the vital role that marine subsidy plays in this population's life history. In the third chapter we use elemental composition of the otoliths to test the hypothesis that the population was resident rather than anadromous. In doing so we not only demonstrated that they are resident but, perhaps more importantly, we discovered a previously undocumented effect of a marine subsidized diet on Sr-based otolith microchemistry. Specifically, otolith chemistry of resident fishes that directly consume and heavily rely on food sources from Pacific salmon can mimic that of fish that have migrated to sea. This effect of diet, rather than migration, is an important methodological finding, and it further emphasizes the importance of salmon in the diet of Dolly Varden that was indicated by the stable isotope results.

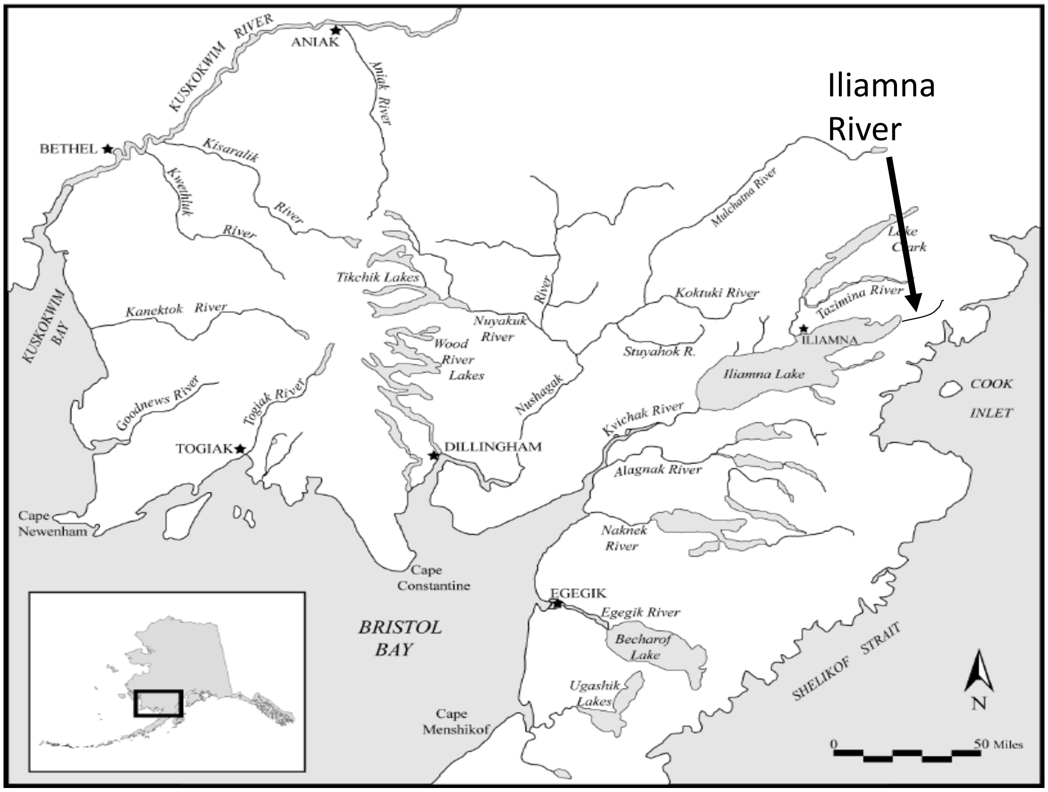


Fig. 1. Bristol Bay and the Iliamna River in southwest Alaska.

Chapter 1: Abundance, age, and growth of an unexploited population of large-bodied riverine Dolly Varden.

Introduction

The dynamics of fish populations are affected by complex combinations of biotic, abiotic and anthropogenic factors. In situations where humans play a dominant role, either through fishing, alteration of the physical habitat or flow manipulation, artificial propagation, or transport of non-native species, it can be difficult to discern natural processes affecting the species. Understanding the natural dynamics of freshwater fish populations in the absence of such anthropogenic disturbances is very important to fisheries managers because this baseline enables them to better assess effects of human activities. Observing populations in undisturbed conditions allows accurate characterization of shifts in density and size composition inherent to the population which could otherwise be misinterpreted as artifacts of disturbance. With the increasing footprint of humans on earth’s ecosystems, undisturbed areas are increasingly rare. Many studies of fish populations are initiated after a threat or damage to the population or surrounding habitat has already occurred and at best, the recovery, or demise, is observed (Johnston and Post 2009). These studies often are snap shots, or short term glimpses into the current status of a population because of limited budgets, lack of personnel, or conflicting priorities. Long term studies that encompass the majority of a species’ lifespan are much less common, despite their obvious importance (Milner et al. 2003).

Recreational fishery managers commonly use regulations to protect fish stocks, maximize sustainable yield, and allow diverse opportunities for anglers. Constraints on fish size allowed for retention, daily and annual bag limits, seasonal and area closures, and gear restrictions are used singly or in combination to achieve a desired effect on a varying spatial, and often species-specific, scale (Noble and Jones 1999). Choosing the most effective regulation depends on understanding the basic dynamics of the population, the quality of the habitat, and angling pressure. Tempering all of these topics into effective regulation can be challenging.

Among the regulations managers use to control harvest, the most conservative and simple is catch-and release; angling is allowed but fish may not be intentionally killed. Gear is often restricted to artificial lures to minimize delayed hooking mortality from fish ingesting baited hooks (Muoneke and Childress 1994). In areas open to retention, there can be a variety of size-related regulation. Size limits may be established to protect juvenile fish until maturity (Noble and Jones 1999) or to allow or prohibit retention of fish of intermediate sizes to protect the largest spawning fish as well as the pre-recruits, or achieve some other management objective (Anderson 1980). Number or “creel” limits regulate the number of fish, often associated with size, to be retained on a daily or annual basis. Retention regulations are successful for species and populations that show little annual variability in abundance. However, static regulations applied to a population that is temporally dynamic in size structure and abundance could have unintended negative effects.

Regulations are particularly applicable in oligotrophic, cold waters inhabited by salmonids where even moderate fishing effort can lead to overexploitation. Salmonid fishes are an important component in commercial and recreational fisheries, but in many cases research is focused on “at risk” populations that may be under special protection after severe depletion due to habitat alteration, over-exploitation or interactions with non-native species. Research in North America has tended to focus on Pacific salmon and trout, genus *Oncorhynchus,* due to both real and perceived higher economic or aesthetic value compared to other salmonids. Charr (*Salvelinus* spp) tend to receive less attention from research and management, with the notable exception of lake charr (*Salvelinus namaycush*) in the North American Great Lakes and introduced populations in western waters, but the diverse life histories that they display across their circum-polar Northern Hemisphere range often pose challenges for managers (Armstrong 1984, Dunham et al. 2008, Reynolds 1994).

Even in areas with intact habitat, charr populations are often exposed to fishing. Angler retention in these areas may affect the size and age distributions as well as growth trajectories of the population through direct removals and alterations in density-dependent processes. If populations naturally fluctuate in size structure or abundance, static regulations allowing size-dependent retention could unequally affect weak year classes pulsing through the system. Additionally, high growth rates within a season could recruit a sub-adult size class to harvest despite an unchanging maturity status and create a biased effect of size-based regulation. However, if the dynamics of an unharvested population are known, it is possible to create predictive models that incorporate natural variability with human perturbations. Long term studies that determine population changes in size, abundance, growth, and maturity provide the inputs for such models and allow managers to make informed decisions on size-limits and harvest that are either flexible or simply conservative but with greater knowledge of natural variation. Therefore, it is important to study the dynamics of population that are largely unaffected by habitat alteration and fishing pressure.

Dolly Varden (*Salvelinus malma*) are found in rivers and lakes draining into the Pacific Rim and Arctic Ocean. This species is understudied in much of its range due to the remote locations of populations, complex and varied migration patterns, and use of different parts of watersheds during juvenile life stages (Decicco 1992). Dolly Varden are distributed from Puget Sound in Washington state, U.S.A., north to the Arctic circle of Alaska and Northwest Territories, to eastern Asia including Siberia, and south to Hokkaido, Japan (Armstrong and Morrow 1980). Although commercial interest in Dolly Varden has been low since the early 20th century, they are often sought by sport fishermen, and can also play an important part of the ecosystems where they live. Dolly Varden display different life history and migration patterns depending on the particular habitat and foraging opportunities of each location across this wide geographic range (Haas and McPhail 1991).

Dolly Varden are iteroparous fall spawners, and are facultatively anadromous. Spawning occurs in headwater areas, usually in September and October. Fry emerge the following spring and rear in headwater areas and small tributaries for up to three years before going to salt water (Armstrong and Morrow 1980) in anadromous populations, or residing in main stems of rivers or in lakes in non-anadromous populations. Dolly Varden may display both anadromous and resident forms within a single watershed (Palmer and King 2005), and have shown inconsistent use of saltwater from year to year (Dunham et al. 2008). Often, within a watershed, populations exhibit stark differences in maximum size, suggesting distinct trophic niches, movement patterns (Denton et al. 2009), and regimes of selection (this thesis Chapter 2).

Understanding differing life histories within intact settings and the processes behind them can allow managers greater insight to conserving and protecting Dolly Varden populations as well as species with similar life histories such as bull charr (*Salvelinus confluentus*). The specialization of life histories displayed by Dolly Varden populations may contribute to increased susceptibility to disturbance. This specialization could amplify the effect of a disturbance; indeed, charr populations have suffered declines due to human impacts directly through fishing (Johnston and Post 2009), habitat degradation (Elliott 1986, Nelson et al. 2002), nonnative species (Rodtka and Volpe 2007), and are constrained by rising temperatures from climate change and effects of wildfires (Isaak et al. 2010). However, it is important to study intact, healthy populations if we are to understand abundance fluctuations, forage and habitat requirements of the species, and thereby gain insights into factors causing declines elsewhere, and potentially build the baseline for proper assessment of future recoveries.

Initial investigations of Dolly Varden in the Iliamna River, Alaska, revealed a large body size distribution and recurring pattern of dominance by a strong year-class (Jaenicke 1999). Sampling in 1996-1997 showed a population dominated by large individuals (ca. 450-550 mm) that declined in abundance with apparently little recruitment in 1997 (Figure 1.1). Subsequent sampling in 2005-2009 revealed a distinct size mode (ca. 300-350 mm) that declined in abundance and increased in body size over time followed by an apparent burst of recruitment. Populations are expected to fluctuate over time, and charr populations within closed systems sometimes cycle (Johnston and Post 2009, Paul et al. 2000), but this dynamic pattern was unexpected in an iteroparous, generally long lived fish such as a Dolly Varden.

The Dolly Varden in the Iliamna grow large for the species (Armstrong and Morrow 1980), likely due to a large marine subsidy provided by strong runs of sockeye salmon (*Oncorhynchus nerka*). The length distribution is similar to that of anadromous populations, but radio telemetry and otolith microchemistry (this thesis Chapter 3) revealed no evidence of anadromy, and limited use of habitats beyond the river itself, despite ready access to Iliamna Lake.

In this study, we used 5 years of mark-recapture data to evaluate demographic and vital rate information for a resident Dolly Varden population that displays large variability in length distribution and abundance in an unaltered setting. Repeated surveys using closed population estimation methods yielded information on abundance, annual and within season growth, length at age and maturity, and shifts in size and maturity structure across the majority of the expected lifespan for this population. These estimates of vital rates provided rare insight into the population dynamics and ecology of this species and highlight areas of concern to be considered in management of resident fishes with similar life histories. In particular we are interested in fluctuations within this population that could lend it and others to periodic overexploitation if managed under the customary theory of protecting sub-adult fish from harvest.

Methods

Study site and field methods

Iliamna Lake, the largest lake in Alaska, offers an excellent setting to study Dolly Varden life history patterns and population dynamics. The lake, its tributaries, and associated smaller lakes, are in a nearly pristine condition in terms of habitat quality, with no logging, agriculture, impassable dams, and limited human population development. It supports very large runs of sockeye salmon, with annual totals of ca. 2 – 6 million adults after well-regulated commercial fisheries, as well as much smaller runs of other Pacific salmon species. The lake system has an entirely native fish fauna, including salmonids such as rainbow trout (*O. mykiss*), Arctic charr (*Salvelinus alpinus*) and Dolly Varden, and also lake charr and a variety of smaller fishes, including but not limited to sculpins (*Cottus aleuticus* and *C. cognatus*), three-spine sticklebacks (*Gasterosteus aculeatus*), nine-spine sticklebacks (*Pungitius pungitus*) and several whitefishes (family Coregonidae).

The Iliamna River Dolly Varden fishery has been regulated for catch-and-release since 1996. There is little angling pressure because it is remote, access to the river is limited seasonally by ice and year round by private ownership. Surrounding critical habitats are intact, allowing researchers to observe movement and population dynamics without interference or confounding influences. Although the river is ca. 45 km long, most Dolly Varden are confined, at least in summer, to ca. 12 km in the middle reach of the river. This range, combined with the modest total population (estimated at 3464 in 2005 to 2012 in 2008 – see details below), provided the opportunity to obtain size and growth samples from a significant proportion of the population, and to use mark-recapture for estimates of growth and survival based on known individuals.

The Iliamna River flows north into the southeast corner of Iliamna Lake. The river is characterized by large cobble bars and high gradient in its upper reaches, and lower velocities, deeper water, and sandy substrate as it nears the lake (Demory et al. 1964). The river can be navigated from Iliamna Lake upstream for ca. 24 km to a steep riffle that is impassable to boats at normal flows. The 12 km reach downstream of this riffle was chosen as the survey area because the 1996 mark-recapture study (Jaenicke 1999) revealed few Dolly Varden outside this area during August, when fish were concentrated to eat eggs from the many sockeye salmon that spawn in this reach.

During August 2005-2009 mark and recapture abundance surveys were conducted by the Alaska Department of Fish and Game, Division of Sport Fish. Dolly Varden > 300 mm fork length were targeted using hook and line techniques within the 12 km survey section. Terminal tackle consisted of 6 mm or 8 mm plastic beads, colored to mimic sockeye salmon eggs, pegged above a small hook. For each fish, length, weight and sex were recorded, an individually numbered T-bar anchor tag was attached below the dorsal fin, and a pelvic or ventral fin was clipped as a secondary mark to assess tag loss. Sex was determined by kype development, deep body morphology and coloration in males and a combination of mottled coloration in the head and abdomen, round body morphology, and smaller jaws in females. Minnow traps were used in 2009 to collect smaller specimens (< 250 mm) for age determination; few juveniles were encountered in the main stem and most were collected in tributaries. Additional sampling with hook and line was conducted in late

September 2009 to assess in-season growth and observe spawning Dolly Varden in headwater areas.

Age determination

Length at age was estimated from a von Bertalanffy growth equation (Weisberg and Frie 1987) using age data taken from sagittal otoliths from all accidental mortalities and from directed lethal sampling apart from the mark-recapture surveys.

Otoliths were mounted on petrographic slides, sulcus side up, using Crystal Bond ™ and ground on wetted sandpaper. The otoliths were then loosened on a hotplate, turned over, and examined under a microscope with transmitted light. Ages reflect the number of winter annuli observed with special consideration given to extra growth on the outer ring due to the date the otoliths were sampled (Dolly Varden in the Iliamna River grow rapidly during late summer and early fall and the outer edge does not necessarily constitute an annulus).

The fork length-at-age plots were fit to the von Bertalanffy growth equation:

$$\hat{L}_i = L_\infty(1 - e^{[-k(t_i - t_0)]}),$$

where $\hat{L}_i$ is the predicted fork length of a fish number i, L_∞ is the asymptotic average maximum fork length, k serves as a growth coefficient, t_0 the time (in years) when fork length = 0 and t_i is the age of the ith fish. Best-fit coefficients were found by maximum likelihood assuming that the errors are normal. Curves from males and females were compared using a likelihood ratio test (function vblrt from the fishmethods package in program R).

Annual and in-season growth, length-at-maturity, and length composition

Annual growth of recaptured individuals was determined using length at capture from individuals who were captured in consecutive years and released. Recaptured individuals were segregated by size class and sex to assess differences between groups. Lengths of Dolly Varden sampled in August 2009 and recaptured in September 2009 (31-50 days later) were compared and proportion of expected annual growth by size/sex was obtained from annual recaptures was calculated.

To calculate the length at first maturity (L50) we predicted the proportion of fish mature (*p*) at a given length (*l*) using the maturity ogive formula:

(1)
$$p = f(l_{50,} l_{95}) = \frac{1}{1 + \exp(\frac{-\ln(19)(l - l_{50})}{l_{95} - l_{50}})}$$

The Bernoulli likelihood (*L*) was used given that the maturity status of a given fish (*i*) was either 0 (immature) or 1 (mature). Thus, if a fish was immature, the likelihood would be *1-p*, whereas for mature fish the likelihood was *p*.

(2)
$$L = \prod_{i=1}^{n} p^{x_i} (1 - p)^{1 - x_i}$$

To determine annual changes in length composition, lengths of unique Dolly Varden sampled were separated by year and sorted into 25 mm bins.

Yearly closed population abundance estimates

Each mark recapture survey was designed as a multi-event, closed population (Schnabel) model under the following assumptions (Seber 1982):

1. The population is closed with no additions or losses between sampling events (i.e., no recruitment, mortality, immigration, or emigration).
2. All fish have an equal capture probability in each sampling event.
3. Marking does not affect capture probability in subsequent capture events.
4. Marks (tags) are not lost between events.
5. All marked fish recaptured during subsequent capture events are correctly identified and recorded.

Failure to satisfy these assumptions would result in a biased estimate; therefore the experiment was designed to test these assumptions.

Assumption 1: Closure

The sampling dates and study area were chosen to coincide with the feeding aggregations of Dolly Varden in the Iliamna River. In late July through early September, Dolly Varden in the Iliamna River aggregate in river km 12-24 to feed on the eggs of sockeye salmon within this reach of the river.

Sampling was conducted over five events, one week long each, in 2005 and four in 2007-2009. The main study site was divided into two, 6 km areas (river km 12 to 18 and 18 to 24, designated areas 2 and 3) and areas below (area 1) and above (area 4) the main study area (Figure 1.2). Areas 2 and 3 were sampled on each of four days during each week with equal time spent in each area. Sampling also occurred once each (in areas 1 and 4) to detect fish movement out of the study area (i.e., assess closure) and to test our assumption that these areas harbored few Dolly Varden. We waited three days between sampling events to allow tagged fish to mix with untagged fish. Sampling was conducted by two anglers with hook and line. All hooked fish were landed as quickly as possible, placed in a tote of fresh water, sampled and released at the site of capture. The amount of angling time was recorded for estimation of CPUE.

The short duration of the experiment helped minimize immigration and emigration of Dolly Varden. If significant immigration occurred, a constant or declining mark to recaptured ratio would be observed. Furthermore, surveys conducted in the Iliamna River in 1996-1997 observed few Dolly Varden outside of areas 2 and 3 during this time period (Jaenicke 1999). Natural mortality was considered insignificant and no subsistence harvest was observed during any of the survey years. Catch-and-release angling effort in the Iliamna River is very low in contrast to most areas and is often focused on rainbow trout. The preferred terminal tackle, a pegged bead 2 cm above a small hook, is an unlikely cause of significant hooking mortality as the hook is rarely swallowed.

Statistical tests for closure were conducted with the program CLOSETEST and chosen dependent upon which abundance estimation model was selected. If Model M_0 or M_h (Otis et al. 1978) was chosen then the closure test developed by Otis et al. (1978) was used. This test compares frequency of capture histories throughout events under the null hypothesis that neither recruitment nor mortality occurred and a z-statistic and probability of closure were calculated. However, this model is likely to commit a type I error if there are time variant capture probabilities. Therefore, if Schnabel (model M_t) (Otis et al. 1978) was chosen, the test of closure developed by Stanley and Burnam (1999) was used. Model M_t serves as a constrained case of the open Jolly Seber model allowing for variation in capture probability through time in this test is compared against variations of the open model which allow for births and/or deaths. Contingency tables of capture probabilities under closed and open models are constructed and a chi square statistic and probability are calculated .

`Assumption 2: Size-selectivity, probability of capture, and mixing

Size-selectivity within the experiment was assessed using Kolmogorov-Smirnov (K-S) tests (Conover 1980), which compare cumulative frequencies of two distributions under the null hypothesis that they are equal. Two series of tests were conducted on each data set for abundance estimation.

The first series of tests evaluated size selective sampling for events 2 through 4 from the perspective that they are "recapture" events. For each event *t* we want inference on capture probability by size, we compared the cumulative length frequency distributions of those fish sampled in event *t* that were recaptured from previous events against all fish marked and released alive in events 1through *t*-1.

The second series of tests evaluates size selective sampling for events 1 through 3 from the perspective that they are "marking" events. For each event *t* that we wanted inference of capture probability by size we compared the cumulative length frequency distributions of those fish captured and inspected for marks during event *t*+1 through event 4 against those fish caught in events t+1 that are recaptures from fish marked in event *t*. If size selectivity was detected, the data would be stratified accordingly to reduce bias.

To determine equal probability of capture, we used two sub-area tests that mimicked those described in Seber (1982) in the Stratified Population Analysis System software package (SPAS) (Arnason et al. 1996) labeled the "Equal Proportions

Test" (EP) and "Mixing Test" (M). The tests are designed for two-event experiments whereby probability of capture in marking and recapture events (and mixing) are assessed with respect to marking and recapture strata (area). Contingency tables were constructed and analyzed to test the null hypothesis that mark status was independent of the area where the fish was inspected (EP test) and that recapture status was independent of the area where the fish was marked (M test). Failure to reject the null hypotheses was considered evidence that the probability of capture in event t was uniform and/or mixing between events and areas took place, and geographic stratification was unnecessary.

Assumption 3: Sampling effects

We carefully and rapidly processed captured fish and no handling and marking induced behavioral effects were anticipated. All fish were resuscitated until they were able to swim strongly, any fish in severely weakened condition was sacrificed for aging purposes.

Assumptions 4 and 5: Fish identification, tag loss, reporting accuracy

In addition to tagging, a different fin clip was applied for each sampling event as a secondary mark to assess tag loss. Event-specific clips allowed us to determine the week when a fish was tagged in the event of tag loss to reconstruct capture histories. However, tag loss was anticipated to be minimal within each year due to the short duration of each survey and careful processing of fish. All fish were thoroughly examined for tags or recent fin clips and all recoveries were by a small number of trained staff rather than relying on angler-reported data. All markings (tag number, tag color, fin clip and/or tag wound) were recorded for each fish.

If no assumptions were violated, the most likely model was a closed multi-event Schnabel mark-recapture model (Ricker 1975, Seber 1982). This model allows for a maximum likelihood estimation of the population abundance when the probability of capture varies over sampling events (Otis et al. 1978). The suite of closed population models described by White et al. (1982) including the Schnabel estimator (M_t as described by White et al. 1982) were examined. The appropriate estimator was selected by examining model AIC's (Burnham and Anderson 2002) and for admissible estimates.

Results

Length at age

In total, 98 Dolly Varden were aged using otoliths. Length-at-age plots revealed rapid growth through age 4 but increasing variability at ages 4-9 (Table 1.1, Figure 1.3). Young-of-the-year were not encountered during this study, likely because they inhabit inaccessible headwater areas where Dolly Varden spawning occurs and are not susceptible to the sampling methods. Male and female Dolly Varden showed no significant difference in length at age (likelihood ratio test for parameters L_∞; p = 0.76, K; p = 0.76, t_0; p = 0.69). Von Bertalanffy equation coefficients were $L_\infty = 850$ mm (SE = 85.4), $k = .2$ (SE = 0.03) and $t_0 = 0.85$ (SE = 0 .09). Accurately determining a difference in male and female length-at-age was constrained by low sample size of larger individuals and difficulties inherent in aging older fish.

From 2005-2009, 2966 unique Dolly Varden were tagged and 89 male and 140 female Dolly Varden were recaptured in consecutive years. Annual growth estimated from recaptured Dolly Varden showed that males and females have similar annual growth rates until they reached 450 mm, at which point males grew faster than females (initial size bins 450 mm, 500 mm, > 550mm; t-test p = 0.02, 0.004, and 0.04 respectively; Table 1.2). Variability in growth between years was greater in males than females of the same size >450 m. All Dolly Varden captured in August 2009 and then recaptured in September 2009 displayed high growth rates in a relatively short period. All Dolly Varden, except one very large individual, grew at least 25 mm and fish < 400 mm grew more than larger individuals. Several smaller Dolly Varden (ca. 300-350 mm) had grown 77-83 mm in ca. 50 days. The proportion of expected annual growth in length of 17 recaptured Dolly Varden examined ranged from 0.32 to 1.78 when compared to growth rates determined by size and/or sex from consecutive annual recaptures from 2005-2009.

Length frequency distributions and maturity ratios from 2005-2009 indicated a population skewed towards smaller fish in 2005 with few adults, shifting to larger sizes (Figure 1.4) and a higher proportion of mature fish (Table 1.4) with little recruitment until 2009. Populations were dominated by the increasingly longer cohort first observed in 2005 until a smaller cohort appeared again in the survey area in 2009. Length at first maturity (L50) was 466 mm (SE=1.98) (Figure 1.5).

Mark and recapture abundance estimates

Closed population estimates were only available for 2005 and 2007-2009 because sampling in 2006 was limited and directed toward assessing length frequency and recapture of tagged individuals for growth estimates.

In 2005 we captured 642 unique Dolly Varden >300 mm in the main survey area, 45 Dolly Varden were recaptured once and three were recaptured twice. Eleven Dolly Varden were not tagged due to hooking injury and two died. A total of 45 Dolly Varden were captured in closure areas (3 in area 1, 42 in area 4), none of the Dolly Varden captured above or below survey areas 2 and 3 immigrated into the survey area, but 5 of the 642 individuals captured within areas 2 and 3 were captured left the core survey areas (none to area 1 and 5 to area 4). Additionally we captured and released untagged, 144 Dolly Varden < 300 mm.

In 2006 we captured 273 unique Dolly Varden >300 mm in the main survey area, three of which were recaptured once and none was recaptured twice. Two Dolly Varden were not tagged due to hooking injury and six died. Sampling in 2006 was not directed toward abundance estimation and closure areas were not sampled. No Dolly Varden <300 mm were captured.

In 2007 we captured 568 unique Dolly Varden >300 mm in the main survey area, 61 Dolly Varden were recaptured once and four were recaptured twice. Eight Dolly Varden were not tagged due to hooking injury and three died. A total of 30 Dolly Varden were captured in closure areas (0 in area 1, 30 in area 4). Of Dolly Varden captured outside the core survey, two immigrated into the core survey areas and two had emigrated out of the core survey areas. No Dolly Varden < 300 mm were captured.

In 2008 we captured 547 unique Dolly Varden >300 mm in the main survey area, 62 Dolly Varden were recaptured once and 2 were recaptured twice. Three Dolly Varden were not tagged due to hooking injury and three died. A total of 14 Dolly Varden were captured in closure areas (0 in area 1, 14 in area 4). Of Dolly Varden captured outside the core survey, two immigrated into the core survey areas and none had emigrated out of the core survey areas. No Dolly Varden < 300 mm were captured.

In 2009 we captured 816 unique Dolly Varden >300 mm in the main survey area, 65 Dolly Varden were recaptured once and one was recaptured twice. Four Dolly Varden were not tagged due to hooking injury and six died. A total of 31 Dolly Varden were captured in closure areas (0 in area 1, 31 in area 4). Of Dolly Varden captured outside the core survey, two immigrated into the core survey areas and none had emigrated out of the core survey areas. Additionally, we captured and released untagged, 87 Dolly Varden < 300 mm.

Tag loss was not encountered within years, and was rare across years. In 2008 and 2009 respectively, three and six Dolly Varden were captured with healed tag wounds and fin clips out of 1558 and 2135 unique fish previously tagged and examined for marks.

Assumptions of closure were satisfied in all years. Closure assessment sampling revealed few Dolly Varden above or below the survey area. The Iliamna River has extremely clear water with a light-colored substrate which creates uniquely excellent viewing conditions. On days when no fish were caught outside of the sampling boundaries, we floated the area (i.e., below or above the core sampling area) to attempt to observe individuals but we rarely saw Dolly Varden.

The proportion of captured fish that had been previously marked increased significantly during each event in all years as expected in the absence of immigrating fish. Tests of closure for both M_t (Stanley and Burnham 1999) and for M_0 (Otis et al. 1978) were not significant for all years.

There was no evidence of size selectivity in any year. However, some comparisons in 2005 were not able to be calculated due to low sample size (Table 1.6).

EP and M tests indicated that there was equal probability of capture and mixing between areas and events, with the exception of 2008, when EP tests indicated a difference in capture probability in the first two events between areas 2 and 3. Inspection of marked-fish movement indicated little mixing of marked fish from the two areas. However, marked to unmarked ratios in these areas during the final event were nearly equal (0.31 and 0.33) indicating that stratification was unnecessary.

With closure and mixing assumptions satisfied, we used the “closedp” function of package Rcapture in the program R to entertain a suite of multi-event closed population models. We used model AIC’s and inspected parameter estimates for admissibility to determine the best model. If models with admissible estimates had very similar AIC’s, the simpler model (fewer parameters) was chosen. Models selected for closed population estimates offered generally high resolution estimates (Table 1.7, Fig. 1.4). The Schnabel estimator (M_t) was selected for each estimate. The number of Dolly Varden ≥ 300 mm estimated each year were: 2005; 3464 (SE = 451), 2007; 2096 (SE = 221), 2008; 2012 (SE = 217), 2009; 3140 (SE = 329). Data collected in 2006 did not provide enough information to generate a comparable estimate. Closed population estimates generally reflect the trend observed in yearly length composition with little or no recruitment until 2009.

Discussion

From 2005-2009, Dolly Varden in the Iliamna River exhibited highly dynamic annual abundance and length frequency composition indicating variable survival rates by length and sex, high growth rates, and pulsed recruitment in a largely unaltered setting. Abundance declined while length frequency distributions increased from 2005-2007 because a sub-adult cohort that dominated the 2005 population suffered low survival but grew quickly and matured. Abundance and length frequency were stable in 2007-2008 and contained mostly large, mature individuals with high apparent survival before recruitment of sub-adults occurred in 2009. Annual growth rates determined by recaptures were rapid and consistent by sex for size classes from 300-450 mm but were differentiated by sex in larger size classes with males growing faster than females. In-season growth rates indicated most fish attained the majority of expected annual length in a short period of time in late summer and fall.

The variable population dynamics displayed by Dolly Varden in the Iliamna River could certainly prove challenging to managers under traditional regulatory constraints and stress the need for conservative management of charr populations. Minimum size limit regulations applied to this population to protect sub-adults could have varying, and at times deleterious effects, on adult components. Applying the mature proportion observed in 2005 to the estimated abundance, there were up to ca. 490 spawning adults as compared to ca. 1596 in 2007 and 1560 in 2008. If equal fishing pressure were applied to all years, mortality of the few adults found in 2005 could have been excessive. It is likely that the fluctuations in this population are not unique but are rather unobserved or incorrectly explained in other areas that experience confounding effects of angler effort and habitat degradation. Managers observing the low adult abundance in 2005 might have implemented angling restrictions, but if the follow-up survey occurred in 2007, conditions would have apparently been corrected.

Similarly, slot-size limits from 2005-2009 would be inadequate to protect long-term population viability. A hypothetical slot size prohibiting retention of 466 mm (approximate length at maturity) to 600 mm would protect the majority of adult fish in 2005 but allow harvest of smaller individuals that already display poor annual survival. This would essentially protect one component of the population while potentially degrading the future adult population. In 2006, this slot-size would protect nearly all fish within the population but would severely restrict the harvest opportunity for anglers. In 2007-2008, the majority of adults would be within the slot-size but a significant number of the largest individuals would be subjected to all potential harvest because there were few fish available below the slot.

Rapid in-season growth presents another challenge to managers. Sub-adult Dolly Varden gained up to 85 mm of length during late summer and fall. Dolly Varden that began the season protected by size limits might grow large enough for retention before the fall spawning period.

Designing regulations in accordance with long-term dynamics of a population would be ideal, but would also be extremely difficult and expensive to implement effectively. In the Iliamna River, each year would require a unique combination of regulations to protect different components of the population and allow limited retention. It would be possible to construct such regulations with current understanding of fluctuations of the Dolly Varden in the Iliamna River, but comparably detailed data would be available for few other populations and such complex regulations would be problematic to implement, enforce, and maintain.

Even in remote locations in Alaska, angler effort from commercial guiding operations, aided by jet-boats and airplanes, can dramatically increase if information about high fishing success is disseminated. If retention is allowed, increased angler effort could quickly lead to detrimental effects and potentially depensation. Regulations that cover large areas do not incorporate local sensitivity to angling pressure experienced by charr populations. Retention limits that pertain to a large river system may not be applicable to a smaller river or tributary with a smaller standing stock of individuals. Conservative and area-specific regulation (i.e. catch-and-release) for these populations is recommended in the absence of background understanding of the demographics of the population.

These insights are useful to researchers and managers when considering not only remote or unexploited areas, but also populations which have experienced deleterious effects from overfishing or habitat alteration. Depleted populations in these circumstances will require extremely conservative regulation and continued study as stocks rebuild. Johnston and Post (2009) observed a bull trout population in recovery after overfishing caused severe reduction in abundance and length composition. Ultimately, abundance and length composition increased which supports the potential resiliency of charr populations. However, the population status at the time of closure highlights the susceptibility of these populations to exploitation under traditional regulation of minimum size limits for harvest with increased angler effort.

Beyond assessment of management schemes, the rates and relationships described in this chapter can also provide baseline parameters for population based models that predict fluctuations as observed in the Iliamna River. Establishing size or age -specific survival rates and gathering more information on juvenile interactions would allow for even deeper understanding of the dynamics of similar populations. With a baseline established, perturbations could be applied to the model to evaluate effects of different disturbances on the abundance of this population.

This study outlines many of the challenges faced by fishery managers. Long term studies in unaltered areas are often expensive and difficult to implement but offer baselines of dynamics that can be applied to other population. Managing fisheries for yield and sustainability require deeper understanding of the mechanisms that naturally control population dynamics so that conservative and flexible regulation can be implemented to compensate accordingly with the intricacies inherent in each population.

Table 1.1. Mean, standard error and range of fork length of Iliamna River Dolly Varden whose ages were determined from otolith examination.

Age (in yrs)	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
n	8	23	26	21	10	5	4	1	1
Mean	73	146	300	424	506	567	585	610	620
S.E.	3.5	5.7	8.0	15.3	14.3	19.4	14.8	na	na
Min	60	102	216	312	444	520	555	610	620
Max	84	192	378	542	607	634	621	610	620

Table 1.2. Annual growth in mm /year and standard error of individually tagged male and female Dolly Varden from the Iliamna River, p = result of t-test for differences between male and female.

Size-class	Male	n	Female	n	p
300-349	124.1 (17.8)	6	122.1 (10.3)	12	0.915
350-399	143.8 (7.7)	5	106.8 (19.5)	6	0.136
400-449	96.1 (9.8)	13	84.6 (5.3)	18	0.277
450-499	80.5 (7.9)	19	48.1 (5.1)	22	0.024
500-549	42.9 (5.15)	21	27.4 (2.5)	56	0.004
>550	28.8 (5.3)	25	15.7 (3.9)	26	0.050

Table 1.3. In season growth and proportion of expected annual growth (from recapture data) of Dolly Varden from the Iliamna River captured in August 2009 and recaptured in September 2009.

Sex	Capture FL	Recap FL	delta FL	Capture WT	Recap WT	delta WT	Days	prop Ann. FL
u	290	345	55	455	731	276	43	0.45
u	305	388	83	503	1027	524	50	0.68
u	320	402	82	553	1075	522	51	0.67
m	356	433	77	750	1399	649	49	0.62
u	356	392	36	651	953	302	37	0.29
u	361	403	42	749	1198	449	31	0.34
u	381	443	62	897	1595	698	44	0.50
u	389	433	44	1052	1454	402	30	0.36
u	410	445	35	1198	1375	177	37	0.28
f	423	458	35	1297	1600	303	31	0.41
m	466	510	44	1453	1980	527	49	0.46
m	470	514	44	1601	2098	497	31	0.46
f	505	533	28	2223	2521	298	31	1.02
f	519	545	26	2052	2101	49	32	0.95
f	536	563	27	2053	2801	748	36	0.99
f	592	620	28	2294	3296	1002	46	1.78
f	640	642	2	3102	3555	453	30	0.13

Table 1.4. Sex composition by number (proportion), male to female ratios and mature proportion of Iliamna River Dolly Varden 2005-2009.

	2005	**2006**	**2007**	**2008**	**2009**
unknown	576 (.86)	111 (.4)	140 (.24)	126 (.23)	493 (.60)
male	40 (.06)	78 (.28)	208 (.35)	121(.22)	101 (.12)
female	55 (.08)	87 (.32)	244 (.41)	313 (.56)	229 (.28)
total	671	276	592	560	823
m/f ratio	0.73	0.90	0.85	0.39	0.44
proportion mature	0.14	0.60	0.76	0.78	0.40

Table 1.5. Summary statistics for Dolly Varden sampling 2005-2009.

	2005	**2006**	**2007**	**2008**	**2009**	**Totals**
Total captures	903	284	685	636	1021	**3529**
Captures for estimate	693	276	637	613	883	**3102**
Recaptures (single)	45	3	61	62	65	**236**
Recaptures (double)	3	0	4	2	1	**10**
Unique histories	642	273	568	547	816	**2846**
Same event recaptures	8	0	7	2	10	**27**
Previously tagged	0	27	80	123	120	**350**
< 300 mm	144	0	0	0	87	**231**
Poor condition	11	2	8	3	4	**28**
Mortality	2	6	3	4	6	**21**
Closure (areas 1,4)	45	0	30	14	31	**120**
DV emigrated	5	0	2	0	0	**7**
DV immigrated	0	0	2	0	2	**4**

Table 1.6. Size selectivity (K-S) tests comparing cumulative length frequencies across events from abundance estimates 2005, 2007-2009.

Year	Event	Marked in Events 1-(t-1)	Recaps in Event t from marks released in Events 1-(t-1)	KS Statistic	p
2005	2	176	7	na	
	3	342	16	0.36	0.04
	4	489	23	0.20	0.32
	5	593	5	na	
2007	2	155	13	0.17	0.87
	3	292	30	0.21	0.16
	4	443	31	0.12	0.76
2008	2	192	6	0.24	0.88
	3	303	23	0.22	0.22
	4	440	38	0.20	0.09
2009	2	218	8	0.25	0.70
	3	411	15	0.24	0.35
	4	528	42	0.20	0.08

Year	Event	Inspected in Events (t+1)-T	Recaps in Events (t+1)-T from marks released in event t	KS Statistic	p
2005	1	490	24	0.19	0.33
	2	335	18	0.17	0.72
	3	181	9	na	na
	4	54	0	na	na
2007	1	417	43	0.16	0.23
	2	281	17	0.31	0.08
	3	128	10	0.32	0.28
2008	1	358	34	0.15	0.41
	2	245	18	0.26	0.19
	3	108	14	0.22	0.56
2009	1	540	33	0.23	0.06
	2	374	12	0.30	0.23
	3	200	18	0.22	0.37

Table 1.7. Abundance estimates of Dolly Varden in the Iliamna River >300 mm within the survey area 2005,2007-2009.

Year	Model	abundance	SE	deviance	parameter
2005	Mt	3464	451	15	6
2006	na	na	na	na	na
2007	Mt	2096	221	11	5
2008	Mt	2012	217	10	5
2009	Mt	3679	381	11	5

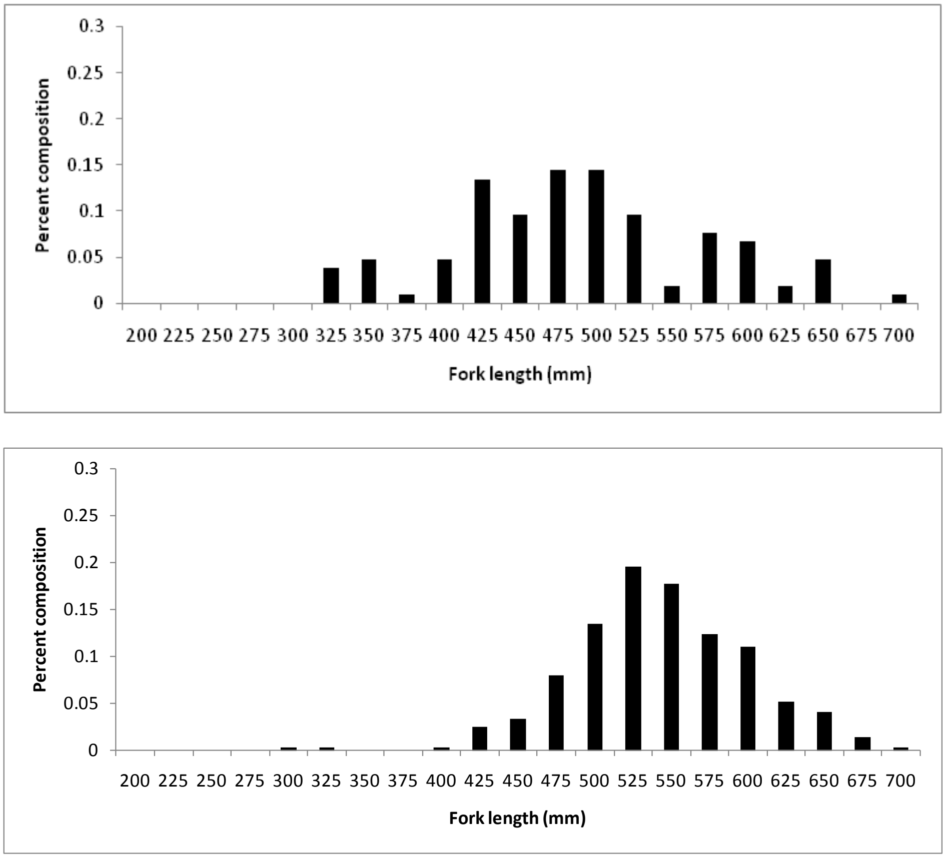


Fig. 1.1. Percent composition of Dolly Varden sampled in 1996-1997

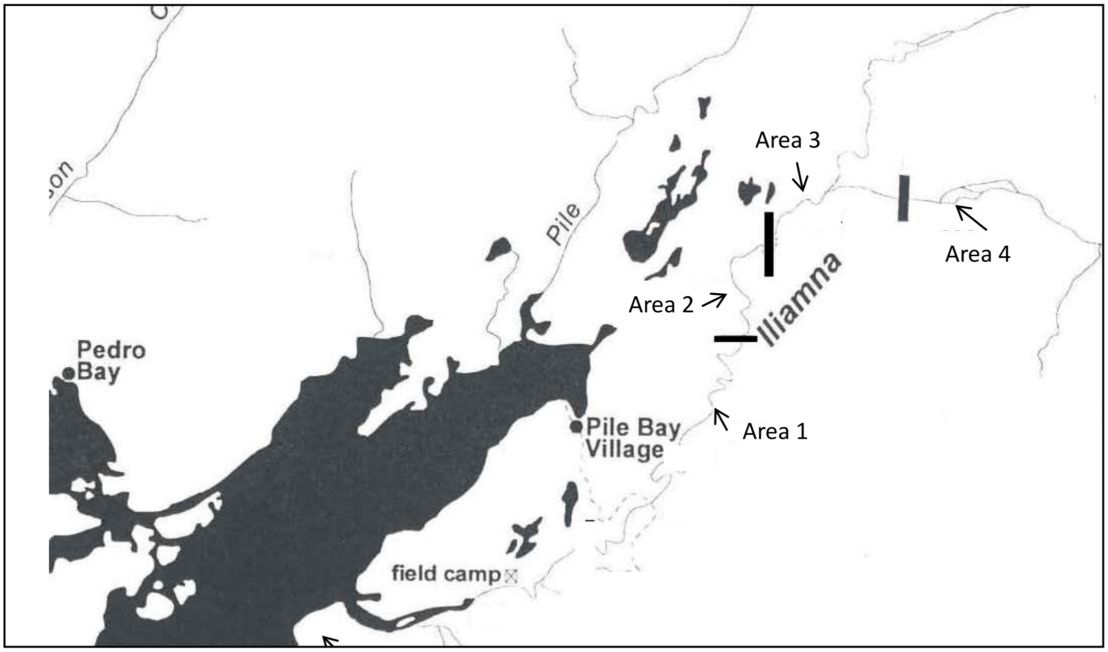


Fig. 1.2. Map of the Iliamna River, indicating areas 1-4, the main survey areas were 2 and 3.

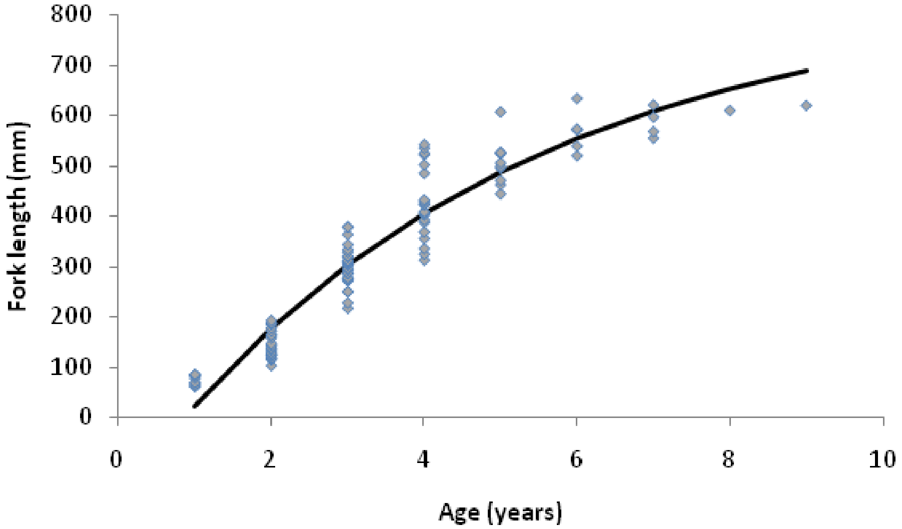


Fig. 1.3. von Bertalanffy growth curve for Iliamna River Dolly Varden based on lengths of individuals whose ages were determined from examination of otoliths.

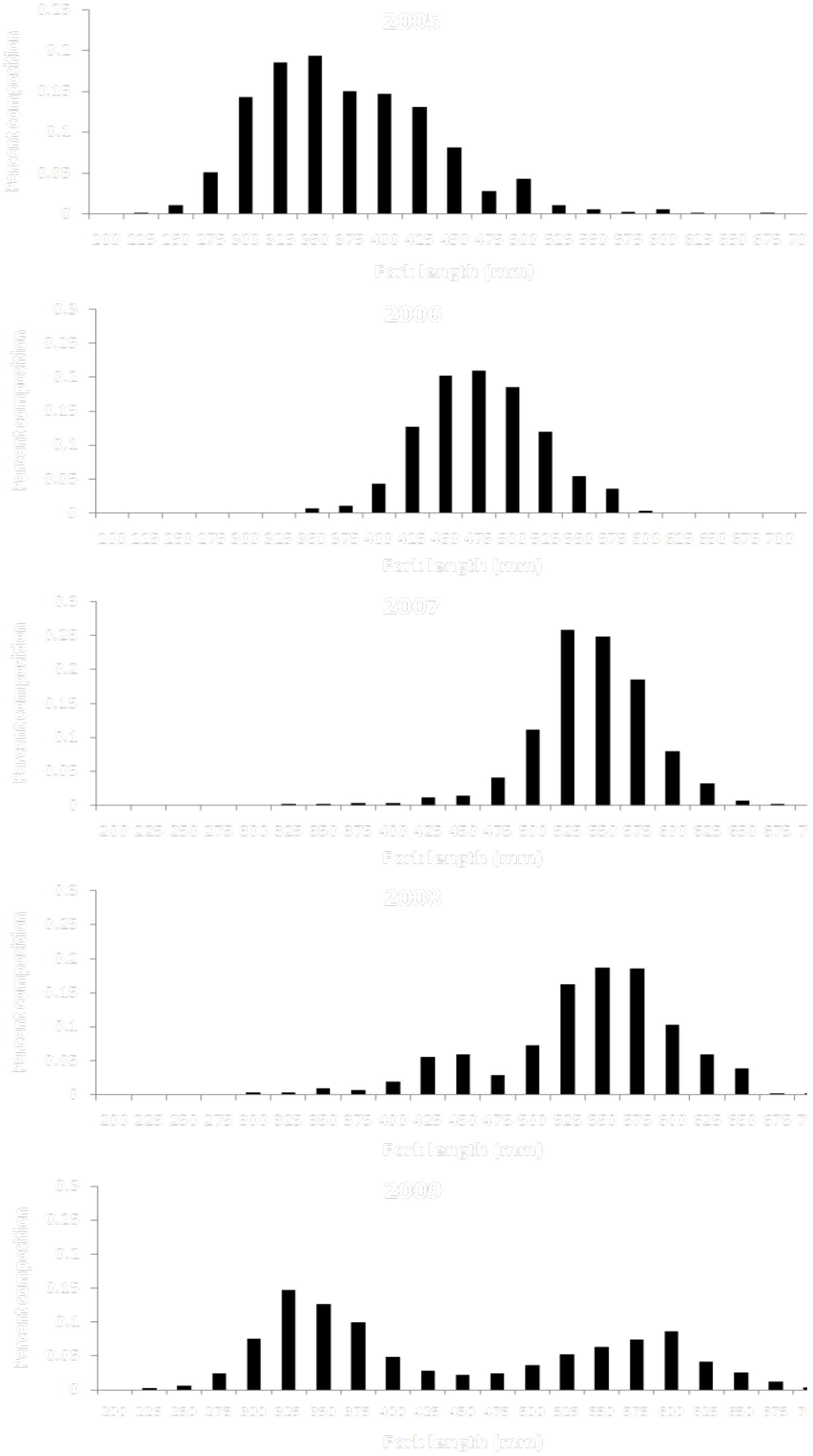


Fig. 1.4. Percent composition by length of Dolly Varden sampled in 2005-2009.

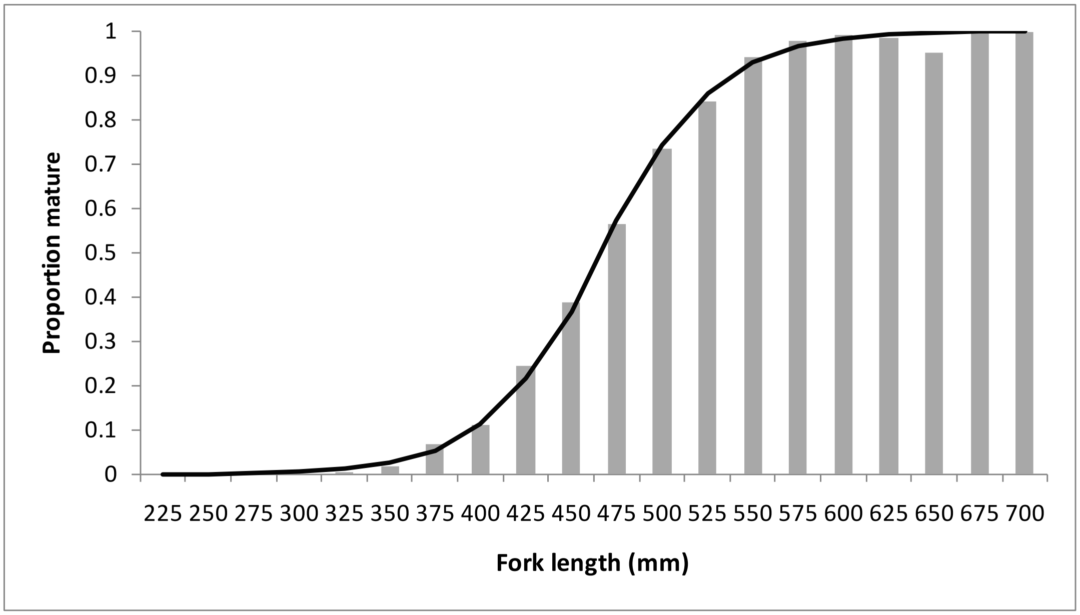


Fig. 1.5. Length frequency with proportion mature (gray bars) of all sampled Dolly Varden in from the Iliamna River 2005-2009 with expected maturity at size (black line).

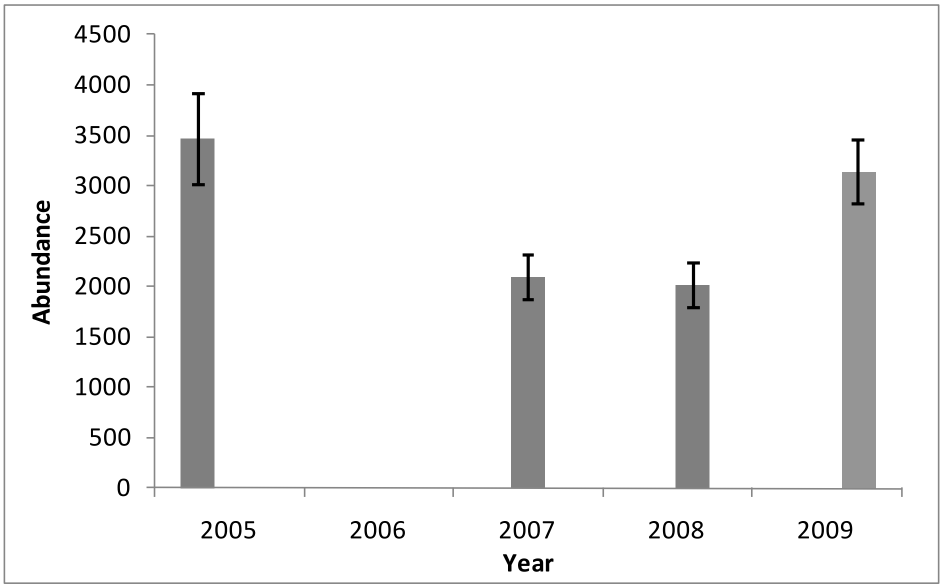


Fig. 1.6. Abundance estimates with standard error of Dolly Varden >300 mm in the Iliamna River.

Chapter 2: Stable isotope analysis reveals ontogenetic shift to dependence on salmon-derived nutrients in Dolly Varden from the Iliamna River

Introduction

Marine subsidy in freshwater systems plays an important role in the ecology of resident fish populations that utilize them through a variety of direct and indirect pathways. This subsidy has been reported in anadromous alosids (MacAvoy et al. 2009) but is most clearly revealed in areas with large runs of semelparous Pacific salmon (*Oncorhynchus* spp) (Janetski et al. 2009). Resident fishes in these areas often experience largely oligotrophic conditions, cold water, and often short growing seasons with limited foraging resources. However, such populations can benefit greatly from pulsed salmon subsidies (Maekawa and Nakano 2002, Wipfli et al. 2003). Marine subsidies in such settings are utilized in some way by nearly all populations of resident fishes within areas of high salmon density throughout Alaska and the Pacific northwest (Schindler et al. 2003) and have been implicated as a factor of success for salmon runs themselves (Adkison 2010). Resident fishes benefit directly by consuming salmon fry in the spring, drifting eggs during spawning in late summer and early fall, flesh from salmon carcasses, and dipteran larvae (maggots) feeding on senescent salmon at the end of the spawning season (Wipfli et al. 2003). Reconstituted eggs, flesh, and maggots from the previous season may also contribute to springtime diets of resident fishes. Salmon also affect the ecology of resident fishes indirectly as engineers. Redd excavation dislodges benthic invertebrates from the substrate, increasing the amount of drift prey available (Field-Dodgson 1987, Scheuerell et al. 2007). Marine nutrients may also have a fertilizing effect, increasing primary production in freshwater (Kline et al. 1990).

The relative importance of salmon subsidies as food and fertilizer has been studied as a factor in the aggregation of adult fishes (Scheuerell et al. 2007), and increased growth in juvenile salmonids (Bilby et al. 1998), and used to compare life histories of sympatric charrs (Denton et al. 2010) but less is known about the role that it plays throughout the lifespan of a resident fish population.

Use of marine subsidy would be predicted to begin when juveniles attained the required gape to ingest eggs (Armstrong 2010) or capture fry (Nowak 2004, Pearsons 1999, Ruggerone 1992) and shift when increased size allowed them to consume larger prey items such as other resident fishes if available. In this scenario, the reliance on salmon products might peak at intermediate body sizes and then decrease as the fish became large. However, considering the quality of marine subsidies as a forage item (i.e., high energy density, visibility, and ease of capture of drifting eggs in a stream) within an oligotrophic stream, continued dependence on salmon-derived resources might be observed even in large-bodied fish. In addition, intraspecific interactions (e.g. competition or predation risk) might reduce availability of the subsidy to smaller size classes in prime feeding habitat, creating a behavioral barrier to maximized subsidy use until they become large enough to compete and avoid predation from larger conspecifics.

The Iliamna River in the southeast corner of the Iliamna Lake system in Bristol Bay in southwestern Alaska, offers an ideal setting to study the use of Pacific salmon marine subsidy by resident fishes. The Iliamna Lake system supports very large runs of sockeye salmon (*Oncorhynchus nerka*), with annual totals of ca. 2 – 6 million adults after well-regulated commercial fisheries, as well as much smaller runs of other Pacific salmon species. The lake system has an entirely native fish fauna, including salmonids such as rainbow trout, *O. mykiss*, Dolly Varden (*Salvelinus malma*), Arctic charr, *S. alpinus,* and lake trout, *S. namaycush*, and a variety of smaller fishes, including but not limited to sculpins (*Cottus aleuticus* and *C. cognatus*), three-spine sticklebacks (*Gasterosteus aculeatus*), nine-spine sticklebacks (*Pungitius pungitus*) and several whitefishes (family Corregonidae). The Iliamna River in particular supports strong and consistent runs of sockeye salmon with up to 200,000 entering the river in late July through August each year. The river itself is free of any major human disturbance, and the sport fishery is lightly used and strictly regulated for catch and release.

Preliminary investigations indicated that Dolly Varden grow rapidly to a large size in this oligotrophic river (this thesis, Chapter 1). It was hypothesized that this growth and maximum body size are related to an energetic subsidy from the eggs, flesh and fly larvae which feed on carcasses (in fall) and fry (in spring) of sockeye salmon. However, it was unknown at what size Dolly Varden began to heavily utilize marine subsidy, and to what extent was it utilized as they became larger. The goal of this study was to quantify the extent to which Dolly Varden of different sizes utilize salmon-derived resources, testing a series of alternative scenarios regarding the ontogeny of foraging. To do so, we used stable isotope analysis of nitrogen and carbon in muscle tissues, because heavier isotopes of nitrogen and carbon (^{15}N and ^{13}C vs ^{14}N and ^{12}C) are more prevalent in marine environments than in freshwater environments, and so serve as an indicator of the derivation of the food resources on which the fish have fed (Fry 2006). Samples taken soon after sockeye salmon fry emerge in the river in June were expected to be lower due to rapid loss of marine signal by salmon fry after emergence and during the salmon spawning season in August they were expected to be high in these isotopes due to salmon eggs and maggots.

Within this population we hypothesized there was one of two definitive size-dependent patterns to marine subsidy use. Within both patterns, we hypothesized that marine subsidy use will first be detected as soon as juvenile Dolly Varden overcome the gape limitation of sockeye salmon eggs at a fork length of ca.70 mm (Denton et al. 2009) and (a) increase with fish size until Dolly Varden became large enough to capture fish, resulting in a mixture of both prey items, or (b) increase quickly to a high level and remain constant through observed the size range. The latter scenario would indicate the ratio of net energy gain to mortality risk (related to piscivory) was not enough to shift foraging patterns. Also, preliminary results showed that juvenile Dolly Varden (< 300 mm) were largely constrained to the upper reaches of the Iliamna River and its tributaries where spawning salmon densities are lower. Sub-adult and adult Dolly Varden (> 300 mm) were encountered wholly in the main stem which suggests juvenile avoidance of adult conspecifics. Thus in both scenarios, it was likely that full utilization of marine subsidy would not be realized until fish were recruited to the main stem.

Methods

Study site and field methods

Dolly Varden were sampled during August of 2008 and 2009 and June of 2009 in the Iliamna River using hook and line techniques and minnow traps in main stem areas and minnow traps in tributaries. Specimens were selected across the available size range to include at least 5 samples for each 50 mm size bin up to 650 mm. All sacrificed fish were identified by sex, weighed, measured for fork length, and otoliths were removed for aging. Muscle tissue samples for stable isotope analysis were taken posterior of the head above the lateral line, and stored frozen in microvials. Otoliths were removed, cleaned and stored dry in microvials.

Diets of sacrificed fish were quantified by item and recorded. Additional diet samples were obtained non-lethally using gastric lavage and stored in ethanol for later analysis. Diets of Dolly Varden captured with minnow traps were not enumerated as they were biased due to the use of salmon eggs as bait and extended length of soak time (18-24 hours) yielded results of either empty stomachs or predictably salmon eggs.

Laboratory protocols

To determine the relative important of food types by size of consumer, lavaged diets were quantified by counts of items or taxa to order. Due to incomplete specimens of most invertebrate prey items, average weight per item was calculated using blotted dry, intact specimens of each taxa and applied to enumerated head pieces.

Tissue samples for isotope analysis were dried at 60° C until a constant mass was reached. Samples were then pulverized into a homogenized powder using a mortar and pestle and ca. 1mg was measured into tin capsules and compressed. All samples were sent to the UC Davis Stable Isotope Facility (http:/stableisotopefacility.ucdavis.edu) and were analyzed for both carbon and nitrogen values with a Europa Hydra 20/20 continuous flow isotope ratio mass spectrometer.

Stable-isotope ratios are expressed as delta values (δ) and measured as the parts per thousand (‰) difference between the sample and that of an international standard according to the formula: $\delta = 1000[(R_{\text{sample}} - R_{\text{standard}})R_{\text{standard}}^{-1}]$, where R = the carbon (^{13}C : ^{12}C) or nitrogen(^{15}N : ^{14}N) of the sample or the standard. UC Davis used three secondary standards to normalize the carbon isotope data on the Pee-Dee belemnite scale for $\delta^{13}C$ (Craig 1957) and the atmospheric nitrogen scale for $\delta^{15}N$ (Mariotti et al. 1983): ammonium sulphate–sucrose, bovine liver (NIST Reference 1577b) and peach material (NIST Reference 1547). These laboratory standards were calibrated against IAEA standards USGS-40 and USGS-41. UC Davis long-term S.D. for their secondary standards are 0.2‰ C and 0.3‰ N.

Data analysis

Diets

The contribution of each prey item was calculated by mean proportion by weight (MW_i) metric (Chipps and Garvey 2007) as:

Where MW_i=mean proportion by weight, P=number of fish with food in their stomachs, Q= number of food types, and W_{ij}=weight of prey type i.

Stable isotopes

To compensate for potential influence of lipid variation on δ^{13}C values of Dolly Varden and end members, all δ^{13}C values were mathematically corrected using the equation for fish muscle tissue (eqn. 5) from (Kiljunen et al. 2006). Previously published values of diet-tissue fractionation for aquatic organisms were used: 2.3 ± 1.6 for δ^{15}N and 0.4 ±1.2 for δ^{13}C (mean ± s.d.) (McCutchan et al. 2003). End member and fractionation stable-isotope ratios are shown in Table 2.1.

Contributions of specific end members to the diet of Dolly Varden were estimated based on the isotopic signatures using the Bayesian mixing model, MixSIR (Moore and Semmens 2008). MixSIR estimates probability distributions of source contributions to a mixture while explicitly accounting for uncertainty associated with multiple sources, fractionation and isotope signatures. End members were chosen based on diet analysis and were separated into two categories: salmon eggs/maggots and benthic invertebrates. Maggots feed on sockeye salmon carcasses and therefore display very similar isotopic signatures to eggs and often co-occur in diet samples. This analysis was repeated across size bins to detect ontogenetic shifts in trophic ecology. End members and their standard deviation were obtained through literature reviews of geographically proximate and topically similar isotopic research (Denton et al. 2010, Moore and Semmens 2008) . MixSIR was run to estimate prey contributions to the diet of each distinct size class to determine size-dependant incorporation of marine subsidy. Dolly Varden were initially divided into 50 mm fork length classes throughout the sample range. Separate MixSIR runs were performed on each consecutively larger size class and similar results were pooled.

Results

Diets

A total of 72 diet samples were collected, 4 during June 2009 and 68 during August 2009. June diet samples were either empty (2) or contained few identifiable items (2) and large amounts of detritus/flotsam including salmon bones, stones and sticks. Prey items observed included a few small benthic invertebrates, the only remnant of fish material observed (the undigested stomach and skin remnants from a small salmonid ca. 60 mm fork length), and three salmon eggs from the previous year. Fish sampled in August revealed a consistent dominance of contents by salmon eggs and maggots (Table 2.2). Samples analyzed from 68 Dolly Varden ranging in fork length from 114 to 620 mm all contained prey items and showed little variation in diet. Stomach contents of Dolly Varden consisted primarily of salmon eggs, maggots and a mix of less common or numerous benthic invertebrates (orders *Ephemeroptera*, *Diptera*, *Plecoptera* and *Tricoptera*).

Stable isotopes

A total of 79 Dolly Varden were sampled for stable-isotope analysis, 23 from a previous study on this population (Denton et al. 2010) collected in 2008, 4 from June 2009 and 52 from August-September 2009. Stable-isotope plots of carbon and nitrogen and results from the MixSIR model runs indicated increasing consumption of salmon eggs and maggots in size classes up to 150 mm fork length (Figure 2.2). Among these size classes, larger fish incorporated more marine subsidy than smaller fish. Larger size classes of Dolly Varden (150 - 650 mm) showed a consistent reliance on the marine subsidy from salmon eggs (Fig. 2.2, Table 2.3). Stable-isotope samples from Dolly Varden sampled in June were similar to those from fish of comparable size (> 400 mm) sampled later in the year (Fig. 2.3), even though there were few marine-derived resources available before June.

Discussion

Overall, stable-isotope analysis reflected the dominance of marine subsidy observed within the diet samples. The diet analysis showed greater reliance on marine subsidies but were somewhat biased because the diets were sampled when salmon eggs were highly available. Both analyses suggest that Dolly Varden in the Iliamna

River forego piscivory and are highly reliant, even as adults, on marine subsidy from sockeye salmon eggs and maggots that have fed on salmon carcasses.

Most surprising of the results was the high marine subsidy from sockeye salmon eggs detected in stable-isotope analysis from Dolly Varden captured in June shortly after peak fry immigration. Although many sockeye salmon fry leave the Iliamna River soon after ice-out to rear in Lake Iliamna, they were not encountered in the diets and stable-isotope samples reflected signatures similar to August. Consumption of sockeye salmon fry cannot be ruled out, but, this subsidy is of a rather short duration because few fry remain in the river after emergence. Capitalizing on migrating fry could also be more difficult than eating sockeye salmon eggs because the fry typically migrate at night in cold water (ca. 3° C) and are evasive, in contrast to the eggs and maggots drifting downstream at summer temperatures up to 10° C when fish are more active. Telemetry studies of this population revealed that few Dolly Varden travel farther than 1 km from the Iliamna River (>200 km from salt water) so other subsidy from marine residency is unlikely.

Mark-recapture data (this thesis Chapter 1) revealed individual Dolly Varden ca. 300 mm long that were captured in August 2009 then recaptured 30-50 days later, by which time they had grown up to 85 mm in length and doubled their mass. Most of the growth that took place over an entire year was accomplished in the brief summer period when the fish consumed eggs and maggots. It is likely that the majority of the yearly ration for Dolly Varden in the Iliamna River comes from consumption of salmon eggs and maggots during August and September when they create large lipid and muscle reserves on which they subsist throughout the winter. Other food sources seem to contribute little to the diet and are maintenance rations at best.

The lack of fish present in either the diets or within the range of observed stable-isotope signatures suggests large Dolly Varden forego piscivory due to the quality and availability of marine subsidies. Freshwater fishes that attain large sizes (> 600mm and > 4 kg) as observed in the Iliamna River, would be expected to shift to a piscivorous diet at least seasonally (Keeley and Grant 2001). Sculpin are a common resident fish within this drainage, however they (or any fish) were very rarely observed in diets. Fish may be, at times, a prey of convenience for Dolly Varden in the Iliamna River, but there is little evidence that it is a major component of their annual energy budget.

Size segregation of fish (< 300 mm in tributaries and > 300 mm in the main stem where sockeye salmon are much more abundant) was hypothesized as the threshold that Dolly Varden must cross to fully utilize marine subsidy in the Iliamna River. However, consistently high levels of marine isotopes in small Dolly Varden (≥ 150 mm) up to the largest individuals sampled (> 600 mm) indicated that near dependence is quickly realize by Dolly Varden in this system. Gape limitation may prevents the smallest Dolly Varden from consuming salmon eggs (Armstrong 2010) but maggots (with a similar isotopic signature) are smaller and may allow juveniles to utilize marine subsidy earlier than expected. Also, sockeye salmon abundance is much higher in the main stem than in tributaries, but relative ration size of sockeye salmon eggs to smaller fish are larger and likely require a less abundant marine subsidy to display the same contribution.

Size segregation observed in the Iliamna River can be explained by several likely hypotheses. Large Dolly Varden found in the main stem would be at risk of predation within the clear, shallow waters of the tributaries. Conversely, smaller Dolly Varden avoid predation or aggression by larger conspecifics (Denton et al. 2010). Juvenile Dolly Varden face a tradeoff between maximizing growth from the much larger amount of available marine subsidy in the sockeye salmon spawning areas in the main stem and minimizing exposure to potential predators (e.g. larger Dolly Varden and rainbow trout that aggregate within sockeye salmon spawning areas) by remaining in tributaries. Although piscivory appears to be a small component of the diet of even the largest Dolly Varden in the Iliamna River, it could be the result of this behavioral segregation. They would likely forage more heavily on smaller conspecifics if given the opportunity.

It was expected that migration of smaller Dolly Varden to the main stem with higher spawning salmon densities would be required for Dolly Varden to maximize marine subsidy use. However, it is clear from stable-isotope analysis that there is sufficient marine subsidy in tributaries for fish > 150 mm fully utilize this resource.

Beyond the dynamics of marine subsidy use by Dolly Varden in the Iliamna River, this study speaks to the importance of Pacific salmon to resident fishes in general. The role of salmon as benefactors of resident fishes, not only as direct providers of marine subsidy but also as system fertilizers (Bilby et al. 1998) and bioengineers (Scheuerell et al. 2007), has been studied in many systems and tissue exploitation by resident fishes is the typical result (Denton et al. 2009). In this study, the role of marine subsidy in its most direct form appears to be a key component in the ecology of this Dolly Varden population. It is utilized to a large degree of every size class > 50 mm and is the key forage item for all fish > 150 mm. It is therefore unlikely that this population could attain the observed size and density (this thesis, Chapter 1) in the least, or maintain its very existence at the most without large inputs of direct marine subsidy. Scheuerel et al. (2007) applied growth models to rainbow trout and Arctic grayling (*Thymallus articus*) that experience large salmon subsidies. Model projections for growth with and without salmon were calculated and revealed severely lower growth for grayling and negative growth for rainbow trout without salmon subsidy. Salmon populations have been depressed throughout much of their range due to habitat degradation, altered flow regimes from dams, pollution from municipal, industrial or agricultural sources and much attention has been given directly to improvements for the sake of salmon themselves. However, the effect of decreased marine subsidy must also be considered as it relates to resident fish populations (Schindler et al. 2003). The remote and generally unaltered and well-managed setting of this study quantifiably highlights how necessary strong salmon runs are to healthy maintenance of resident fish populations and the need to include this aspect of salmon biology in restoration and preservation efforts.

Table 2.1. Fractionation and end member inputs used in MixSIR analysis, values taken from literature.

	$\delta^{15}N$	S.D.	$\delta^{13}C$	S.D.
Fractionation	2.3	1.61	0.4	1.21
Eggs/maggots	2.25	1.00	-20.88	0.90
Benthic insects	4.12	0.33	-27.09	0.35

Table 2.2. Proportion by mean weight(MW_i)and frequency of occurrence (O_i) from Iliamna Dolly Varden sampled in the Iliamna River during August.

Prey	MW_i	S.E.	O_i
Eggs	96%	1.4%	100%
Maggots	3%	1.3%	64%
Benthic	1%	0.4%	43%

Table 2.3. Proportional diet contributions eggs/ maggots versus benthic invertebrates to different sizes of Dolly Varden in the Iliamna River in August, based on results of the stable isotope mixing model.

	Fork length (mm)									
	50-99	100-124	125-149	150-199	200-249	250-299	300-349	350-399	400-499	500+
Eggs/maggots	0.29	0.54	0.53	0.84	0.82	0.89	0.82	0.85	0.78	0.81
Benthic	0.71	0.46	0.47	0.17	0.18	0.11	0.18	0.15	0.22	0.19

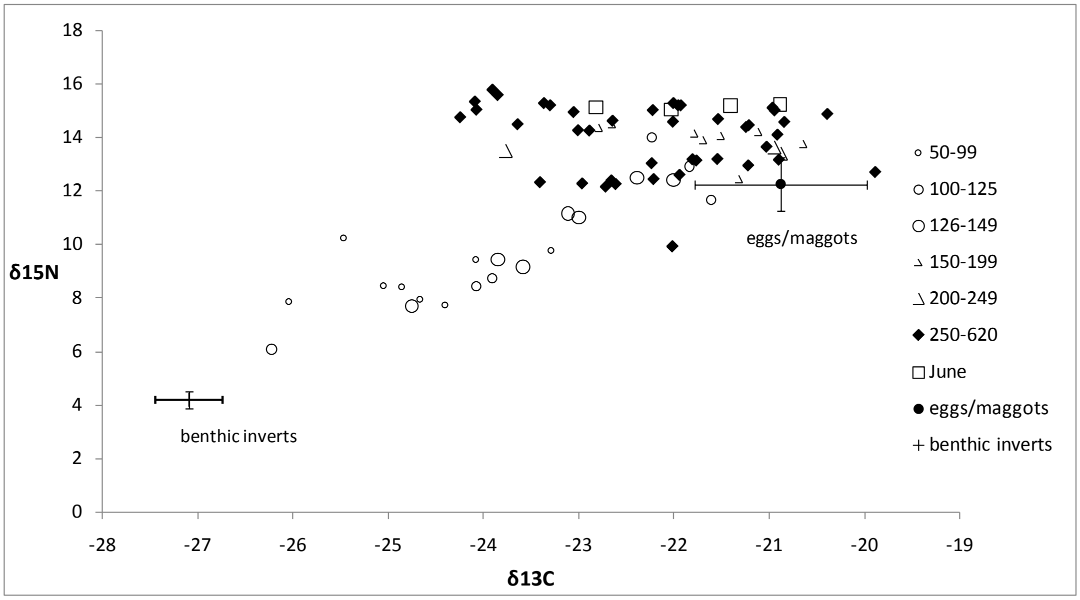
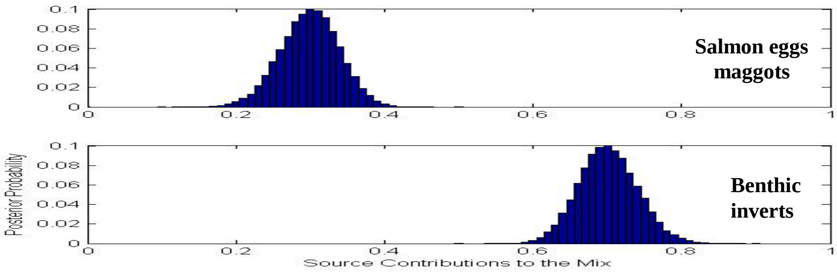
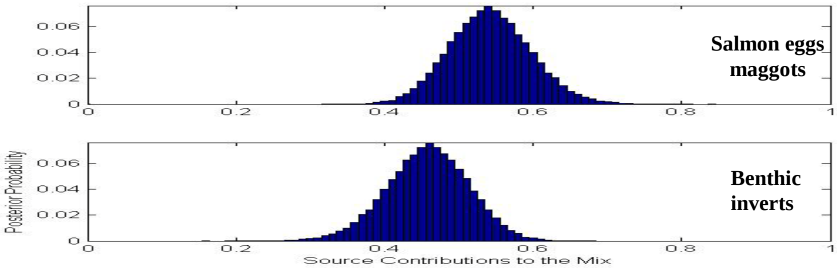


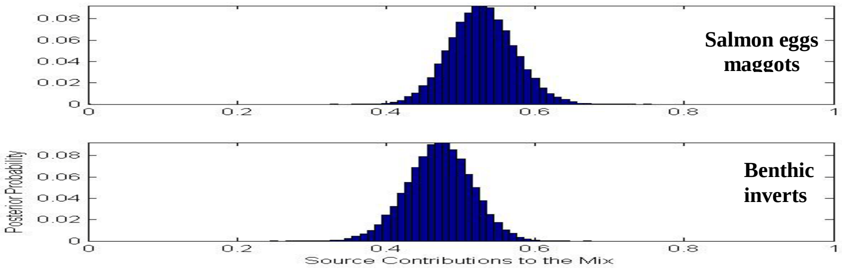
Fig. 2.1. Stable-isotope ratio plots from Iliamna River Dolly Varden with literature isotope values for benthic invertebrates and eggs/maggots as end members.



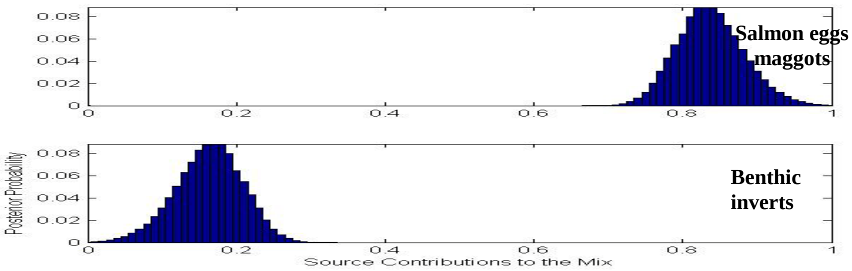
50-99 mm



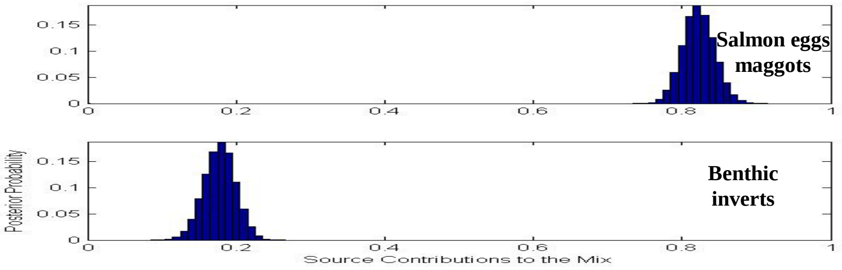
100-124 mm



125-149 mm

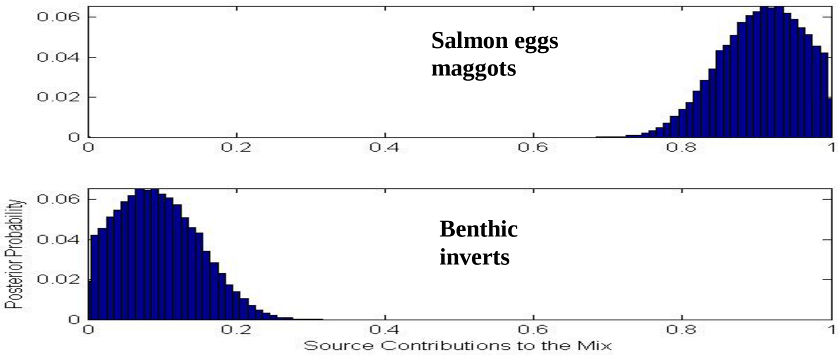


150-199 mm



200-620 mm

Fig. 2.2. MixSIR plots of stable-isotope analyses source contributions of Iliamna River Dolly Varden sampled in August across encountered size ranges.



June

Fig. 2.3. MixSIR plots of stable-isotope analyses source contributions of Iliamna River Dolly Varden sampled in June (fork length > 450 mm).

Chapter 3: Dietary reliance on Pacific salmon eggs creates Sr/Ca signatures that mimic anadromy in otoliths of resident Dolly Varden *Salvelinus malma*

Introduction

Otolith microchemistry has proven useful for documenting the chronology of diadromous migration in many species of teleost fishes. Sagittal otoliths serve as chemical storage devices which, when compared to elemental gradients in different environments, can reveal fish migration patterns. In particular, the ratio of strontium (Sr) to calcium (Ca) across annuli of otoliths has been widely used to determine migration patterns because higher Sr concentrations are typically found in marine compared to freshwater environments, and Sr passively replaces calcium in bony structures such as otoliths (Brenkman et al. 2007, Campana 1999, Elsdon and Gillanders 2004, Volk et al. 2000). Conversely, barium (Ba) is more abundant in freshwater systems compared to saltwater but acts much like Sr in Ca replacement within otoliths, and has also been used to indicate fish migrations (Allen et al. 2009, de Vries et al. 2005, Elsdon and Gillanders 2005). Since these elements are rarely found in high concentration concurrently, there is little information about their interactions with each other. However, at low salinities, Sr spiked water has been found to increase Ba uptake (Collingsworth et al. 2010, de Vries et al. 2005). These methods have proven useful as indicators of diadromy but they are based on the assumption that there is a marked difference between fresh and saltwater concentrations in these elements, and that groundwater sources and diet are at most minor contributors to elemental concentrations in otoliths (Walther and Thorrold 2006).

In most cases there is insufficient marine-derived material in the environment or diets of freshwater fishes to be a significant source of Sr, but the extremely high densities of adult semelparous Pacific salmon present the possibility that the otolith chemistry signals of freshwater resident fishes might mimic those of anadromous individuals. Strontium from marine sources can be made available to freshwater fishes through two pathways. First, elevated levels of Sr from the breakdown of large numbers of dead salmon within confined areas (i.e. a small stream or pond) could elevate ambient concentrations. Second, the uptake of Sr through a diet dominated by marine sources such as salmon eggs and flesh (Scheuerell et al. 2007, Wipfli et al. 2003) could make a detectable contribution to Sr levels in resident fish.

For otolith microchemistry to be a viable tool in assessing migration history of anadromous fishes, extreme situations need to be assessed to test the limits of its applicability. If “pseudo-anadromy” can occur in populations associated with heavy marine subsidy, then considerable care would have to be exercised when using this technique on resident fishes in situations where anadromous species also occur at high densities.

Charr, fishes of the genus *Salvelinus*, exhibit a high degree of life history plasticity including multiple morphs within and among systems throughout their circumpolar range. Dolly Varden , *S.malma*, occur in drainages of the northern Pacific Ocean, from northern Japan and the Kamchatka Peninsula of Russia to Alaska and both Arctic and Pacific Canada and south to Washington state. Throughout their range, Dolly Varden grow larger in body size and are more often anadromous at higher latitudes (Maekawa and Nakano 2002). In areas where they are sympatric with anadromous Pacific salmon, they often feed heavily in late summer and fall on salmon eggs, carcass tissue, and terrestrial insects that have been scavenging salmon carcasses (this thesis, Chapter 2), and also feed heavily in spring on juvenile salmon (Denton et al. 2009, 2010).

Preliminary examination of chemical signals in otoliths from six Dolly Varden collected in 2006 yielded evidence that they were anadromous, based on the elevated Sr/Ca ratios after several years of life. However, radio-tracking conducted in 2007-2008 failed to detect Dolly Varden migrating any appreciable distance from the river into Iliamna Lake much less to sea. Also, at this time we were becoming aware of the extreme reliance on sockeye salmon, *Oncorhynchus nerka,* eggs and other salmon tissue sources as food for this population and another, small-bodied population of Dolly Varden in a series of spring-fed ponds nearby, at the village of Pedro Bay, and to a lesser degree in Arctic charr, *S. alpinus,* in Iliamna Lake (Denton et al. 2009, 2010). Accordingly, we sampled additional Dolly Varden from the Iliamna River as well as the Pedro Bay ponds, and also Arctic char from Iliamna Lake for comparison between lacustrine and riverine fish. These results were consistent with the earlier results, suggesting anadromy in both populations of Dolly Varden but not the Arctic char. Finding these results inconsistent with the radio-tracking in the case of the Iliamna River fish, and the very small body size (ca. 20 cm) of the Pedro Bay pond fish, we commenced additional sampling to critically test the hypothesis of anadromy by processing otoliths from both Dolly Varden populations for Ba/Ca and Sr/Ca to discern if these elements would display opposite trends in concentration, as expected if marine migration had occurred. As an additional comparison, we processed otoliths from rainbow trout collected from the Iliamna River as they have access to similar prey as the Dolly Varden but are not known to be anadromous in this part of the species' range. We also collected water samples from the pond, river and lake areas to assess background levels from geologic sources. To assess Sr incorporation due to chemical deposition from salmon carcasses, water samples were collected from reaches above, within, and below the high density areas of spawning salmon, and also prior to, during, and after the spawning period in the Iliamna River.

The comparisons of Ba/Ca and Sr/Ca from the same specimens and the water samples were designed to distinguish between three competing hypotheses. First, if the fish had migrated to sea and back, we would expect elevated Sr/Ca ratios after a few years of life, once they became large enough to accomplish the migration. We would also expect Ba/Ca ratios to decline during periods of high Sr/Ca, reflecting the opposing concentrations in marine and freshwater as indicated in studies of known anadromous salmonids. The water samples from the river would be expected to show low Sr/Ca ratios if the high Sr levels in otoliths came from the marine environment rather than the river. Second, if the fish had not migrated to sea but the elevated Sr/Ca levels resulted from saturation of the Iliamna River water with chemicals from the decaying carcasses of the salmon, water samples prior to the arrival of salmon and those taken above the region used for spawning would differ from those taken during and after spawning in the reach used for spawning and the reach below it. These latter samples would be elevated in Sr/Ca ratio if the carcasses had been the source of the Sr.

The third hypothesis was that the consumption of sockeye salmon eggs produced the elevated Sr/Ca levels in the Dolly Varden. In this case, the Sr/Ca ratios would be periodically high and the Ba/Ca data would show consistent ratios near freshwater values with little fluctuation or increase in parallel with Sr, reflecting the stability of Ba in freshwater or the positive relationship of these elements suggested by laboratory experiments.

In this paper we first present the preliminary data from otoliths collected from the Iliamna River fish in 2006 and the comparison to specimens of the species from populations known to be resident and anadromous. We then present the data from subsequent samples (Pedro Bay pond Dolly Varden, Arctic char from Iliamna Lake and additional Iliamna River Dolly Varden). Finally we present water chemistry data and dual elemental analysis of Sr/Ca and Ba/Ca data (from the same otoliths) from Dolly Varden from the Pedro Bay ponds and Iliamna River and also from rainbow trout sampled in the Iliamna River. Collectively, these samples allow us to distinguish among the three competing hypotheses for the elevated Sr/Ca ratios in the Dolly Varden from the Iliamna Lake populations, and conclude that extreme reliance on salmon-derived resources and especially eggs generated the false impression of anadromy in these resident fish. This is important both from the methodological standpoint but also for the implications regarding the ecological link between salmon and resident fishes.

Methods

Study site and field methods

Iliamna Lake, its tributaries, and associated smaller lakes, are in a nearly pristine condition in terms of habitat quality, with no logging, agriculture, impassable dams, and limited human population development. The lake is geologically diverse, with steep mountains and deep, island-rich waters in the eastern end of the lake, transitioning to shallower water and low-lying tundra and fewer rivers on the western end (Rich 2006), where it flows 97 km via the Kvichak River into Bristol Bay. It supports very large runs of sockeye salmon, with annual totals of ca. 2 – 6 million after well-regulated commercial fisheries, as well as much smaller runs of other Pacific salmon species. The lake system has an entirely native fish fauna, including salmonids such as rainbow trout, Arctic charr and Dolly Varden, and also lake trout, *S. namaycush*, and a variety of smaller fishes, including but not limited to sculpins (*Cottus aleuticus* and *C. cognatus*), three-spine sticklebacks (*Gasterosteus aculeatus*) and nine-spine sticklebacks (*Pungitius pungitus*).

Dolly Varden and Arctic charr were caught using seines and hook and line from the Pedro Bay ponds in 2008, Iliamna River in 2006-2009 and Iliamna Lake in 2008. Captured fish were identified by sex and sampled for length and weight. Otoliths were removed, and stored dry in microvials. Gut contents were either enumerated or stored in ethanol for later analysis and samples for stable-isotope analysis were taken as reported in Denton et al. (2010) and this thesis, Chapter 2.

Otolith microchemistry

Initial otolith microchemistry analysis

Initial otolith micro chemistry for Sr/Ca levels was conducted on six Dolly Varden sampled in 2006 from the Iliamna River. Otoliths were analyzed in accordance with methods outlined in Brown and Severin (2007). One otolith from each fish was thin-sectioned through the core and mounted on a glass slide. Each section was 200–300 µm thick, and growth increments from the core region to the margin were visible with transmitted light. They were polished on a lapidary wheel with 1 µm diamond abrasive and coated with a conductive layer of carbon in preparation for microprobe analyses.

A wavelength-dispersive electron microprobe (microprobe) was used for chemical analyses of otoliths. The technology functions by directing a focused beam of electrons to points on a sample surface. Atoms within the material are ionized by the electron beam and emit X-rays unique to each element. Spectrometers are tuned to count the X-rays from elements of interest. The electron beam used here was 5 µm in diameter and was operated at an accelerating voltage of 15 kilo-electron volts and a nominal current of 20 nanoamperes. According to Gunn et al. (1992), the electron beam penetrates less than 3 µm into otolith material. Strontium and Ca X-rays were counted for 25 s at each point along a core-to-margin transect (core precipitated early in life, margin precipitated late in life) for each otolith. Center-to-center distance between points was 8 µm. Element specific X-ray counts at each point are proportional to the concentration of the element in the sampled material (Goldstein 2003, Reed 1997). Strontianite and calcite standards were used with established quantitative procedures to develop conversion factors between X-ray count data and elemental concentration estimates in units of mg*kg–1, as detailed by Brown et al. (2007). Elemental concentrations of Sr, Ba and Ca throughout all otolith microchemistry and water analysis were converted to molar concentrations using the following equivalencies:

and

and

Comparison with resident species

Otoliths from 10 Dolly Varden from the Iliamna River and five from the Pedro Bay pond complex as well as five Arctic char from Iliamna Lake were collected in 2008 and analyzed to better define results observed in initial analyses. Iliamna River fish were included to confirm patterns observed in 2006, Pedro Bay pond Dolly Varden and Iliamna Lake Arctic char were included to represent presumably resident populations. The Pedro Bay ponds Dolly Varden were considered resident due to their small size (max length ca. 250 mm) and Arctic char due to known migration history of this population. One sagittal otolith from each fish was embedded in epoxy (Epo-Thin, Buehler Ltd.) and a transverse section was cut through the core using a diamond wafering saw. Otolith mounting and preparation followed the methods of Donohoe and Zimmerman (2010). The transverse section was glued to a cover slip attached to a glass slide on one edge and ground with 2000-grit sandpaper to remove saw marks. The section was then polished with a slurry of 0.05 µm alumina paste. The cover slip was cut with a scribe so that several prepared otoliths could be mounted on a petrographic slide for microprobe analysis. The petrographic slide containing several otoliths was rinsed with deionized water, air dried, and carbon coated. Elemental analysis was conducted with a JEOL JXA-8800L wavelength dispersive microprobe. A 15 kV, 50 nA, 10 µm-diameter beam was used for all analyses (Zimmerman and Nielsen 2003). Strontiantite ($SrCO_3$) and calcite ($CaCO_3$) were used as standards for Sr and Ca, respectively. Each element was analyzed simultaneously; and a counting time of 40 s was used to maximize precision (Toole and Nielsen 1992). Sr was measured using the TAP crystal and Ca was measured using the PET crystal. A transect of points with a spacing of 10 to 25 µm was measured from the center of the core to the edge of the otolith. After microchemical analysis, the carbon layer was cleaned from the surface of the otoliths and each otolith was photographed at a 45x magnification using a digital camera connected to a dissecting microscope. The otolith was placed on a black background and reflected light was used to accentuate the presumed annuli. The age of each fish was determined by counting alternating translucent and opaque regions. Under reflected light, annuli correspond to the translucent zone (Kalish 1995). The distance from the center of the core to each annulus was measured along a standardized transect. A single observer conducted all measurements.

Dual elemental analysis

Otoliths from Iliamna River and Pedro Bay ponds Dolly Varden were prepared for dual elemental analysis using standard methods to minimize contamination (Miller 2009). Otoliths were mounted on a petrographic slide with thermoplastic cement, sulcus side up, and then ground with 1200 grit sand paper to near the core. Otoliths were then heated to loosen the resin, turned and ground laterally with increasingly fine lapping paper to reveal all annuli. Otoliths were then sonicated in nanopure water and dried in a clean room. Otolith ^{43}Ca, ^{86}Sr, and ^{138}Ba data were collected using a VG PQ ExCell inductively coupled plasma mass spectrometer (ICPMS) with a New Wave DUV193 excimer laser. The laser was set at a pulse rate of 10 Hz with a 40 µm diameter spot size and travelled at 5 µm s^{-1}. Limits of detection (ppm) were calculated as 3 standard deviations of background measurements: Ca = 0.02, Sr = 0.03, and Ba = 0.008. Normalized ion ratios were converted to elemental ratios as described in Miller (2007), converted to molar ratios based on the molar mass of Ca, Sr, and Ba, and presented as mmol mol^{-1} for Sr/Ca and µmol mol–1 for Ba/Ca. The mean percent relative standard deviations (%RSD) for NIST 612 glass during data collection were ^{43}Ca = 3.2, ^{86}Sr = 4.1, and ^{138}Ba = 4.4%. A calcium carbonate standard of known composition developed by the US Geological Survey (USGS MACS-2) provided an estimate of accuracy: measured values were within 2% of known values for both Sr/Ca and Ba/Ca.

Water chemistry

Water samples were collected in late July, August and September 2009 from the Iliamna River, Pedro Bay pond complex and Iliamna Lake. The timing of collections was intended to encompass the beginning, middle and end of sockeye salmon abundance to determine if the increasing number of senescent salmon was associated with increasing Sr concentrations. Similarly, the Iliamna River was sampled at the river km 3 (below most spawning), r km18 (in the area of high salmon density) and r km 30 (above the area where most salmon spawn) to determine if there were any spatial patterns in chemistry related to salmon density. Samples (250 ml) were collected in acid-washed bottles and analyzed using ICP-MS for concentrations of Sr, Ba and Ca. Ratios were calculated using concentrations and compared to levels observed in analyzed otoliths and also with levels established in literature to assess relative concentrations. Increase in concentrations during the salmon run would denote elemental deposition due to senescent salmon, consistent concentrations or levels well below observed rates in otoliths would rule out ambient water as an elemental source.

Results

Otolith microchemistry

Initial otolith microchemistry analysis

Initial analysis of samples collected in 2006 revealed generally low and consistent Sr/Ca levels near the otolith core with periodic fluctuations beginning at points corresponding to the second to third annulus and continuing through the rest of the fish's life. The ratios observed at the peak of these fluctuations were indicative of saltwater migrations in other salmonids. These scans, when compared with images from well-studied resident and anadromous Dolly Varden populations from Northwest Alaska (Figure 3.1) show periodic variability consistent with annual events that cause a significant rise and then fall in Sr/Ca. Interpretation of otolith microchemistry analysis is not as much a matter of absolute numbers but the relationship of each scan across the otolith patterns signifying chemical changes in the environment throughout the life of the fish. However, within normal water chemistry constraints, 1.5-1.7 mmol/mol Sr/Ca is a level that strongly indicates saltwater residence (Randy Brown, United States Fish and Wildlife Service, 101 12th Avenue, Room 110, Fairbanks, AK, 99701, personal communication). All Dolly Varden otoliths analyzed reached or exceeded this level at least once, suggesting that Dolly Varden from the Iliamna River made annual migrations to saltwater as seen in many populations of the species.

Otolith microchemistry comparison with resident populations

ICPMS otolith scans of Dolly Varden from the Iliamna River and Pedro Bay ponds collected in 2008 revealed similar results to the original scans. Not only the larger-bodied Iliamna River Dolly Varden (Figure 3.2) but, more surprisingly, the smaller Pedro Bay pond fish had otolith chemistry patterns consistent with anadromy (Figure 3.3). Lower Sr/Ca levels in areas near the core were followed by periodic fluctuations in both Dolly Varden populations representing apparent migrations to marine waters. Pedro Bay ponds Dolly Varden displayed slightly higher Sr/Ca near core areas but similar periodic fluctuations through the remaining annuli. As expected, Arctic char from Iliamna Lake exhibited consistently lower Sr/Ca ratios than those of either Dolly Varden population, and no periodic fluctuations that would indicate migration (Figure 3.3). Thus these otoliths were consistent with non-anadromous fish.

Dual elemental analysis

Dual elemental analysis of Dolly Varden from both the Iliamna River (Figure 3.4a) and Pedro Bay ponds (Figure 3.4b)showed Sr/Ca patterns consistent with former analyses (i.e., high and fluctuating levels of Sr/Ca that were consistent with anadromy) in all otoliths examined. However, Ba/Ca levels remained at or above levels typical of freshwater systems. (ca. 5 mmol/mol). Ba/Ca ratios indicated that the fish had continuously resided in freshwater, (Figure 3.4), thus the uptake of high levels of Sr had taken place in freshwater. Ba/Ca was expected to remain near freshwater values with little variation, but instead fluctuated positively with Sr/Ca to relatively high levels synchronously with high Sr/Ca values. Rainbow trout otoliths did not display the same degree of fluctuation as Dolly Varden otoliths but low Sr/Ca near the core area and first several annuli, followed by high Sr/Ca near the otolith margin, approaching those that might be seen in anadromous fish (Figure 3.4c)

Water chemistry

Elemental water analysis established that the background ratios for the Iliamna River, Pedro Bay Ponds and Iliamna Lake that were all well within published freshwater ranges for Sr/Ca (ca. 2.39 mmol/mol in freshwater and 8.54 mmol/mol in saltwater)(Brown and Severin 2009) and Ba/Ca (ca.1.4 mmol/mol in freshwater and

0.005 mmol/mol in saltwater)(Miller et al. 2010) (Table 3.1). Neither temporal nor spatial differences were detected within the Iliamna River, indicating that sockeye salmon carcass deposition did not determine the patterns found in otoliths. However, Sr/Ca and Ba/Ca in the water samples differed between locations. Iliamna Lake displayed the lowest Sr/Ca and Ba/Ca (2.21 mmol/mol and 0.24 mmol/mol respectively). The Pedro Bay Ponds displayed the highest Sr/Ca (3.83 mmol/mol) and the Iliamna River displayed the highest Ba/Ca (1.03 mmol/mol).

Discussion

Based on previous research, the elevated Sr/Ca ratios observed in the Dolly Varden from the Iliamna River and Pedro Bay ponds would be interpreted as indicative of anadromous individuals. It was therefore imperative to establish the actual migration histories of both populations before defining a source. The hypothesis of continual freshwater residency was strongly supported by dual-elemental analysis of Sr/Ca and Ba/Ca. Sr and Ba are found at stable concentrations in both fresh and saltwater, but with opposite gradients in each medium. Comparisons of Sr/Ca and Ba/Ca conducted in known anadromous fish have exhibited the expected transposition of concentrations when moving from fresh to saltwater (Elsdon and Gillanders 2005, Tabouret et al. 2010). However, dual elemental analyses of Dolly Varden in this study showed that the lowest observed Ba/Ca values were well above those observed in saltwater and indicate that none of the Dolly Varden had been to saltwater.

A plausible alternative explanation would have been exceptionally high Sr concentrations in the freshwater environment. However, water chemistry analysis offered no indication that there was a geologic source of high levels for Sr, nor any evidence that decaying salmon carcasses were releasing elements that might give the false impression of anadromy.

Given the data from the water samples, indicating levels of Sr that were not unusual, and dual elemental analysis, that neither population had experienced saltwater, the parsimonious explanation is that the elemental Sr/Ca levels that mimicked a marine migration were generated by a very Sr-rich diet. It has been recognized that diet can affect otolith chemistry but results have varied from little to no effect in marine fishes (Farrell and Campana 1996, Marohn et al. 2009, Walther and Thorrold 2006) to limited increases in Sr/Ca in freshwater fishes (Limburg 1995).

Diet analysis (this thesis, Chapter 2 and Denton et al. 2009, 2010) clearly indicate that these two Dolly Varden populations rely very heavily on salmon tissue (eggs and flesh from carcasses), maggots that had consumed salmon tissue, and salmon fry. Prior to the annual arrival of adult salmon and the opportunity to feed on eggs, flesh and maggots, the Dolly Varden feed at low apparent rates, as only a few insects were found in their stomachs during this time period. Dolly Varden in the Iliamna River and Pedro Bay ponds have full access to a high Sr diet in particular through sockeye salmon eggs. Salmon eggs are largely developed in saltwater (Volk et al. 2000) and reflect the high Sr content of ocean conditions (ca. 3 ppm) (Waite et al. 2008) to the extent that they result in the formation of elevated Sr/Ca levels in the core of anadromous fish otoliths. Additionally, Sr in salmon eggs is in solution and thus more likely to be incorporated intestinally than Sr from hard structures (e.g. bones or shells) or flesh and extremely abundant during a period of high fish growth rates.

Dietary Sr uptake from sockeye salmon eggs occurs in a full freshwater environment with low background Sr levels so any dietary effect is less likely to be masked as may occur in high Sr marine conditions. Arctic char diet analysis did not show as heavy of a reliance on sockeye salmon subsidies (in particular, salmon eggs) and this may explain the lack of fluctuations that were observed in the Dolly Varden populations. Specifically, Arctic char had fed on snails and three-spine sticklebacks but none had eaten salmon eggs or juvenile salmon at the time of capture. Rainbow trout otoliths showed increased Sr/Ca later in life to near anadromous levels, but did not display the sharp contrasts and continued periodicity detected in the Dolly Varden otoliths. Although rainbow trout feed heavily on sockeye salmon eggs, they also utilize a greater area of the Iliamna Lake system. For example, 3 of 183 tagged rainbow trout released in the Iliamna River were captured more than 60 km away from the Iliamna River within 21-40 days of their initial capture (compared to none of > 2000 tagged Dolly Varden, this thesis, Chapter 1) and may have access to more diverse forage sources. However, the marked increase from base Sr/Ca levels observed in rainbow trout otoliths suggested a similar, but less defined dietary effect.

Although the positive relationship observed between Sr/Ca and Ba/Ca in the Dolly Varden otoliths did not reflect the low variability hypothesized, it did confirm continual freshwater residency. Similar variability was also observed in controlled experiments using Sr-spiked water (Collingsworth et al. 2010, de Vries et al. 2005) . Laboratory experiments conducted at varying salinities using spiked Sr concentrations revealed that in brackish waters, high Sr concentrations facilitated increased uptake of Ba into otoliths, but there was no effect in full saltwater. This effect was more pronounced in freshwater and could explain the positive relationship observed between Sr and Ca in Dolly Varden otoliths as abnormally large amounts of Sr (through consumption of sockeye salmon eggs) were available in the normally high Ba level environment experienced in freshwater.

While the argument could be made that the scenario in this study is extreme in the context of otolith microchemistry research, it does highlight aspects of aquatic systems and fish life histories that need to be addressed in future investigations. Otolith Sr/Ca analyses cannot be held as the litmus test alone without also considering and exploring other sources of information such as freshwater chemistry, complementary elemental ratios such as Ba/Ca, potential for marine subsidy, diet, radio-telemetry and other kinds of information about life history and movement.

Dolly Varden are sympatric with high densities of sockeye and other Pacific salmon throughout much of their northern range, and often utilize marine subsidy in both anadromous and resident populations so the populations in this paper are not unique in regard to potential for pseudo anadromy using otolith microchemistry techniques. Thus it remains to be seen if other populations thought to be resident may also show elevated Sr/Ca. Conversely, there may be populations thought to be anadromous due to Sr/Ca analysis that may contain a subpopulation that exhibit freshwater Ba/Ca as the Dolly Varden studied in this paper.

Throughout this investigation, chemical otolith analysis provided information contrary to raw observation, requiring further refinement of methods to test all assumptions and establish a likely conclusion. Knowledge gained from this study is certainly most pertinent to researchers within the range of healthy runs of Pacific salmon but bears a broader applicability to the discipline of otolith microchemistry as it establishes what conditions may lead to misleading results, and a strategy to discern the difference.

Table 3.1. Elemental concentrations and molecular ratios of Ba/Ca and Sr/Ca in freshwater sampled during the early, middle and late stages (late July, August and September) of the sockeye salmon run in the Iliamna Lake area.

	Early		Middle		Late	
	Ba (µg/L)	Ba/Ca (mmol/mol)	Ba (µg/L)	Ba/Ca (mmol/mol)	Ba (µg/L)	Ba/Ca (mmol/mol)
Iliamna River-Bottom	7.77	1.03	8.74	1.03	8.57	0.94
Iliamna River-Middle	8.48	1.14	9.05	1.07	8.53	0.95
Iliamna River-Top	6.99	1.12	7.79	1.08	8.76	1.03
Pedro Bay Ponds	4.02	0.54	3.89	0.53	3.76	0.52
Lake Iliamna	4.67	0.25	4.96	0.24	4.78	0.24
	Sr (µg/L)	Sr/Ca (mmol/mol)	Sr (µg/L)	Sr/Ca (mmol/mol)	Sr (µg/L)	Sr/Ca (mmol/mol)
Iliamna River-Bottom	13.28	2.77	14.78	2.73	15.52	2.67
Iliamna River-Middle	14.17	2.99	15.92	2.95	16.05	2.81
Iliamna River-Top	10.26	2.58	12.93	2.80	16.47	3.03
Pedro Bay Ponds	18.25	3.82	17.72	3.78	17.63	3.83
Lake Iliamna	26.82	2.24	29.35	2.21	28.56	2.23
	Ca (mg/L)		Ca (mg/L)		Ca (mg/L)	
Iliamna River-Bottom	2.20		2.48		2.66	
Iliamna River-Middle	2.16		2.47		2.61	
Iliamna River-Top	1.82		2.11		2.49	
Pedro Bay Ponds	2.19		2.14		2.10	
Lake Iliamna	5.49		6.07		5.85	

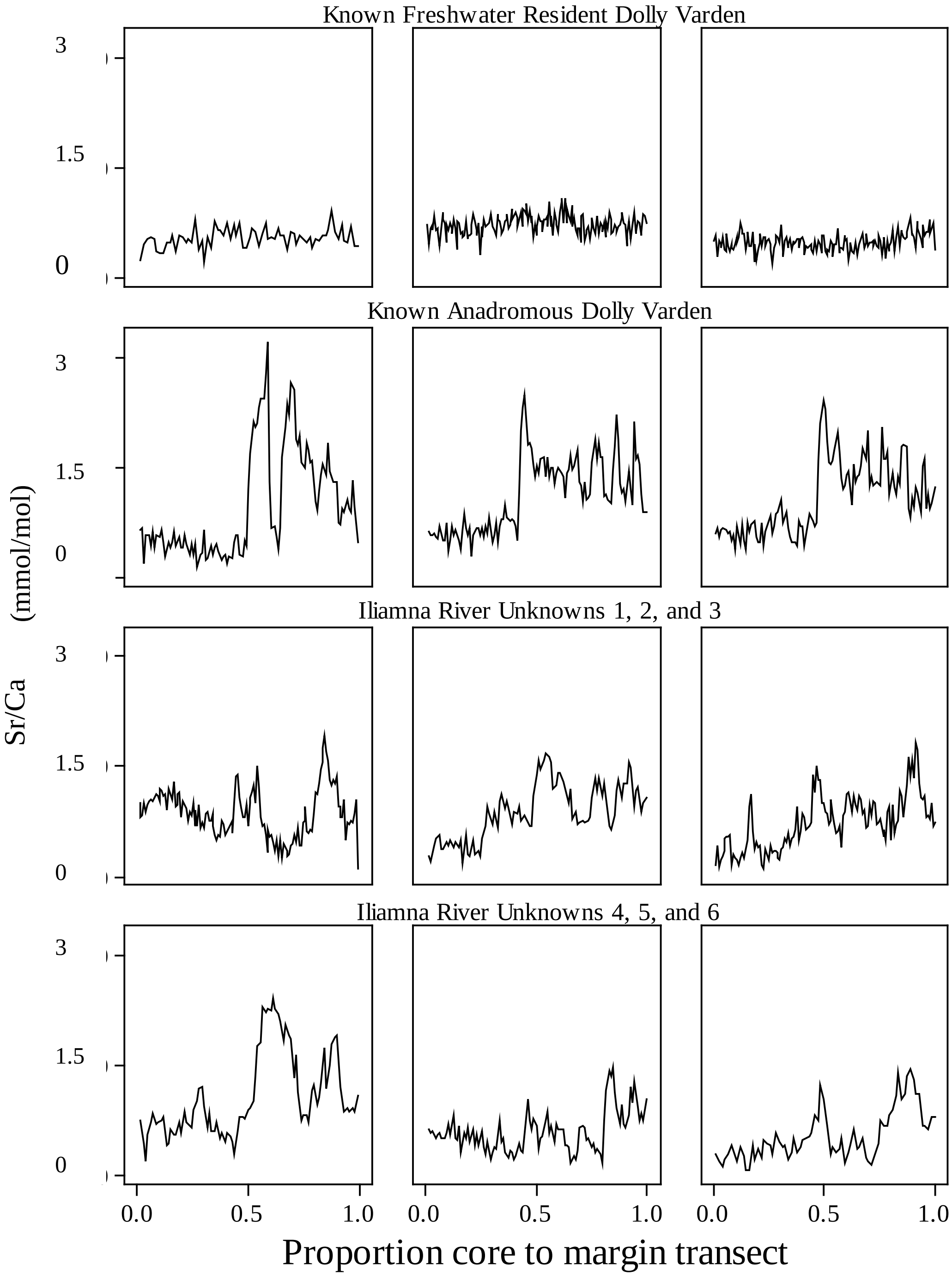


Fig. 3.1. Otolith scans from Dolly Varden from known resident populations (row 1: residual male from Wulik River, Alaska and adults from Amiloyak and Walker lakes, Alaska), known anadromous populations (row 2;Wulik and Hulahula Rivers, Alaska), and Dolly Varden from the Iliamna River (rows 3 and 4).

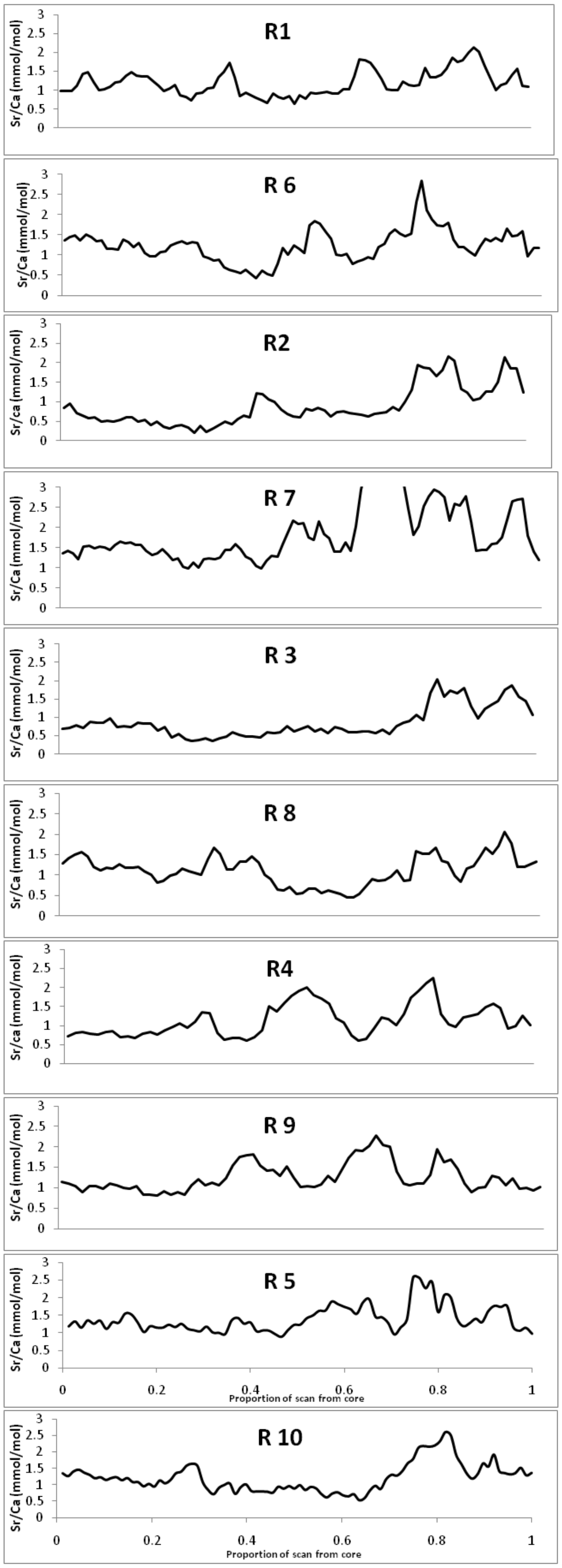


Fig. 3.2. Otolith scans of Sr/Ca from core to margin of Dolly Varden from the Iliamna River.

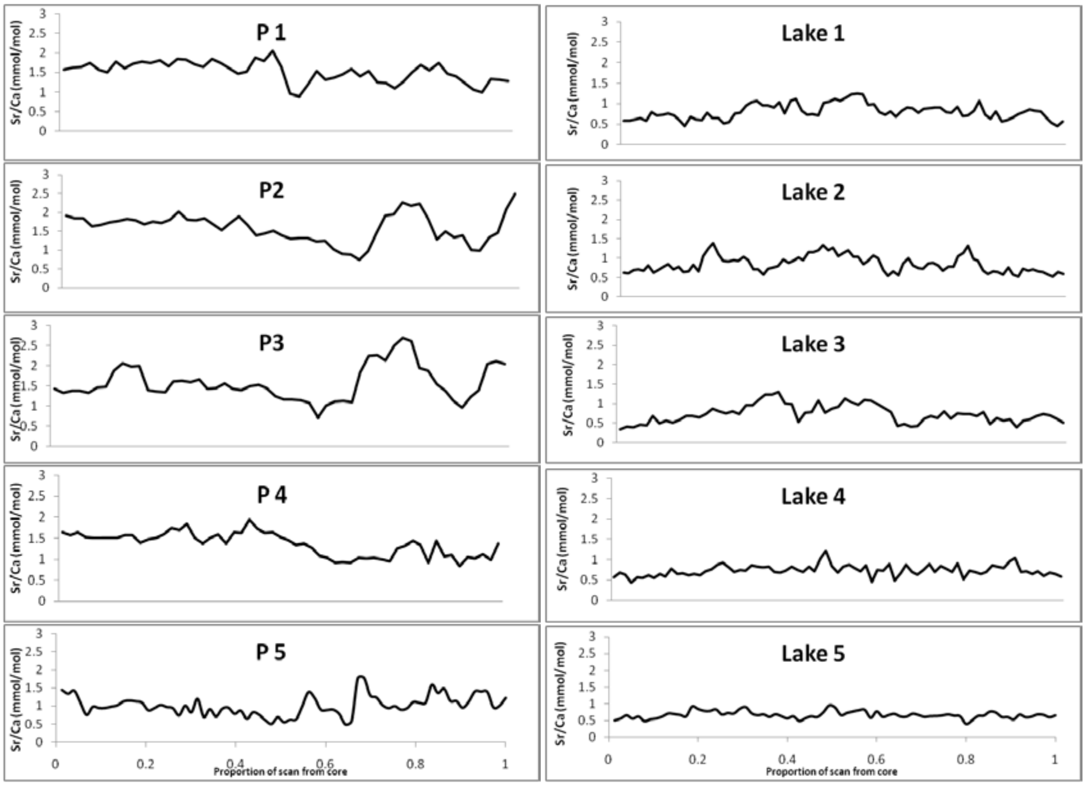


Fig. 3.3. Otolith scans of Sr/Ca from core to margin of Dolly Varden from the Pedro Bay ponds (left) and Arctic char from Iliamna Lake (right).

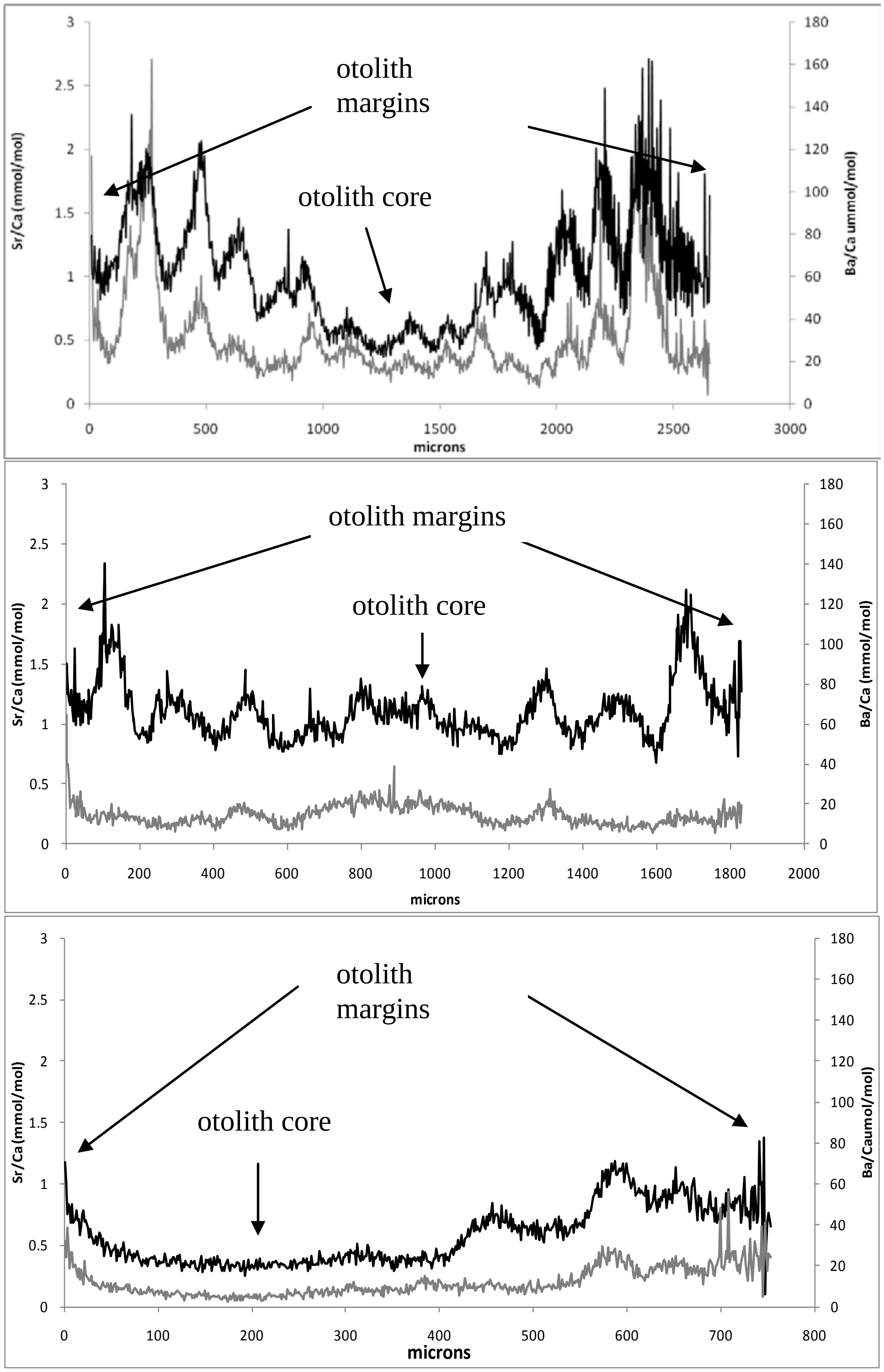


Fig. 3.4. Dual elemental otolith analysis of (a) a Dolly Varden from the Iliamna River (age 6), (b) a Dolly Varden from the Pedro bay ponds (age 3), and (c) a rainbow trout from the Iliamna River (age 6) with Sr/Ca in black on the left axis, Ba/Ca in gray on the right.

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