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# Salmon in the Arctic and How They Avoid Lethal Low Temperatures

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Abstract: With climate change, scientists and others are interested in the future of Pacific salmon in the Arctic. Chum, pink, sockeye, coho, and chinook salmon have been encountered in the Beaufort Sea, well within Canadian Arctic waters. Chum is the only salmon species regarded as natal to the Mackenzie River watershed, although both pink and chum salmon appear to be natal to Alaska's North Slope rivers. It is not possible to say whether apparent recent increases in the frequency of occurrence of salmonids in the Arctic is an effect of climate change, but it appears there are either increases in the survival of natal fish from the Mackenzie, or in the wandering of non-natal fish to the Mackenzie, or both. We propose three hypotheses to explain how chum salmon survive cold marine winter conditions, and thereby persist in the North American Arctic: (1) Bering Sea Refuge – young salmon migrate to the Bering Sea and Gulf of Alaska where they remain until they are ready to return to spawn; (2) Atlantic Layer Beaufort Refuge – salmon remain in the Beaufort Sea, wintering offshore deep under pack ice; and (3) Freshwater Beaufort Refuge – salmon remain in the Beaufort Sea region, wintering in the brackish, under-ice Mackenzie River plume or in fresh water adjacent to the Beaufort Sea. As a preliminary test of these hypotheses, we examined the strontium-to-calcium ratios (Sr:Ca) of otoliths from chum salmon from the Colville (Alaska's North Slope) and Tanana (Yukon River drainage) rivers. Yukon River chum salmon were assumed to reside in the Gulf of Alaska and the Bering Sea. Otolith Sr:Ca ratios were similar between rivers, implying that fish from each group lived in similar environments, but also exhibited significant fluctuations often associated with migrations between freshwater and marine environments. Age compositions and sizes of adult chum salmon from the upper Mackenzie River watershed did not differ from chum from a Yukon River tributary. We are not able to refute any of our hypotheses, but the most parsimonious explanation is that arctic chum salmon live in the North Pacific for most of their marine life, rather than in the Beaufort Sea region. Because of the long distance to migrate between the mouth of the Mackenzie and the North Pacific Ocean, we suggest salmon may spend their first winter deep within the Beaufort Sea (i.e., a combination of Hypotheses 1 and 2). Additional elemental and isotopic signature measurements will enable a more thorough testing of these hypotheses, allow us to understand how chum salmon survive cold winter conditions, and thereby better predict potential climate change effects on salmon in the Arctic.

Keywords: salmon, Arctic, Beaufort Sea, Bering Sea, chum salmon, climate change, oceanography, Mackenzie River; low temperature

## INTRODUCTION

The subarctic North Pacific Ocean, especially the Bering Sea and Gulf of Alaska (Fig. 1), is a major rearing area for many Pacific salmon. Differences in the distribution and growth of salmon in this region between warm and cold years imply that salmon productivity and growth closely track the thermal regimes and productivity of marine waters. Thus, future effects of climate change may be significant. Northward ecological community shifts must have occurred at the end of the last ice age, and recent shifts have been documented in the Bering Sea (Mueter and Litzkow 2008). Extensive shifts in species distributions are projected in consequence to changing sea-ice and temperature distributions (Vermeij and Roopnarine 2008). Kaeriyama (2008) predicts distributional changes for chum salmon, with the Arctic becoming increasingly important as ecosystems continue to shift over time.

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What is the potential of the Arctic Ocean, including the Chukchi and Beaufort seas for Pacific salmon? With climate change, will this area become a major salmon rearing environment? Will arctic watersheds become important salmon producers? In order to answer these types of questions, we need to better understand the current importance of the Arctic for Pacific salmon, the factors that currently limit salmon production there, and how these factors are likely to respond to climate change.

After briefly describing the oceanography of North American Arctic Ocean and reviewing the status of Pacific salmon in it, we propose three hypotheses to explain the persistence of salmon in the Arctic. The Bering Sea Refuge, the Atlantic Layer Beaufort Refuge, and the Freshwater Beaufort Refuge hypotheses differ primarily in where salmon are purported to spend their winters. We present results on strontium-to-calcium ratios (Sr:Ca) of otoliths from northern chum salmon, examine size and age-frequency data as a preliminary testing of these hypotheses, and identify additional research to further test these hypotheses. Understanding how salmon from the Arctic are able to survive winter will enable us to better anticipate future climate change impacts.

## OCEANOGRAPHY

We focus on the North American portion of the Arctic known to have Pacific salmon, which includes Alaska's North Slope and the Western Canadian Arctic. Various rivers, including the Colville, drain this portion of the coast, but the Mackenzie River, with a mean annual discharge of 9130 $m^3/s$ (Water Survey of Canada, http://www.wsc.ec.gc.ca/staflo/index_e.cfm?cname=main_e.cfm, accessed 12 June 2009), is by far the largest (Fig. 1).

Although the oceanography of the Arctic Ocean is perhaps not as thoroughly observed as most ocean areas to the south due to difficulty of year-round access, a reasonable understanding of ice motion, stratification, seasonality of shelf regions, and ocean currents has been developed during the past three decades. There is a vigorous inflow through Bering Strait (85 km wide, 50 m sill depth; Woodgate and

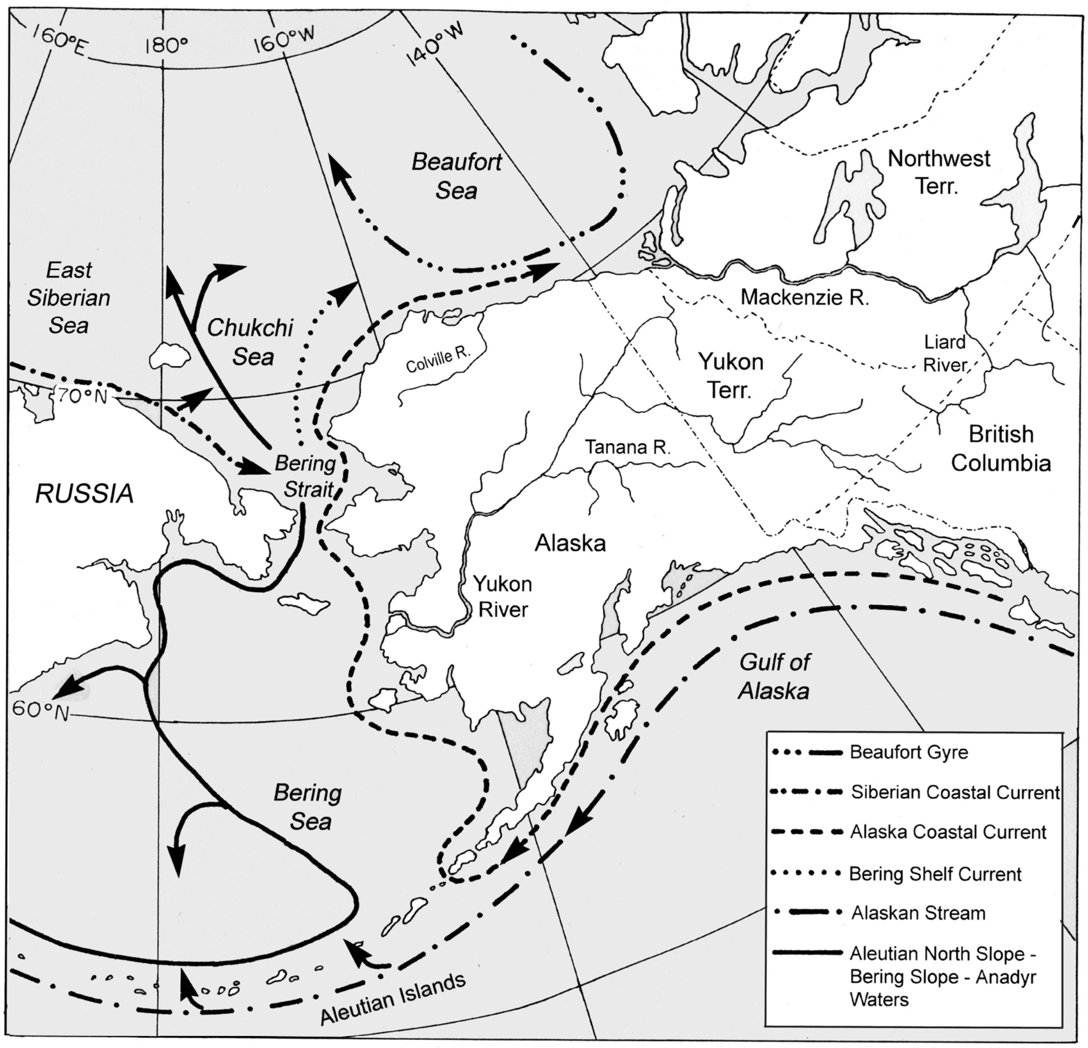


**Fig. 1.** Study area showing major rivers and ocean currents.

Aagaard 2005) into the western Arctic Ocean, and ice motion of the permanent pack is characterized by a clockwise drift within the Beaufort Gyre (Fig. 1; Aagaard 1984). Due to the strong inflow, the upper layers of the western Arctic Ocean derive largely from the Pacific Ocean (McLaughlin et al. 1996; Yamamoto-Kawai et al. 2008), whereas the deeper water below 200 m or so originates in the Atlantic Ocean (Macdonald et al. 1989). Surface waters (< 50 m) tend to be less salty because of freshwater inflow from the large pan-arctic drainage basin (Carmack et al. 2008). Surface water also undergoes a strong modulation in temperature, exhibiting near freezing temperatures (-1.2 to -1.8 °C) in winter and warmer temperatures in open water around the ocean margin in summer. Below the surface water there is a cold halocline that exhibits near freezing temperatures throughout the year (50–200 m). Below about 200 m where Atlantic water is encountered, the temperatures exceed 0°C throughout the year and salinity increases to above 34.8 (Fig. 2; Carmack et al. 1989). The Alaska Coastal Current forms part of a long transport system that moves fresh water, contained in low-salinity surface water, northward along the North American coast and into the Chukchi Sea where the current then moves eastward along the Alaskan northern coast. Below the surface waters, however, the Beaufort Undercurrent runs eastward along the shelf slope (Aagaard 1984). Carmack and Macdonald (2002) describe the complex seasonal influence of the Mackenzie River on the oceanography of the Beaufort Sea; whether the Mackenzie River plume goes west into the Beaufort Gyre, or east into Amundsen Gulf, is influenced each year by the amount of persistent summer ice cover, its proximity to shore, and the direction, strength, and persistence of prevailing winds.

## STATUS OF PACIFIC SALMON IN THE ARCTIC

Of all Pacific salmon, chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon have the broadest distributions, occasionally being encountered west of the Lena River in Siberia, and east of Canada's Mackenzie River (Heard 1991; Salo 1991; Stephenson 2006). Documentation from the 1881 Alaskan voyage of the Revenue-Steamer Corwin (Bean 1883), to our knowledge, provides the first published records of Pacific salmon in Arctic North America. Bean (1883) reported pink and chum salmon in the Bering Strait, chum salmon in Hotham Inlet (Kotzebue Sound), and pink salmon in the Colville River. There is also anecdotal evidence of increased numbers of pink salmon in northern-draining rivers of the Russian north (V. Karpenko, Kamchatka Research Institute of Fisheries and Oceanography, Petropavlovsk-Kamchatsky, Russia, pers. comm.). Recent reviews of salmon in the Canadian Arctic (Babaluk et al. 2000; Stephenson 2006; Irvine et al. 2009) document the capture of Chinook (*O. tschwatscha*), sockeye (*O. nerka*), and coho (*O. kisutch*) salmon, in addition to chum and pink salmon, but note there is no clear evidence of recent increases in abundance. Numbers of chum salmon estimated at individual locations in the Western Canadian Arctic over the years ranged from 1 to 5000 (Stephenson 2006); Irvine et al. (2009) estimated that at least several hundred chum salmon returned to the Liard River in the upper Mackenzie River watershed (Fig. 1) during two years of intensive study.

Coho, sockeye, and Chinook salmon are rare east of Point Hope (western North Slope Alaska), and pink salmon east of Prudhoe Bay (central North Slope Alaska) are generally considered to be vagrants (Craig and Haldorson 1986). Chum salmon appear to be the only species natal to the Mackenzie River watershed as they are the only spe-

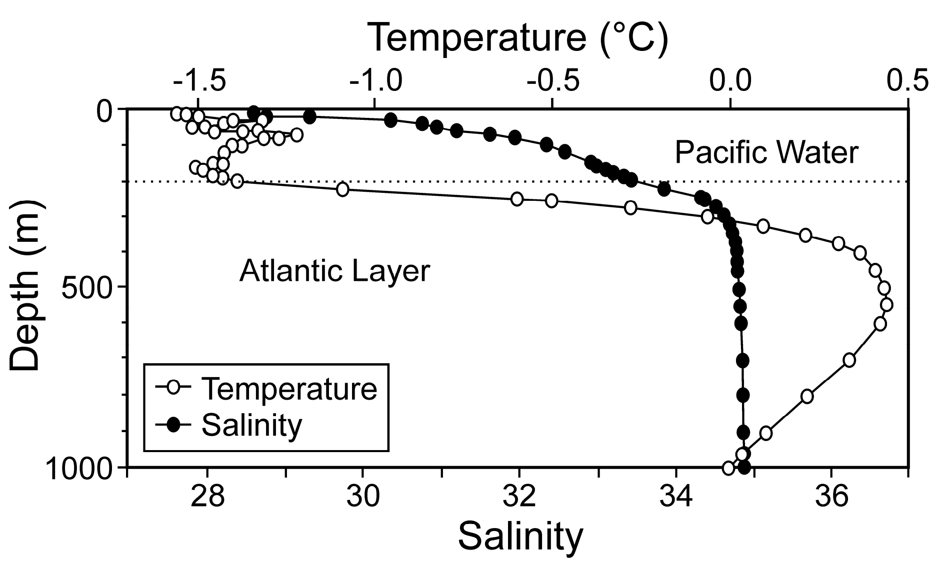


**Fig. 2.** Typical vertical profiles of temperature (open circles) and salinity (closed circles) for the southern Beaufort Sea of the Canada Basin. Water above about 200 m is cold and comes predominantly from the Pacific Ocean via Bering Strait, whereas water deeper than 200 m is warmer and comes from the Atlantic Ocean via the Barents Sea and Fram Strait.

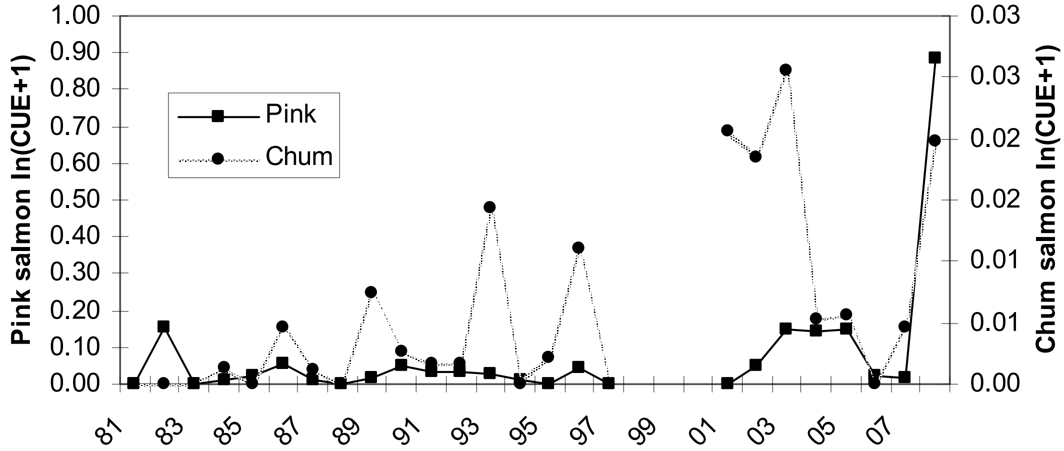


**Fig. 3.** Catch per unit effort for pink and chum salmon from a nearshore marine fyke net survey in the North Slope, Alaska (data from Fechhelm et al. (2008) and Bob Fechhelm, LGL Ecological Research Associates, Bryan, Texas, USA, pers. comm.).

cies consistently captured in good numbers in upstream areas with many individuals exhibiting pre-reproductive development. Traditional knowledge supports this theory; chum is the only salmon species with a name in the Inuvialuktun and Dene languages of this area (Coad and Reist 2004; Stephenson 2006). Closer to the Bering Strait, both pink and chum salmon are reported from various rivers in the Prudhoe Bay area, including the Colville (Craig and Haldorson 1986). We assume pink and chum are natal in many of these streams, but this has not been confirmed.

Salmon abundance time series are rare. One exception is the monitoring program operated ~50 km west of Prudhoe Bay to evaluate potential effects of oil and gas exploration in the area (Craig and Haldorson 1986; Fechhelm et al. 2008). Small numbers of pink and chum salmon have been caught in most years in a nearshore fyke net, which has been maintained since 1981, and larger numbers of pink salmon were caught in 2008 (Fig. 3). It is impossible to know if the high 2008 pink salmon catches reflect a spike in actual abundance, or are some sort of artefacts.

The Canadian Arctic Salmon Sampling Program monitors salmon caught by subsistence harvesters, aboriginal and commercial fishers, and others in and near the Mackenzie River. During the past decade, salmon catches have increased, especially for pink and chum salmon (J. Reist, unpubl. data). While it is not possible to know if the apparent increase in frequency of occurrence is a climate change effect, something appears to have changed to either increase the survival of natal fish from the Mackenzie, the wandering of non-natal fish to the Mackenzie, or both.

To summarise, salmon in the Arctic are uncommon. All five species have been captured, and while there is some evidence implying recent increases in abundance, this does not necessarily mean additional spawning in the Arctic. Chum and pink salmon are encountered more frequently than coho, sockeye, and Chinook salmon, and there is general agreement that only chum salmon are natal to the Mackenzie River watershed while chum and pink salmon are probably natal to several rivers in Alaska's North Slope.

## WHERE DO ARCTIC SALMON OVERWINTER?

While recent dramatic reductions in the extent of summer ice coverage in the Arctic have been well-documented (e.g., Stroeve et al. 2008), ice coverage during winter continues to extend beyond the Arctic Ocean southward into the Bering Sea. The ability of salmonids to tolerate cold waters varies among species, but in general, acclimatized salmon can survive subzero temperatures provided they do not come in contact with ice crystals (Brett and Alderdice 1958; Fletcher et al. 1988).

We focus here on chum salmon because they are the only species thought to return regularly to the Mackenzie River. We present three hypotheses (Bering Sea Refuge, Atlantic Layer Beaufort Refuge, and Freshwater Beaufort Refuge) to explain how chum salmon are able to persist in the Arctic. In all cases, chum salmon fry are transported downstream by river flows, arriving at the mouth of the Mackenzie (or other) River in June/July of the year following spawning. We assume chum usually spend three winters at sea (occasionally two or four) as found by Irvine et al. (2009) for chum from the Liard River, returning to the mouth of their spawning river in late summer or early autumn. Each hypothesis differs in where chum spend their winters, meaning that the temperatures and salinities fish are exposed to in the marine environment also vary. Although incomplete, our understanding of the physical and chemical oceanography of the Arctic Ocean is sufficient to speculate on the influence of these conditions on chum salmon.

### Hypothesis 1 - Bering Sea Refuge

According to this hypothesis, after arriving in the ocean, young-of–the-year chum salmon are carried north (offshore)

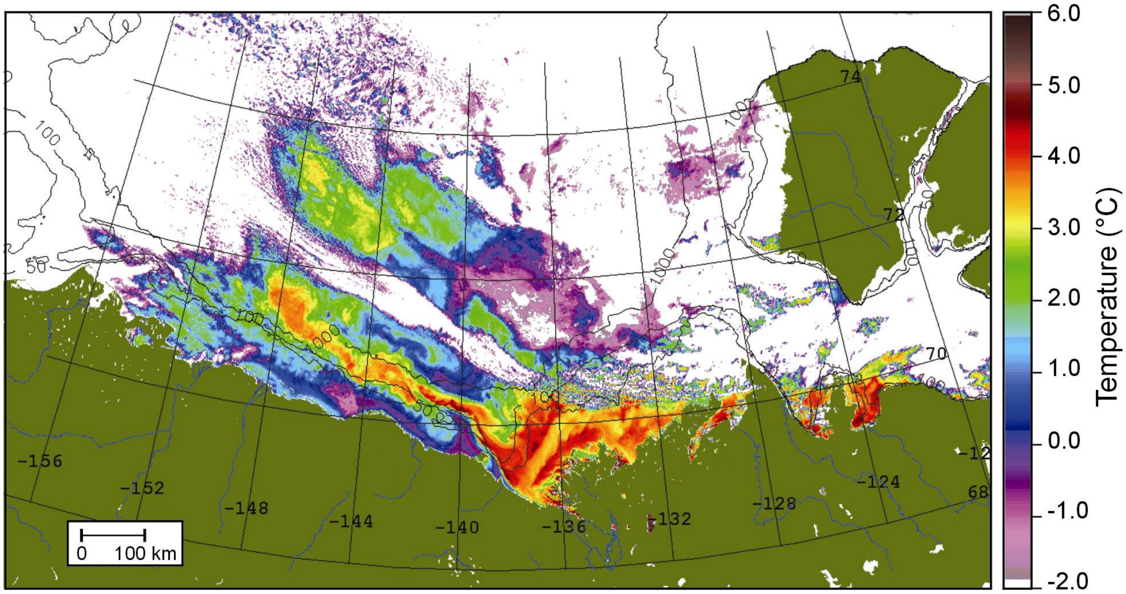


**Fig. 4.** A satellite thermal image taken of the Southern Beaufort Sea on 17 September 2008. The influence of the Mackenzie Plume likely extends westward at least as far as 142° W where it connects with a continuous band of what is probably warm Alaskan coastal water (SeaWiFs data were obtained from OCDP Archive, NASA/Goddard Space Flight Center).

and sometimes west towards the icepack in the Mackenzie plume (Fig. 4). From there young chum are transported west towards the Chukchi Sea either by means of wind-driven longshore currents, as proposed by Fechhelm and Fissel (1988) for Arctic cisco (*Coregonus autumnalis*), and/or by taking advantage of the westerly flowing Beaufort Gyre near the ice edge, which in some years also transports substantial amounts of Mackenzie River water (Macdonald et al. 1999). To arrive in the Bering Sea before freeze-up, young Mackenzie River chum salmon need to cover the distance (~1800 km) at a speed of ~24 km/d (assuming 75 days to complete the migration). Young chum salmon from Alaskan North Slope rivers, with a shorter distance to swim to reach the Bering Strait, rely chiefly on wind-driven currents to move them west.

Because the dominant flow leaving the Bering Sea is northward (Woodgate and Aagaard 2005), young chum exiting the Chukchi Sea would normally have to swim against the current, perhaps saving energy by remaining close to the Asian side of the Bering Strait where currents are generally slowest (Fig. 1). Alternatively, fish could be assisted by occasional southerly flow reversals consequent to periods of northerly winds (see Woodgate et al. 2006).

Once in the Bering Sea, arctic chum salmon probably adopt a migratory strategy similar to that proposed by Myers et al. (2007) in their conceptual model for Pacific salmon in the open ocean. According to Myers et al., salmon move southeastward towards the Gulf of Alaska in fall, and back to the Bering Sea in summer. After typically three winters in the Bering Sea and Gulf of Alaska, arctic chum salmon return to the Mackenzie (or other) River, taking advantage of the Alaska Coastal current, arriving at the mouth of their natal river in late summer or early autumn.

Although this hypothesis requires young chum salmon to migrate a long distance, it is attractive because for the majority of their life, arctic chum salmon occupy the same environment as many chum from the North Pacific.

### Hypothesis 2 - Atlantic Layer Beaufort Refuge

This hypothesis proposes that young-of-the-year chum salmon carried north towards the icepack avoid freezing temperatures by swimming down to water of Atlantic origin (> 200 m) in fall. After wintering at depth in these waters, which exceed 0°C throughout the year (Fig. 2), chum return towards the surface, and spend the ice-free period within the Beaufort Sea actively feeding and growing. This seasonal vertical migratory pattern is repeated typically during three years at which point the salmon return to the Mackenzie (or other) River and migrate upstream to spawn.

This hypothesis is appealing from the standpoint that salmon do not need to migrate over the long distance required to reach the Chukchi Sea, or swim against the current to enter the Bering Sea. Furthermore, from what we know about the replenishment process for the Atlantic layer, heat has been sustained here reliably over a long time-frame and is not affected by either local ice conditions or weather. Other studies have reported chum in the North Pacific at the depths and temperatures required under this hypothesis. For instance, Walker et al. (2000) recorded chum in very cold waters (-1°C to 1°C), possibly several hundred metres deep. Ueno (1992) found that chum salmon were frequently caught in trawls at depths exceeding 200 m.

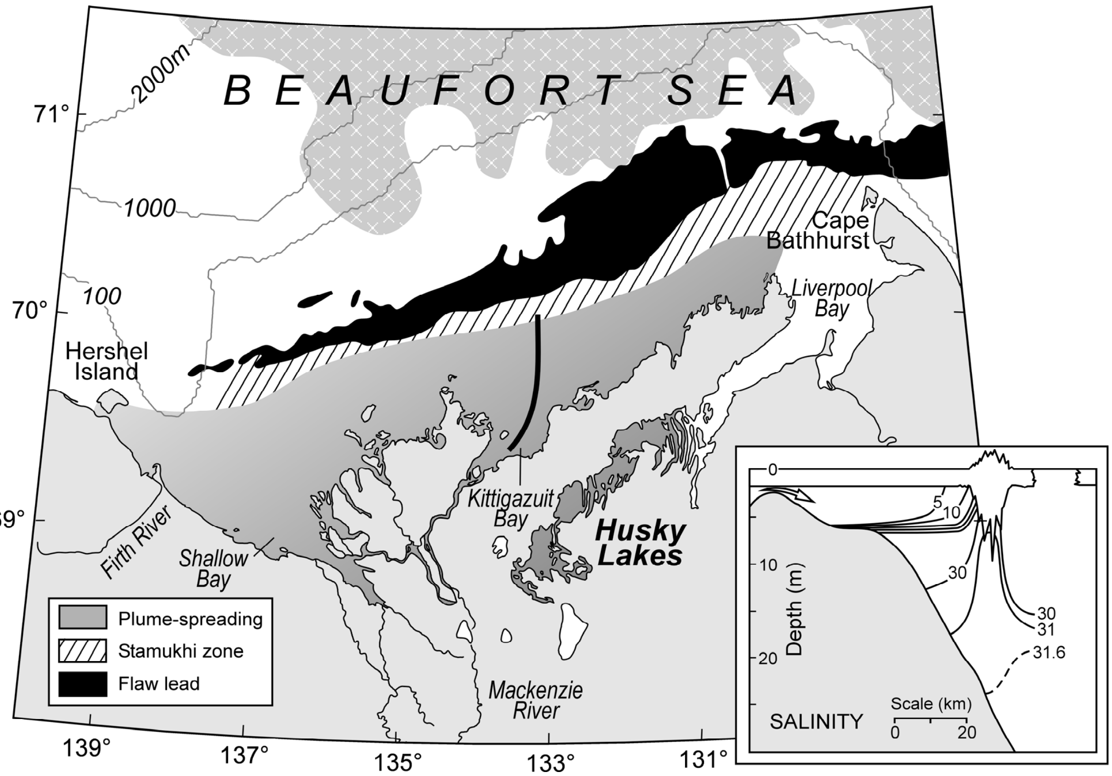


**Fig. 5.** A diagram showing the disposition toward the end of winter (May) of Mackenzie River water that has invaded the nearshore under the ice of the Canadian Beaufort Shelf. The inset section shows the depth and salinity of the brackish water, which extends out to the rough ice (stamukhi) located at the end of the landfast ice zone. This seasonal, under-ice lake covers approximately 16,000 km$^2$ by the end of winter (Macdonald et al. 1995).

### Hypothesis 3 - Freshwater Beaufort Refuge

In this case, chum salmon adopt a strategy similar to other arctic fish species. For instance, Dolly Varden (*Salvelinus malma*) and several coregonine species common in the Arctic spend their summers in the Beaufort Sea, typically near the coast, but retreat into fresh or brackish waters, at temperatures at or close to zero in winter, thereby avoiding sub-zero (-1.9 °C) temperatures associated with more saline water during winter (Fig. 2; Craig 1984; Craig 1989). Fish may also over-winter in groundwater-influenced stream environments, near the bottoms of coastal lakes, or within parts of the Mackenzie River plume that flows underneath a large portion of the landfast ice (Fig. 5; Macdonald et al. 1995).

The Freshwater Beaufort Refuge Hypothesis is also attractive because salmon do not have to migrate long distances, including an upstream migration through the Bering Strait. However, as chum salmon elsewhere are not known to rely on fresh or brackish refugia as a means of avoiding cold marine environments, if it occurs, this strategy would likely be a specific adaptation to the Arctic. Furthermore, fish over-wintering in the plume under the ice would endure very uncertain conditions where they might be exposed to either below-freezing water near the bottom or frazil ice formation at interfaces.

## PRELIMINARY TESTING OF HYPOTHESES

While the most direct way to test these hypotheses would be to sample the proposed winter environments for arctic chum salmon, the likelihood of capturing salmon during winter in the Arctic is extremely low. Most winter fish sampling techniques are not only dangerous but tend to be passive, and unlikely to catch uncommon non-migrating fish. If arctic salmon are in the Bering Sea, they will be mixed with many more numerous salmon populations. Genetic techniques could theoretically be applied to identify arctic salmon in the Bering Sea, but an inadequate baseline for arctic salmon and small sample sizes makes this approach impractical at this time. Fortunately we can take advantage of the different chemical signatures of the various environments potentially used by arctic salmon to evaluate the hypotheses. We can also compare growth and age patterns of salmon from the Arctic with salmon from other northern areas.

If Hypothesis 1 (Bering Sea Refuge) is correct, salmon are exposed to relatively constant salinity (maximum 34.45) during their marine period, but significant seasonal variability in temperatures (~2.7 to 15.6 °C, Azumaya et al. 2007). If Hypothesis 2 (Atlantic Layer Beaufort Refuge) is correct, fish are exposed to winter salinities similar to those in Hypothesis 1, but reduced summer salinities, and lower minimum and maximum temperatures (~1 and ~8 °C). With Hypothesis 3 (Freshwater Beaufort Refuge), salinity profiles are much more variable, with the lowest minimum values for fish retreating to fresh or brackish water in winter. In addition, salmon wintering in the Mackenzie plume would probably be exposed to colder winter temperatures than those retreating to fresh water.

As a preliminary test of the Freshwater Beaufort Refuge Hypothesis, we examined the Sr:Ca ratios of otoliths from six returning adult chum salmon collected in the Colville River and six returning adult chum salmon collected in the Tanana River, a major tributary of the Yukon River (Fig. 1). Secor et al. (1995), Zimmerman (2005), and others have documented that the ratio of Sr to Ca is generally greater in otolith material precipitated in marine rather than in fresh water, and that analysis of Sr:Ca ratios across fish otoliths can reveal their migratory histories between marine and freshwater environments. We also compared the size and age of chum salmon from the Liard River with those caught in the Porcupine River, another tributary of the upper Yukon River. The life history of chum salmon from the Yukon River and tributaries is similar to that of other non-arctic chum; they migrate to the ocean during their first summer and remain in marine waters until they return to spawn (Salo 1991). We hypothesized that if Colville River chum salmon overwintered in marine waters of the Bering Sea/Gulf of Alaska, similar to Yukon River chum salmon, then the two groups would have similar otolith Sr:Ca profiles, sizes, and age compositions. If Colville chum wintered deep within the Beaufort Sea, or within the freshened water of the Mackenzie River plume or adjacent areas (i.e., Hypotheses 2 and 3), their otolith Sr:Ca profiles might exhibit larger oscillations, particularly for Hypothesis 3. Otolith Sr:Ca profiles for chum wintering in fresh or brackish waters should exhibit larger oscillations than Tanana River chum salmon, similar to those of Arctic char *Salvelinus alpinus* (Halden et al. 1995), inconnu *Stenodus leucichthys* (Howland et al. 2001), and other anadromous salmonids that annually migrate between high and low salinity environments. If chum salmon remain in the Beaufort Sea region, their growth (i.e., size at age) should

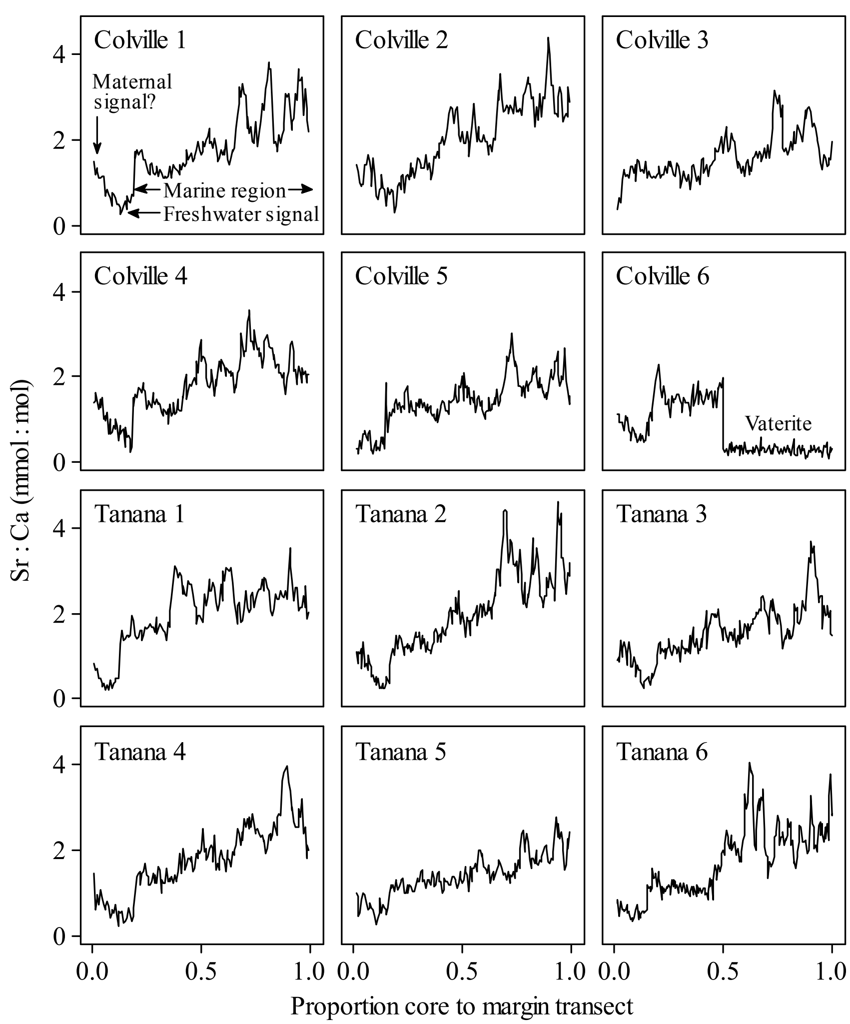


**Fig. 6.** Lifetime otolith Sr:Ca profiles of six Colville River chum salmon (top two rows) and six Tanana River (Yukon River drainage) chum salmon (bottom two rows).

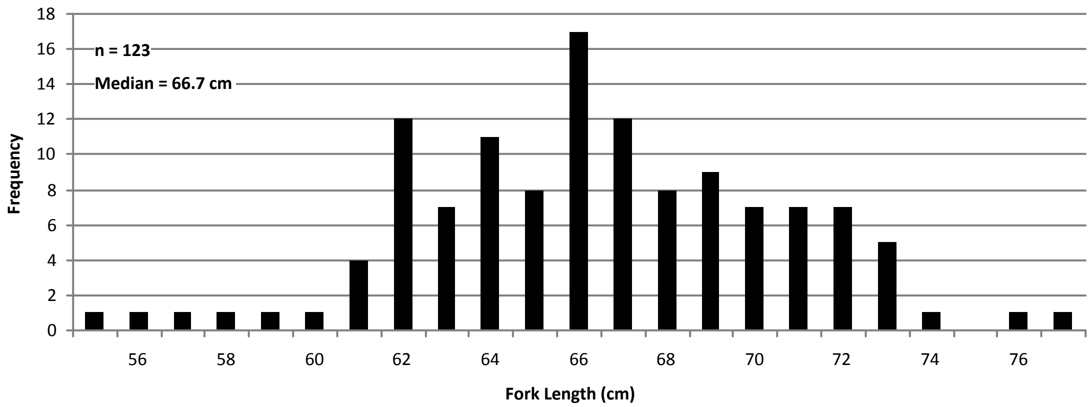


**Fig. 7.** Length frequency distribution of adult chum salmon from the Liard River (from Irvine et al. 2009).

be depressed compared to fish in the Bering Sea and North Pacific Ocean, and perhaps they might return to spawn as older fish, due to the colder winter temperatures.

Using methods described by Brown et al. (2007), Sr and Ca concentrations were measured in chum salmon from the Tanana and Colville rivers, at a series of points from the core of each otolith (precipitated early in life) to its margin (precipitated late in life). These data were converted to molar ratios of Sr:Ca using equivalency equations presented by Brown and Severin (2008), and plotted as ontogenetic profiles (Fig. 6). In these preliminary analyses, comparisons were limited to descriptive assessments of patterns of Sr:Ca variation (Fig. 6).

Strontium:Ca profiles of the Colville River chum salmon were similar to those of Tanana River chum salmon (Fig. 6), suggesting these fish experienced similar environments throughout life. Freshwater regions near the core were narrow and all fell in the range of Sr:Ca < 1 mmol:mol. Several members of each group had an elevated region of Sr:Ca (> 1 mmol:mol) in the core that is probably a maternal contribution of marine Sr via the egg, a phenomenon documented by Arai and Miyazaki (2002) for chum and Volk et al. (2000) for other anadromous salmonids. All chum salmon from the Colville and Tanana river groups exhibited an initial rise in Sr:Ca to levels ranging between approximately 1 and 2 mmol:mol. A general increasing ontogenetic Sr:Ca trend was evident for chum salmon within both groups rising to maximum levels ranging from just under 3 mmol:mol (Fig. 6, Colville 5 and Tanana 5) to just over 4 mmol:mol (Fig. 6, Colville 2 and Tanana 2). An exception to this trend was sample Colville 6, for which the outer region consisted of vaterite. Vaterite regions of otoliths are visually distinctive and have been shown to exhibit very low levels of Sr that do not reflect environmental chemistry (Brown and Severin 1999; Tzeng et al. 2007).

Somewhat surprisingly, chum salmon from both groups exhibited Sr:Ca oscillations in the latter portion of their profiles that spanned as much as 2 mmol:mol. Oscillations of this magnitude are normally associated with migrations between freshwater and marine environments (e.g., Brenkman et al. 2007). Because the Tanana River chum salmon are not thought to migrate annually between marine and fresh waters, the oscillations seen in their Sr:Ca profiles may reflect physiological responses within the marine environment, as reported by Arai and Miyazaki (2002) for chum salmon from the Otsuchi River in Japan. We are not able to refute any of our hypotheses based on these results.

Chum salmon captured in the Liard River ranged between 55 and 78 cm fork length (Fig. 7) and 2000 and 6200 g. Four-year-old fish predominated, with some three- and five-year-olds also caught; approximately 61% of the catch was male, and 39% female (n = 167, Irvine et al. 2009). Irvine et al. (2009) compared these results with those for chum from the Yukon River watershed as documented by Boyce (2001, 2002), Boyce and Vust (2002), and Boyce and Wilson (2001). In the Porcupine River, a tributary of the Yukon, for the four years considered, returning chum ranged in age from three to six years. The majority were age three to five with age-four fish being the most common, the same as found for chum from the Liard. Male and female chum caught in weirs in the Yukon did not differ in abundance, while in the Liard, males were caught most frequently, perhaps a result of sex-biased sampling by gill nets. Irvine et al. (2009) did not find significant differences between the sizes of male and female chum of each age caught in the Liard and those in the Yukon, although in some cases, sample sizes from the Liard River were small.

Similar growth patterns for chum from the Mackenzie and Yukon rivers support Hypothesis 1 (Bering Sea Refuge). Furthermore, if chum salmon are living in the Beaufort Sea region (Hypotheses 2 and 3) for a significant period of their lives, one would expect that subadult fish would have been reported in some of the many sampling projects that have been conducted along the Beaufort Sea coast of Canada and Alaska (e.g., Kendel et al. 1975; Percy 1975; Bond 1982; Craig 1984; Craig et al. 1985; Bond and Erickson 1989, 1992; Jarvela and Thorsteinson 1999; Brown 2008; Fechhelm et al. 2008; and many more); yet subadult size chum salmon have never been reported, other than in recent surveys in the Chukchi Sea (Kondzela et al. 2009; Moss et al. 2009). We believe these lines of evidence are most consistent with the Bering Sea Refuge Hypothesis although the long distance chum would need to migrate between the Canadian Arctic and the Bering Sea needs to be considered.

The speed required for chum to reach the Bering Sea in their first season (~24 km/d) is significantly greater than their normal swimming speed. Even if the chum migration is assisted by currents, it may not be possible to reach the Chukchi Sea in the first year, so perhaps chum spend their first winter in the Beaufort Sea below 200 m to avoid freezing temperatures. Adopting this strategy would give them extra time to complete their migration, and also provide them the opportunity to reach a larger size, when they would presumably be more capable of migrating against the current to reach the Bering Sea. We note that Japanese chum salmon spend their first winter in a narrow region of the western North Pacific, arriving at the Bering Sea in their second summer-fall (Myers et al. 2007).

Although we are unable to exclude any of the three hypotheses based on our preliminary evaluation, the most parsimonious explanation is that arctic chum salmon live in the North Pacific for most of their marine life, rather than the Beaufort Sea region. Because of the long distance to migrate between the mouth of the Mackenzie and the North Pacific Ocean, they may spend their first winter deep within the Beaufort Sea (i.e., a combination of Hypotheses 1 and 2). However, it is not possible to eliminate the Freshwater Beaufort Refuge Hypothesis due to the surprising range of otolith Sr:Ca values for chum salmon from the Colville and Tanana river samples.

## FUTURE WORK NEEDED TO TEST HYPOTHESES

We recommend additional elemental and isotope analyses to fully test our hypotheses. For instance, Arai and Hirata (2006) found that, in addition to Sr, concentrations of Mg, Zn, and Ba also differed between the freshwater and seawater growth zones of chum otoliths. Unfortunately, elemental results can sometimes be confusing due to natural variability in elemental concentrations within environments. In addition, temperature and salinity, the two primary environmental parameters to differentiate among our hypotheses, can have an interactive effect on otolith microchemistry (Elsdon and Gillanders 2002). In contrast, the $^{87}Sr$:$^{86}Sr$ ratios for particular freshwater systems tend to be constant and often different from those in the ocean (Kennedy et al. 2002). Milton and Chenery (2003) described anadromous migrations of a tropical shad by examining variation in the ratio of $^{87}Sr$:$^{86}Sr$ isotopes, along linear transects. The dietary history of a fish is recorded in the organic matrix of its otolith; $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$ are particularly useful at tracing this history since these stable isotopes are more enriched in marine versus freshwater prey (Hesslein et al. 1993; Doucett et al. 1999; Weber et al. 2002; L. Godbout, unpubl. data). Measures of these stable isotopes in prey from locations associated with the hypotheses (Gulf of Alaska, Bering Sea, Beaufort Sea, Mackenzie River plume and nearby freshwater habitats) as well as in salmon otoliths from Mackenzie River chum salmon will allow one to determine in which environments salmon are most likely to have lived. Isotopic signatures of salmon prey are likely to differ among the various locations, as there is evidence for differences in salinities and food webs among locations. For instance, $\delta^{13}C$ is enriched in Bering Sea zooplankton compared to Beaufort Sea zooplankton (Saupe et al. 1989) and this difference is likely to occur at other trophic levels.

Measures of stable oxygen isotopes can also be used to reconstruct the water temperatures at which fish lived. This is possible because there is temperature-dependent fractionation during the formation of the otolith; increases in water temperature result in lower $\delta^{18}O$ (Høie et al. 2004). Because the slopes of fractionation equations are constant among species (Storm-Suke et al. 2007), a general fractionation equation could be used to describe the thermal conditions in relative terms. This approach would be useful to differentiate between the Bering Sea Refuge and Atlantic Layer Beaufort Refuge hypotheses.

Additional exploration can be done at lower levels of temporal resolution of life histories by measuring isotopic signatures from tissue samples such as muscle and scales. Finally, additional fish growth patterns, as reflected by otolith and/or scale growth, should be compared among arctic salmon and other reference fish of known history.

In summary, to thoroughly evaluate the hypotheses proposed, which would allow one to evaluate potential climate change effects on arctic salmon, we recommend that elemental and isotopic signatures be measured in:

- Otoliths and tissue from arctic and more southerly salmon populations;
- Tissue from fish of known habitats; and
- Prey and water samples from the Bering Sea, Beaufort Sea, Mackenzie River plume and nearby freshwater habitats

Fortunately some of this work has been completed. For instance, the Canadian Arctic Salmon Sampling Program has been gathering salmon samples from the western Canadian Arctic since 1986. The U.S. Fish and Wildlife Service have access to salmon samples from the Prudhoe Bay region. Similarly, reference fish samples are available from all areas, and some have been analysed for elemental and isotopic ratio levels. However, fewer environmental samples, especially of salmon prey, have been collected and essentially no relevant laboratory analyses of these samples have been completed.

Anticipating climate effects on arctic salmon is an international issue. Much valuable information has resulted from events such as the International Polar Year, and through the cooperative research by agencies such as the North Pacific

Anadromous Fish Commission. We encourage a continuing collaborative approach among scientists to better understand likely impacts of climate on salmon and other creatures in the Arctic.

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## REFERENCES

Aagaard, K. 1984. The Beaufort Undercurrent. *In* The Alaskan Beaufort Sea: Ecosystems and environments. *Edited by* P.W. Barnes, D. M. Schell, and E. Reimnitz. Academic Press, New York. pp. 47–71.

Arai, T., and T. Hirata. 2006. Determination of trace elements in otoliths of chum salmon *Oncorhynchus keta* by laser ablation-ICP-mass spectrometry. Fish. Sci. 72: 977–984.

Arai, T., and N. Miyazaki. 2002. Analysis of otolith microchemistry of chum salmon, *Oncorhynchus keta*, collected in Otsuchi Bay, northeastern Japan. Otsuchi Mar. Sci. 27: 13–16.

Azumaya, T., T. Nagasawa, O.S. Temnykh, and G.V. Khen. 2007. Regional and seasonal differences in temperature and salinity limitations of Pacific salmon. N. Pac. Anadr. Fish Comm. Bull. 4: 179–187.

Babaluk, J.A., J.D. Reist, J.D. Johnson, and L. Johnson. 2000. First records of sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) from Banks Island and other records of Pacific salmon in Northwest Territories, Canada. Arctic 53(2): 161–164.

Bean, T.H. 1883. List of fishes known to occur in the Arctic Ocean north of Bering Strait. *In* Cruise of the Revenue-Steamer Corwin in Alaska in the N.W. Arctic Ocean in 1881. *Edited by* I.C. Rosse. Government Printing Office, Washington. pp. 118–120.

Bond, W. A. 1982. A study of the fishery resources of Tuktoyaktuk Harbour, southern Beaufort Sea coast, with special reference to life histories of anadromous coregonids. Can. Tech. Rep. Fish. Aquat. Sci. No. 1119, Winnipeg.

Bond, W.A., and R.N. Erickson. 1989. Summer studies of the nearshore fish community at Phillips Bay, Beaufort Sea coast, Yukon. Can. Tech. Rep. Fish. Aquat. Sci. No. 1676, Winnipeg.

Bond, W.A., and R.N. Erickson. 1992. Fishery data from the Anderson River estuary, Northwest Territories, 1990. Can. Man. Rep. Fish. Aquat. Sci. No. 2171, Winnipeg.

Boyce, I. 2001. Enumeration of adult chum salmon, *Oncorhynchus keta*, in the Fishing Branch River, Yukon Territory, 1995. Can. Man. Rep. Fish. Aquat. Sci. 2563. 33 pp.

Boyce, I. 2002. Enumeration of adult chum salmon, *Oncorhynchus keta*, in the Fishing Branch River, Yukon Territory, 1996. Can. Man. Rep. Fish. Aquat. Sci. 2594. 33 pp.

Boyce, I., and V. Vust. 2002. Enumeration of adult chum salmon, *Oncorhynchus keta*, in the Fishing Branch River, Yukon Territory, 1997. Can. Man. Rep. Fish. Aquat. Sci. 2585. 35 pp.

Boyce, I., and B. Wilson. 2001. Enumeration of adult chum salmon, *Oncorhynchus keta*, in the Fishing Branch River, Yukon Territory, 1998. Can. Man. Rep. Fish. Aquat. Sci. 2499. 25 pp.

Brenkman, S.J., S.C. Corbett, and E.C. Volk. 2007. Use of otolith chemistry and radiotelemetry to determine age-specific migratory patterns of anadromous bull trout in the Hoh River, Washington. Trans. Am. Fish. Soc. 136: 1–11.

Brett, J.R., and D.F. Alderdice. 1958. The resistance of cultured young chum and sockeye salmon to temperatures below 0 degree C. J. Fish. Res. Board Can. 15: 805–813.

Brown, R.J. 2008. Life history and demographic characteristics of Arctic cisco, Dolly Varden, and other fish species in the Barter Island region of northern Alaska. U.S. Fish Wildl. Serv., Alaska Fish. Tech. Rep. No. 101, Fairbanks.

Brown, R.J., N. Bickford, and K. Severin. 2007. Otolith trace element chemistry as an indicator of anadromy in Yukon River drainage Coregonine fishes. Trans. Am. Fish. Soc. 136: 678–690.

Brown, R., and K.R. Severin. 1999. Elemental distribution within polymorphic inconnu (*Stenodus leucichthys*) otoliths is affected by crystal structure. Can. J. Fish. Aquat. Sci. 56: 1898–1903.

Brown, R.J., and K.P. Severin. 2008. A preliminary otolith microchemical examination of the diadromous migrations of Atlantic tarpon *Megalops atlanticus*. *In* Biology and management of the world tarpon and bonefish fisheries. *Edited by* J.S. Ault. CRC Press, Boca Raton, Florida. pp. 259–274.

Carmack, E.C., and R.W. Macdonald. 2002. Oceanography of the Canadian shelf of the Beaufort Sea: a setting for marine life. Arctic 55(Suppl.1): 29–45.

Carmack, E.C., R.W. Macdonald, and J.E. Papadakis. 1989. Water mass structure and boundaries in the Mackenzie shelf estuary. J. Geophys. Res. 94(C12): 18043–18055.

Carmack, E.C., F.A. McLaughlin, M. Yamamoto-Kawai, M. Itoh, K. Shimada, R. Krishfield, and A. Proshutinsky. 2008. Freshwater storage in the Northern Ocean and the special role of the Beaufort Gyre. *In* Arctic - Subarctic

Ocean Fluxes. *Edited by* R.R. Dickson, J. Meincke, and P. Rhines. Springer. pp. 145–170.

Coad, B.W., and J.D. Reist. 2004. Annotated list of the Arctic marine fishes of Canada. Can. Man. Rep. Fish. Aquat. Sci. 2674. 112 pp.

Craig, P.C. 1984. Fish use of coastal waters of the Alaskan Beaufort Sea: a review. Trans. Am. Fish. Soc. 113: 265–282.

Craig, P.C. 1989. An introduction to anadromous fishes in the Alaskan Arctic. Biological Papers of the University of Alaska 24: 27–54.

Craig, P.C., W.B. Griffiths, L. Haldorson, and H. McElderry. 1985. Distributional patterns of fishes in an Alaskan Arctic lagoon. Polar Biol. 4: 9–18.

Craig, P., and L. Haldorson. 1986. Pacific salmon in the North American Arctic. Arctic 39(1): 2–7.

Doucett, R.R., W. Hooper, and G. Power. 1999. Identification of anadromous and nonanadromous adult brook trout and their progeny in the Tabusintac River, New Brunswick, by means of multiple-stable isotope analysis. Trans. Am. Fish. Soc. 128: 278–288.

Elsdon, T.S., and B.M. Gillanders. 2002. Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fish. Can. J. Fish. Aquat. Sci. 59: 1796–1808.

Fechhelm, R.G., and D.B. Fissel. 1988. Wind-aided recruitment of Canadian Arctic cisco (*Coregonus autumnalis*) into Alaskan waters. Can. J. Fish. Aquat. Sci. 45: 986–910.

Fechhelm, R.G., B.W. Williams, M.J. Daigneault, and M.R. Link. 2008. Year 25 of the long-term monitoring of nearshore Beaufort Sea fishes in the Prudhoe Bay region, 2007. Report for BP Exploration (Alaska) Inc. by LGL Alaska Research Associates, Inc., Anchorage, Alaska. 80 pp.

Fletcher, G.L., M.H. Kao, and J.B. Dempson. 1988. Lethal freezing temperatures of Arctic char and other salmonids in the presence of ice. Aquaculture 71: 369–378.

Heard, W.R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. UBC Press, Vancouver. pp. 119–230.

Halden, N.M., J.A. Babaluk, J.L. Campbell, and W.J. Teesdale. 1995. Scanning proton microprobe analysis of strontium in an Arctic charr, *Salvelinus alpinus*, otolith: implications for the interpretation of anadromy. Environ. Biol. Fish. 43: 333–339.

Hesslein, R.H., K.A. Hallard, and P. Ramlal. 1993. Replacement of sulfur, carbon and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$. Can. J. Fish. Aquat. Sci. 50: 2071–2076.

Høie, H., E. Otterlei, and A. Folkvord. 2004. Temperature-dependent fractionation of stable oxygen isotopes in otoliths of juvenile cod (*Gadus morhua* L.). ICES J. Mar. Sci. 61: 243–251.

Howland, K.L., W.M.Tonn, J.A. Babaluk, and R.F. Tallman. 2001. Identification of freshwater and anadromous inconnu in the Mackenzie River system by analysis of otolith strontium. Trans. Am. Fish. Soc. 130: 725–741.

Irvine, J.R., E. Linn, K. Gillespie, C. McLeod, and J.D. Reist. 2009. Pacific salmon in Canada's Arctic draining rivers, with emphasis on those in British Columbia and the Yukon. Pacific Fisheries Resource Conservation Council. Vancouver B.C. (Available at http://www.fish.bc.ca/files/R-59_StockStatusArcticSalmon2009.pdf).

Jarvela, L.E., and L.K. Thorsteinson. 1999. The epipelagic fish community of Beaufort Sea coastal waters, Alaska. Arctic 52: 80–94.

Kaeriyama, M. 2008. Ecosystem-based sustainable conservation and management of Pacific salmon. *In* Fisheries for Global Welfare and Environment. Proceedings of 5th World Fisheries Congress. *Edited by* K. Tsukamoto, T. Kawamura, T. Takeuchi, T.D. Beard, Jr., and M.J. Kaiser. TerraPub., Japan. pp. 371–380.

Kendel, R.E., R.A. C. Johnston, U. Lobsinger, and M.D. Kozak. 1975. Fishes of the Yukon coast. Department of the Environment, Fisheries and Marine Service, Northern Operations Branch. Beaufort Sea Technical Report No. 6, Whitehorse.

Kennedy, B.P., A. Klaue, J.D. Blum, C.L. Folt, and K. Nislow. 2002. Reconstructing the lives of salmon using Sr isotopes in otoliths. Can. J. Fish. Aquat. Sci. 59: 925–929.

Kondzela, C.M., M.R. Garvin, R. Riley, J.M. Murphy, J.H. Moss, S.A. Fuller, and A. Gharrett. 2009. Preliminary genetic analysis of juvenile chum salmon from the Chukchi Sea and Bering Strait. N. Pac. Anadr. Fish Comm. Bull. 5: 25–27. (Available at www.npafc.org).

Macdonald, R.W., E.C. Carmack, F.A. McLaughlin, K.K. Falkner, and J.H. Swift. 1999. Connections among ice, runoff and atmospheric forcing in the Beaufort Gyre. Geophys. Res. Lett. 26: 2223–2226.

Macdonald, R.W., E.C. Carmack, F.A. McLaughlin, K. Iseki, D.M. Macdonald, and M.O. O'Brien. 1989. Composition and modification of water masses in the Mackenzie Shelf Estuary. J. Geophys. Res. 94(C12): 18057–18070.

Macdonald, R.W., D.W. Paton, E.C. Carmack, and A. Omstedt. 1995. The freshwater budget and under-ice spreading of Mackenzie River water in the Canadian Beaufort Sea based on salinity and $^{18}O/^{16}O$ measurements in water and ice. J. Geophys. Res. 100(C1): 895–919.

McLaughlin, F.A., E.C. Carmack, R.W. Macdonald, and J.K. Bishop. 1996. Physical and geochemical properties across the Atlantic/Pacific water mass front in the southern Canadian Basin. J. Geophys. Res. 101(C1): 1183–1197.

Moss, J.H., J.M. Murphy, E.V. Farley, Jr., L.B. Eisner, and

A.G. Andrews. 2009. Juvenile pink and chum salmon distribution, diet, and growth in the northern Bering and Chukchi seas. N. Pac. Anadr. Fish Comm. Bull. 5: 191–196. (Available at www.npafc.org).

Milton, D.A., and S.R. Chenery. 2003. Movement patterns of the tropical shad hilsa (*Tenualosa ilisha*) inferred from transects of 87Sr/86Sr isotope ratios in their otoliths. Can. J. Fish. Aquat. Sci. 60: 1376–1385.

Mueter, F.J., and M.A. Litzow. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecol. Appl. 18(2): 309–320.

Myers, K.W., N.V. Klovach, O.F. Gritsenko, S. Urawa, and T.C. Royer. 2007. Stock-specific distributions of Asian and North American salmon in the open ocean, interannual changes, and oceanographic conditions. N. Pac. Anadr. Fish Comm. Bull 4: 159–177. (Available at www.npafc.org).

Percy, R. 1975. Fishes of the outer Mackenzie Delta. Department of the Environment, Fisheries and Marine Service, Environment Canada. Beaufort Sea Technical Report No. 8, Winnipeg.

Salo. 1991. Life history of chum salmon (*Oncorhynchus keta*). *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. UBC Press, Vancouver. pp. 231–310.

Saupe, S.M., D.M. Schell, and W.B. Griffiths. 1989. Carbon-isotope ratio gradients in western arctic zooplankton. Mar. Biol. 103: 427–432.

Secor, D.H., A. Henderson-Arzapalo, and P.M. Piccoli. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fish? J. Exp. Mar. Biol. Ecol. 192: 15–33.

Storm-Suke. A., J.B. Dempson, J. Reist, and M. Power. 2007. A field-derived oxygen isotope fractionation equation for *Salvelinus* species. Mass Spectrom. 21: 4109–4116.

Stephenson, S.A. 2006. A review of the occurrence of Pacific salmon (*Oncorhynchus* spp.) in the Canadian Western Arctic. Arctic 59(1): 37–46.

Stroeve, J., M. Serreze, S. Drobot, S, Gearheard, M. Holland, J. Maslanik, W. Meier, and T. Scambos. 2008. Arctic sea ice extent plummets in 2007. Eos, Trans. Am. Geophys. Union 89: 13–14.

Tzeng, W.N., C.W. Chang, C.H. Wang, J.C. Shiao, Y. Iizuka, Y.J. Yang, C.F. You, and L. Ložys. 2007. Misidentification of the migratory history of anguillid eels by Sr/Ca ratios of vaterite otoliths. Mar. Ecol. Prog. Ser. 348: 285–295, doi: 10.3354/meps07022.

Ueno, Y. 1992. Deepwater migrations of chum salmon (*Oncorhynchus keta*) along the Pacific coast of northern Japan. Can. J. Fish. Aquat. Sci. 29: 2307–2312.

Vermeij, G.J., and P.D. Roopnarine. 2008. The coming Arctic invasion. Science 321: 780–781.

Volk, E.C., A. Blakley, S.L. Schroder, and S.M. Kuehner. 2000. Otolith chemistry reflects migratory characteristics of Pacific salmonids: using otolith core chemistry to distinguish maternal associations with sea and fresh waters. Fish. Res. 46: 251–266.

Walker, R.V., K.W. Myers, N.D. Davis, K.Y. Aydin, K.D. Friedland, H.R. Carlson, G.W. Boehlert, S. Urawa, Y. Ueno, and G. Anma. 2000. Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags. Fish. Oceanogr. 9: 171–186.

Weber, P.K., I.D. Hutcheon, K.D. McKeegan, and B.L. Ingram. 2002. Otolith sulfur isotope method to reconstruct salmon (*Oncorhynchus tshawytscha*) life history. Can. J. Fish. Aquat. Sci. 59: 587–591.

Woodgate, R.A., and K. Aagaard. 2005. Revising the Bering Strait freshwater flux into the Arctic Ocean. Geophys. Res. Lett. 32: L02602.

Woodgate, R.A., K. Aagaard, and T.J. Weingartner. 2006. Interannual changes in the Bering Strait fluxes of volume, heat and freshwater between 1991 and 2004. Geophys. Res. Lett. 33: L15609.

Yamamoto-Kawai, M., F.A. McLaughlin, E.C. Carmack, S. Nishino, and K. Shimada. 2008. Freshwater budget of the Canada Basin, Arctic Ocean from geochemical tracer data. J. Geophys. Res. 113, C01007, doi:10.1029/2006JC003858.

Zimmerman, C.E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. Can. J. Fish. Aquat. Sci. 62: 88–97.