

Pacific Salmon in the Arctic: Harbingers of Change

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Abstract

Pacific salmon appear to be expanding their range into Arctic ecosystems and may be acting as effective sentinels of climate change. Salmon harvests voluntarily reported through the Pacific Salmon Collection Program (PSCP) suggest recent increases in both the abundance and distribution of Pacific salmon in the Arctic over the past decade. In the Canadian western Arctic, chum salmon have been harvested annually since 1997 and more abundant harvests appear to have increased in frequency. Pink salmon harvest has increased from the sporadic catch of individual fish prior to 2003 to 41 pink salmon reported in 2004, 18 reported in 2008, three reported in 2011, and eight reported in 2012 (i.e., predominantly in even-numbered years). Recent reports

also expand the known distribution of this species upstream in the Mackenzie River, eastward in the Beaufort Sea and one putative pink salmon was recorded off the east coast of Greenland. Since 2003, one kokanee, one coho, seven Chinook, and ten sockeye salmon have also been reported in the Mackenzie River watershed. Multiple fish identified by local subsistence harvesters as “unusual” were captured near Arctic Bay, Nunavut, in 2011 and 2012. Although abundance and distribution data obtained from voluntary harvest reports need to be interpreted with caution, Pacific salmon may be following thermally suitable habitat northward and benefiting from increased productivity in the Arctic. Reduced sea ice extent and longer durations of open water in the Arctic may also facilitate expanded marine migrations of juvenile and adult salmon. Efforts to document the harvest of Pacific salmon will continue. Pacific salmon may be demonstrating new marine pathways that facilitate the expansion of other similarly opportunistic species and, as such, may be harbingers highlighting major arctic changes.

Introduction

Climate change is affecting the terrestrial, freshwater, and marine ecosystems in the Arctic through changes to important physical, chemical, and biological processes (Reist et al. 2006, Prowse et al. 2009). In the marine ecosystem, warming temperatures and changes to other oceanographic variables such as sea ice, advection, and turbulence influence vital biotic processes including growth rate, reproductive rate, phenology, swimming speed, mortality, recruitment, and distribution (Drinkwater et al. 2010). Therefore, shifts in species distribution, which are occurring in the Arctic as temperature barriers lessen due to climate warming (Vermeij and Roopnarine 2008, Post et al. 2009), may reflect ecosystem-level changes. Pacific salmon *Oncorhynchus* spp. may be effective biological indicators of these ecosystem changes (Irvine and Riddell 2007) because they appear to be naturally colonizing arctic habitats as conditions become more favorable (Babaluk et al. 2000b, Grebmeier et al. 2006). Chum *Oncorhynchus keta* and pink *O. gorbuscha* salmon have a relatively small but historical presence in the Arctic and are the only species of Pacific salmon with natal populations in the Arctic (reviewed in Nielsen et al. 2013). Vagrant adult Chinook *O. tshawytscha*, coho *O. kisutch*, sockeye *O. nerka*, and kokanee (i.e., freshwater-resident *O. nerka*) salmon have also been found in the Arctic, although rarely (reviewed in Nielsen et al. 2013). Although the marine migration routes of Pacific salmon harvested in the Arctic are not currently known, it is likely that these fish have either migrated from marine overwintering habitat in the Pacific Ocean or have overwintered in the Arctic Ocean. We hypothesize that the marine pathways facilitating expansion of salmon into the Arctic are related to increased

temperatures contributing to expanded marine habitat availability, including surface water distributional shifts and potential deepwater arctic refugia, and increased marine productivity facilitating survival and growth of Pacific salmon in the Arctic Ocean.

As Pacific salmon in the offshore marine environment primarily use the upper portion of the water column (within the top 40-60 m; Walker et al. 2007), warming sea-surface temperatures (SST) are predicted to affect ocean distributions of salmon (Myers et al. 2007, Abdul-Aziz et al. 2011). The current conceptual model for Pacific salmon distribution in the open ocean, based primarily on pink, chum, and sockeye salmon, posits that the salmon occupy the Bering Sea during the summer and fall feeding season, and migrate south and east for winter habitat (Myers et al. 2007). Pacific salmon actively change migration routes, timing, and rates based on spring SST and follow the northwest progression of the 2°C isotherm during open ocean migrations to summer habitat (Myers et al. 2007). The southern distributional limit of Pacific salmon in the open ocean is also related to species-specific thermal limits in SST; sockeye salmon have the coldest upper thermal limit (8.9°C), followed by coho (9.4°C) and chum and pink (10.4°C) salmon (Welch et al. 1995, 1998). Future climatic projections of warming SST in the North Pacific Ocean and Bering Sea shift this southern thermal limit northward, potentially shrinking the availability of thermally suitable habitat (Welch et al. 1995, 1998). However, this same warming SST may similarly shift the northern thermal limit northward (Welch et al. 1998), perhaps into the Chukchi or Beaufort Seas (Kaeriyama 2008). Warming climatic conditions producing warmer winters and earlier springs have resulted in the earlier return of mature salmon to spawning grounds and the earlier arrival of maturing salmon to the feeding grounds in the Bering Sea (Myers et al. 2007). Relatively high abundances of juvenile pink and chum salmon were caught in the Chukchi Sea in 2007 (Eisner et al. 2013) and demonstrated higher growth rates compared to those caught in the Bering Strait (Moss et al. 2009). This indicates northward-shifting distributions in the marine environment coupled with increased productivity that would benefit colonizing species.

Feeding behavior and prey preference may also be contributing to the range extension of Pacific salmon into the Arctic because the availability of key prey species may be increasing in the Arctic with reductions in sea ice and the apparent associated increase in production (Moore and Laidre 2006, Moore and Huntington 2008). Sockeye salmon have the narrowest food spectrum of all Pacific salmon species in the marine environment, and feed primarily on crustaceans, including euphausiids, hyperiids, and copepods, but also consume fish and squid (Karpenko et al. 2007). Pink salmon diet overlaps that of sockeye salmon, and also includes a wider variety of prey items (Karpenko et al. 2007). Chum salmon are the most flexible consumers (Karpenko et

al. 2007) and can survive on large quantities of low calorie prey items (Gritsenko et al. 2000). The retreating sea ice supports a phytoplankton bloom (Perrette et al. 2011), which may contribute to increases in zooplankton and upper trophic level species at the ice edge (Hunt et al. 2002). Strong phytoplankton blooms have been recorded in the Canadian archipelago and elsewhere in the Arctic (Perrette et al. 2011) and large under-ice phytoplankton blooms were also recently reported, presumably due to reductions in sea ice thickness and presence of melt ponds that allow sufficient light penetration (Arrigo et al. 2012). These shifts in productivity may increase feeding opportunity for Pacific salmon in the Arctic and are an example of ecosystem-level changes due to warming temperatures (Grebmeier et al. 2006).

Other sentinel species may also be opportunistically expanding northward due to increased feeding opportunity and suitable habitat conditions for longer periods of time in novel locations. Similar to Pacific salmon, bowhead whales *Balaena mysticetus* feed on zooplankton, especially euphausiids and copepods (Ashjian et al. 2010), and reductions in sea ice may be benefiting this species through increased feeding opportunities (Moore and Laidre 2006) and opportunities for dispersal (Heide-Jørgensen et al. 2012). Pacific-origin populations of bowhead whales migrate between the Bering Sea and the Canadian Arctic in the spring and fall, passing near Barrow, Alaska, where they form feeding aggregations (Moore et al. 2010). These aggregations may be indicating concentrations of prey that would be similarly suitable for Pacific salmon. Also, reductions in sea ice in the Northwest Passage are creating opportunities for increased movement of bowhead whales through this area and may eventually allow bowhead whales from populations originating in the Pacific and Atlantic Oceans to travel between the different oceans (Heide-Jørgensen et al. 2012). Seasonally migrant whales may also benefit from reductions in sea ice, feeding on forage fish that benefit from increased production resulting from reduced sea ice (Moore and Huntington 2008). Sections of the McClure Strait to Lancaster Sound support large populations of marine mammals and seabirds, suggesting higher productivity in these areas (McLaughlin et al. 2004). As Pacific salmon and certain species of ice-associated or seasonally migrant whales feed on similar prey items and undergo long seasonal marine migrations, it is possible that the benefits of reduced sea ice they experience are similarly experienced by Pacific salmon.

The warmer and more saline Atlantic layer, which occurs below 200 m in the Arctic (Carmack et al. 1989), may provide an overwintering refuge for salmon in the Arctic Ocean (as reviewed in Irvine et al. 2009). Gray whales *Eschrichtius robustus* have been recorded overwintering in the Beaufort Sea (Moore et al. 2006) and arctic cod *Arctogadus glacialis* may use this habitat during winter as they prefer warmer temperatures (Crawford et al. 2012). Pacific salmon undergo daily vertical migrations

to optimize growth and maturation by behavioral regulation of body temperature (Azumaya and Ishida 2005) and salinity (Quinn 2005), to optimize feeding on prey species that also migrate vertically (Walker et al. 2007) or as a mechanism for open-ocean orientation (Friedland et al. 2001). Sockeye salmon generally have the shallowest vertical distribution of all Pacific salmon species, typically less than 40 m, followed by pink, coho, chum, and Chinook salmon, although there are exceptions (Walker et al. 2007). Chinook and chum salmon occasionally attain depths exceeding 300 m in the offshore marine environment and more consistently attain depths of up to 350 m daily during migrations in coastal waters during the fall, likely to avoid higher surface water temperatures (Tanaka et al. 2000, Walker et al. 2007). Chum salmon were found to experience a wide range of temperatures in the marine environment (-1 to 22°C), likely coinciding with these vertical migrations (Walker et al. 2000). Therefore, it may be possible for Pacific salmon that make deep vertical migrations to adopt a strategy that allows them to benefit from thermoregulation in cold water while reducing the energetic costs of long migrations (Moore and Huntington 2008, Irvine et al. 2009).

Pacific salmon may be effective indicators of marine ecosystem changes associated with climate warming due to their expanding distribution and increased abundance in recent years. Thus, the objectives of this paper are to: (1) summarize the recent trends of relative abundance and the expansion of the known geographic distribution of Pacific salmon in the Canadian Arctic since previous reviews (Stephenson 2006, Nielsen et al. 2013); and (2) use the marine ecology of Pacific salmon (i.e., thermal preference, vertical distribution, swimming speed, and prey preference), coupled with changes in oceanographic conditions resulting from warming temperatures, to discuss possible marine pathways facilitating this observed expansion. If the trends of warming ocean temperatures, sea ice retreat, and associated changes in oceanographic conditions continue, Pacific salmon harvest throughout the Arctic may indicate marine pathways facilitating northward expansion of other opportunistic colonizing fauna.

Materials and methods

The Pacific Salmon Collection Program (PSCP) was established by Fisheries and Oceans Canada, Central and Arctic Region, in 2000 to record the capture of salmon by aboriginal and non-aboriginal harvesters in the Northwest Territories (Babaluk et al. 2000b, Stephenson 2006). As Pacific salmon are not specifically targeted in the Northwest Territories, establishment of the PSCP did not affect fishing effort for Pacific salmon, but rather provided an incentive to report harvested Pacific salmon to more accurately document actual numbers and

locations of harvested salmon and to verify species identification. All communities in the Mackenzie River watershed as well as coastal communities in the Beaufort Sea voluntarily participate in the PSCP. As Pacific salmon harvest had already been documented to occur throughout the Mackenzie River and in many Beaufort Sea communities (Stephenson 2006), the establishment of the PSCP did not increase the number of communities reporting harvest of Pacific salmon in the Mackenzie River watershed. Rather, it facilitated the documentation of more rarely harvested Pacific salmon species (i.e., pink, Chinook, coho, sockeye, and kokanee salmon) in communities that regularly reported chum salmon harvest, and allows observation of trends in year-to-year abundance and distribution of Pacific salmon harvested in Mackenzie River watershed and Beaufort Sea communities.

Reports of Pacific salmon harvested from 2004 to 2012 in the Canadian western Arctic, that were made available to Fisheries and Oceans Canada through the PSCP, are provided herein. Species identification was verified from actual specimens using keys of morphological and meristic counts (e.g., Scott and Crossman 1973), except as otherwise noted. A kokanee captured in 2005 was initially identified using meristic character data from Scott and Crossman (1973), and the life-history form was confirmed using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) analyses of the otolith to determine the pattern of strontium distribution (see methods in Swanson et al. 2010). In 2011, efforts to promote the PSCP increased and many local community organizations (i.e., Renewable Resource Councils, Hunters and Trappers Committees) became involved, which increased local communication and the convenience of reporting harvest. Through this program, it is possible to monitor overall trends in abundance of salmon as well as document capture dates and locations by species.

These reports of Pacific salmon harvested between 2004 and 2012 are compared to the data provided in Stephenson (2006), who reviewed the total reported Pacific salmon harvest in the Canadian western Arctic to 2003. Trends in salmon abundance were estimated by comparing: (1) frequency of exceptional years and (2) total harvest reported per year, although different collection methods for harvests reported prior to 2003 and those reported after 2003 restrict interpretation regarding trends using absolute numbers. To determine harvest to 2003, Stephenson (2006) included the subsistence and commercial fisheries; salmon captured during nondirected research by consultants, government, and university researchers; and salmon reported through the PSCP between 2000 and 2003. Total reported chum salmon harvest per year in Stephenson (2006) was tallied from 1931 to 2003. Where a range of harvest values was provided in Stephenson (2006) the maximum was used here, and where a range of years of harvest was provided the harvest was included in the latter year. The harvest reported by the

PSCP was separated from the reported harvest included in Stephenson (2006) when overlap occurred (i.e., 2000 to 2003). This allowed a comparison of historical harvest trends to more recent years. Related recent information regarding Pacific salmon on the Alaska North Slope is also summarized from information obtained from the literature.

The PSCP does not currently extend beyond the Northwest Territories. Therefore, no formal ongoing collections are under way for Pacific salmon obtained from the subsistence fisheries in the Canadian eastern Arctic, and very little data exist regarding incidental harvest of Pacific salmon in Nunavut. However, observations of vagrant salmon or "unusual fish" elsewhere in the Arctic are reported. The fish were tentatively identified to species by sending out high resolution photographs without any associated harvest location information independently to up to eight researchers specializing in Pacific salmon (*Oncorhynchus* spp.) or chars (*Salvelinus* spp.). These individuals provided their opinion regarding species using morphological information and/or meristic counts obtained from the photographs including criteria such as the size, shape, and color of the fish, the length and pigment of the lower jaw, the presence or absence of spots, the shape and size of the eye, the size of the caudal peduncle, the number of fin rays, and the number of scales above and below the lateral line. Unfortunately, actual specimens are not available to verify these species identification efforts.

Results

Canadian western Arctic

Chum salmon abundance appears to have increased in the Mackenzie River over the past decade. Although chum salmon are historically known from the Canadian western Arctic, more abundant harvests have been reported more frequently in recent years. Higher chum salmon harvest in the Canadian Arctic has been noted in 1978-1980, 1987, 1998, and 2003 using total reported harvest by multiple activities including subsistence and commercial catch, incidental catch by government, university researchers, and consultants, and those salmon reported to the Pacific Salmon Collection Program (Fig. 1). Using only harvest reported to the PSCP, higher chum salmon harvest is noted in 2004, 2005, 2007, 2008, 2011, and 2012 (Fig. 1). Therefore, since 2003 there have been only three years with fewer than 10 chum salmon reported to the PSCP. It is possible these years with lower harvest are simply due to lower incidence of reporting, not necessarily to a lower harvest of salmon, and it is possible that the years with higher harvest are simply due to increased incidence of reporting. However, the reporting of specimens to the PSCP reflects subsistence harvest trends; as harvest increases, so do voluntary reports of harvest.

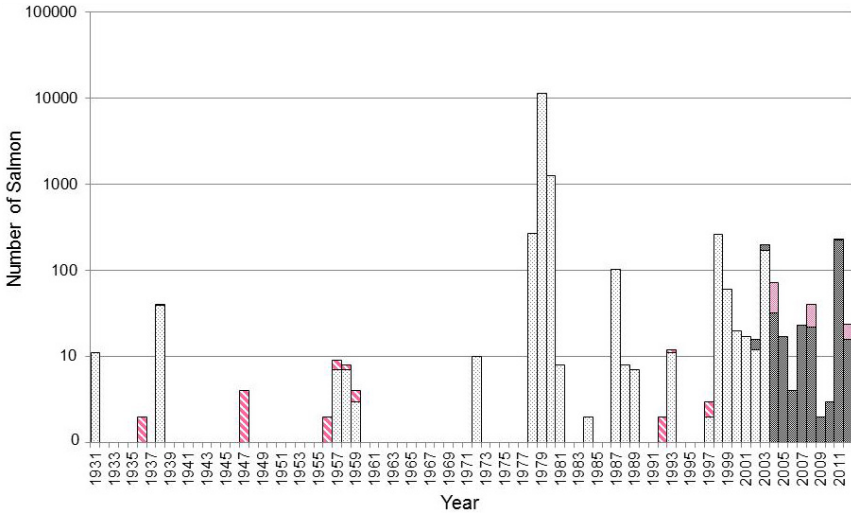


Figure 1. Data prior to 2003 were compiled by Stephenson (2006) from the literature and Fisheries and Oceans Canada (DFO) catch records (chum salmon = dotted white bars; pink salmon = pink striped bars); those from 2004 and onward (inclusive) are from the Pacific Salmon Collection Program (PSCP) (chum salmon = crosshatch bars, pink salmon = pink crosshatch bars), conducted by DFO. In 2002 and 2003, the reported chum salmon harvest obtained from the PSCP is indicated separately from the harvest reported by other methods included in Stephenson (2006). No salmon were obtained from the PSCP in 2000 and 2001.

Pink salmon have also become more common in the western Arctic, and they are being caught in more places in recent years. In the Canadian Arctic, pink salmon harvest increased from captures of mostly single specimens prior to 2003 to 41 pink salmon reported to the PSCP in 2004, 18 reported in 2008, three reported in 2011, and eight reported in 2012 (Fig. 1). Four pink salmon were harvested at the confluence of the Arctic Red and Mackenzie Rivers near Tsiigehtchic in 2004 and one was harvested in the Beaufort Sea near Paulatuk in 2012, expanding the known distribution of this species upstream in the Mackenzie River and eastward in the Beaufort Sea (Fig. 2).

Kokanee, sockeye, coho, and Chinook salmon have all been found in small numbers in the Canadian western Arctic (Babaluk et al. 2000a,b; Stephenson 2006). Since 2004, one additional kokanee, likely from the Peace River, British Columbia/Alberta system, was captured in the Slave River near Fort Smith on October 5, 2005, bringing the total captured

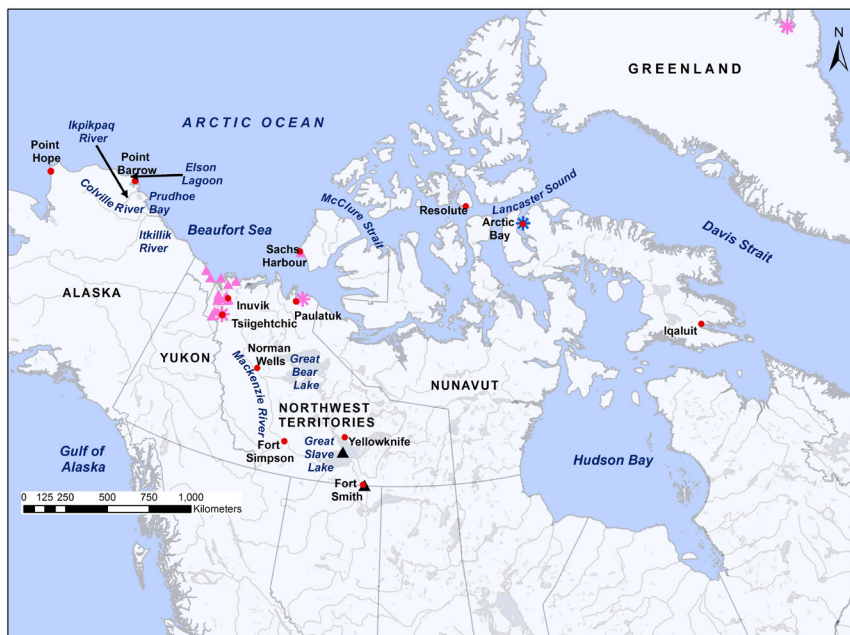


Figure 2. Overview of the Arctic showing the place names included in the text and the harvest locations of Pacific salmon species that have expanded their distribution since 2003. Historic pink salmon harvest locations (pink triangles) are shown and each symbol may represent the capture of more than one fish over several years. New capture sites (pink stars near Tsiigehtchic and Paulatuk, Northwest Territories, and east Greenland) for pink salmon are also included. Kokanee salmon harvest is represented by black triangles. The “unusual fish” (blue star) were harvested at Arctic Bay, Nunavut, in 2011 and 2012.

in the Canadian Arctic to two fish (Fig. 2). The strontium (Sr) profile for this 4+ year old salmon was indicative of freshwater residency, and was compared to a kokanee previously caught in the Mackenzie River watershed and a sockeye salmon previously harvested near Sachs Harbour (Fig. 3; Babaluk et al. 2000a). The low, relatively flat Sr signal (~500 ppm) early in each fish’s life (0 to ~500 microns) indicated that all three fish occupied a freshwater habitat during this period after which the sockeye salmon migrated to the sea where it spent the duration of its life, as indicated by the elevated Sr signal. Both kokanee remained in freshwater habitats for the duration of their lives, as indicated by the continuation of the low Sr signals. From 2004 to 2012, 10 additional sockeye

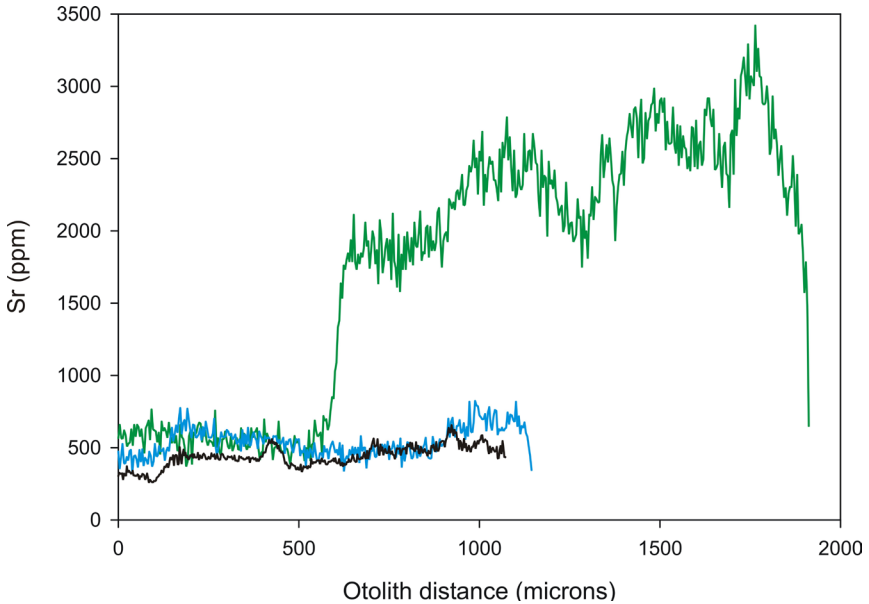


Figure 3. Strontium distributions from line-scans of otoliths from a sockeye salmon captured at Sachs Harbour, Northwest Territories, in late August 1993 (green line, scanning proton micro-probe analysis); a kokanee captured in Great Slave Lake, Northwest Territories, on August 11, 1991 (blue line, scanning proton micro-probe analysis); and a kokanee captured in the Slave River at Fort Smith, Northwest Territories, on October 5, 2005 (black line, LA-ICP-MS analysis).

salmon have been reported from the subsistence fishery: seven were harvested in 2004, two were reported in 2005, and one was reported in 2011. These captures did not extend the known distribution of sockeye salmon in the Canadian western Arctic. A coho salmon was captured in the Canadian Arctic in 2011 near the confluence of the Arctic Red River and the Mackenzie River at Tsiigehtchic, bringing the total number of coho salmon captured and reported in the Canadian western Arctic to three fish. This capture did not extend the known distribution of coho salmon in the Mackenzie River watershed. Seven additional Chinook salmon have been captured in the Mackenzie River since 2003: five in 2004, one in 2005, and one in 2008. Likewise, these captures did not extend the known distribution of Chinook salmon.

Canadian Eastern Arctic

Although the Canadian eastern Arctic is not included in the PSCP, residents of Arctic Bay, Nunavut, reported harvest of an unknown number of “unusual fish” in 2011 and 2012 (Figs. 2, 4). Several harvesters were catching these fish using gillnets in August to early September of each year, and the fish were all silver in color (i.e., non-spawning) when captured. Unfortunately, species identification cannot be verified from actual specimens. Using a high resolution photograph of a representative specimen, these fish have been placed both in the genus *Oncorhynchus* by five scientists knowledgeable in Pacific salmon ($n = 2$ suggest sockeye salmon, $n = 2$ suggest chum salmon, and $n = 1$ said either sockeye or chum salmon), and in the genus *Salvelinus* (most likely arctic char *Salvelinus alpinus*) by three scientists knowledgeable in chars. Thus, the difficulties of correctly identifying a fish using a photograph are highlighted. However, the local subsistence harvesters in Arctic Bay have repeatedly captured fish over two years that they have independently self-identified as “unusual,” suggesting that these fish were somehow different from the char normally harvested. Efforts to obtain actual samples of subsequent catches to identify these “unusual fish” to species will continue in future years.

Greenland

Researchers from the Greenland Institute of Natural Resources incidentally caught a pink salmon on the east coast of Greenland ($70^{\circ}20'53.11''N$, $28^{\circ}9'21.24''W$) on August 24, 2012 (Figs. 2, 4). While the specimen was not preserved, the species was identified as a pink salmon from a high resolution photograph which clearly showed the development of a distinctive “humped-back” shape and the large black spots on the dorsal surface and on both lobes of the caudal fin (Fig. 5). All scientists who viewed this photograph ($n = 7$) independently agreed that this fish was a pink salmon. This record documents the first known pink salmon captured on the east coast of Greenland.

Discussion

In the past 10 years, the geographic distribution and relative abundance of Pacific salmon in the Arctic has changed. The frequency of exceptional years of chum salmon harvest in the Mackenzie River watershed has increased and the harvest of pink salmon has changed from the sporadic capture of individuals to the reported capture of between eight and 41 pink salmon in several even years since 2004. The known geographic distribution of Pacific salmon in the Arctic has also increased with the pink salmon captured near Paulatuk, Northwest Territories, and the putative pink salmon captured on the east coast of Greenland

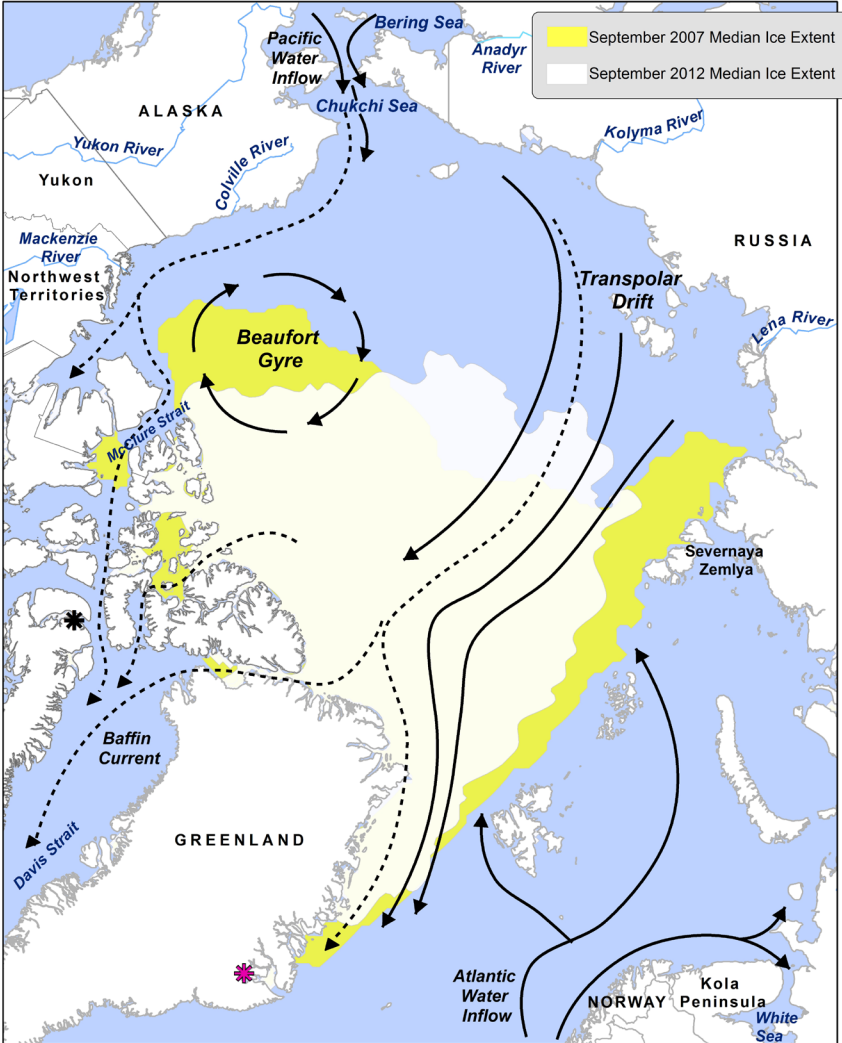


Figure 4. Schematic of the Pacific upper-water current and Atlantic deepwater current inflows in the Arctic Ocean, and the median sea ice extent in September 2007 and 2012. The solid lines depict ice drift and ocean currents, while the dotted lines are pathways for Pacific origin waters within and exiting the Arctic Ocean. The harvest location of the pink salmon on the east coast of Greenland (pink star) and the “unusual fish” at Arctic Bay, Nunavut (black star), are shown.



Figure 5. Photograph of the pink salmon captured on the east coast of Greenland on August 24, 2012. Photo credit: Mads Peter Heide-Jørgensen.

(Fig. 2). This range expansion and increase in relative abundance may be indicative of overall changes in the Arctic marine environment that facilitate increased survival and dispersal and highlight the importance of continuing to monitor Pacific salmon as sentinels of arctic change.

Increases in the harvest of chum salmon in the Canadian Arctic may be attributed to increased survival of natal populations, increased vagrants from outside sources, or both, as chum salmon is the only Pacific salmon species natal to the Canadian Arctic (Stephenson 2006, Irvine et al. 2009). On the Alaska North Slope, evidence of spawning also exists for chum salmon in several drainages between Point Hope and Prudhoe Bay (Craig and Haldorson 1986, Johnson and Blanche 2011) and juvenile chum salmon have been captured in the Colville River Delta (Moulton 2001 as reported in Fechhelm et al. 2009). Natal chum salmon may survive lethal low temperatures associated with arctic marine winters by migrating to the North Pacific, overwintering in the Beaufort Sea in the warm Atlantic layer, or behaving similar to other anadromous salmonids and finding suitable fresh or brackish water for overwintering (as reviewed in Irvine et al. 2009). Vagrant chum salmon may be similarly following feeding opportunities into the Arctic and end up in subsistence gillnets in the Mackenzie River. The increased frequency of exceptional chum salmon years since 2004 suggests that survival has increased in the freshwater, the marine environment, or both. However, changes to freshwater habitats resulting from warmer temperatures are apparent (Prowse et al. 2009) and could also contribute to the increased frequency of exceptional years of chum salmon in the Arctic (i.e., greater survival of the freshwater phase for fish of this species).

The larger harvests of pink salmon that have occurred in the Canadian Arctic in several even years since 2004 may be similarly reflecting changes facilitating increased dispersal and survival. Although robust self-sustaining spawning populations of pink salmon in the North American Arctic have not been confirmed through the capture of juveniles (Nielson et al. 2013), directed efforts to capture juvenile pink salmon have not been conducted to our knowledge, and would be difficult due to the coincidental timing of outmigration and spring melt. Pink salmon have the highest straying rate of the Pacific salmon species, so the capture of vagrants is not uncommon (Hendry et al. 2004). On the Alaska North Slope, pink salmon are now suspected to spawn in 11 drainages west of Point Barrow, Alaska (Woods and Carothers 2011), which has increased from the eight drainages suspected by Craig and Haldorson (1986). Their status east of Point Barrow is less well known although local knowledge suggests that pink salmon may spawn in the Ikpikpaq and Itkillik Rivers (George et al. 2009). Pink salmon are regularly caught daily in the subsistence fishery at Elson Lagoon, Alaska, during summer (George et al. 2009). The pink salmon harvest on the Alaska North Slope was exceptionally high in 2008: 19,531 pink salmon were harvested from Elson Lagoon (Woods and Carothers 2011) and catch-per-unit-effort information from a 26-year monitoring project at Prudhoe Bay shows a high catch of pink salmon in 2008 compared to other years (Fechhelm et al. 2009). Therefore, the possibility of a self-sustaining population of pink salmon along the Alaska North Slope exists and warrants further investigation. If verified, the vagrant pink salmon captured in the Canadian Arctic may be sourced from established populations along the Alaska North Slope. Alternatively, the pink salmon captured along the North Slope could be vagrants from populations farther away in North America or Russia. These fish presumably follow the current conceptual model for open ocean distribution and migrate to summer feeding grounds in the Bering Sea (Myers et al. 2007), and then follow marine pathways similar to other marine species to feeding opportunities in the Arctic.

The appearance of the pink salmon on the east coast of Greenland is an interesting anomaly, not only because this is the first record of a Pacific salmon captured on the east coast of Greenland, but also because the potential origin and migration routes of this pink salmon suggest significant changes have occurred in the Arctic. Confidence in identifying this fish as a pink salmon is high, albeit from a photograph, because of the distinct morphological characteristics present and because the fish was beginning to develop secondary sexual characteristics, making those distinguishing characteristics more pronounced (Fig. 5). Presumably, the captured pink salmon was entrained in the transpolar current, a Pacific origin water mass moving across the polar cap and extending south past the east coast of Greenland through the Denmark

Strait (Fig. 4). The lowest sea ice extent ever recorded was in 2012 and a section of sea ice connecting the polar ice cap to the Severnaya Zemlya islands melted for the first time (National Snow and Ice Data Center 2012; Fig. 4). This may have provided opportunity for pink salmon to follow the transpolar current from small natal runs in the Lena River or farther east, skirting and perhaps actively feeding at the ice edge to east Greenland (approximately 2500 nautical miles, nm; Fig. 4). Assuming pink salmon are approximately 0.5 m in length, and travel at 1 body length per second (Drenner et al. 2012), a pink salmon would travel at 23.3 nm per day and take approximately 107 days to reach the capture site. Presumably entrained in the transpolar current, which moves ice between 5 and 20 cm per second (2.3 to 9.3 nm per day) toward Fram Strait (Polyak et al. 2010), this fish would have reached the capture site in approximately 10 to 30 fewer days. Therefore, active swimming following retreating ice coupled with passive movement while entrained in ocean currents may have resulted in this possible extension to the distribution of Pacific salmon in the Arctic.

Alternative origin and migration route options are also possible, although less likely. The pink salmon captured in east Greenland may have originated from the self-sustaining odd-year population of introduced pink salmon to the Kola Peninsula (Gordeeva and Salmenkova 2011, ICES 2013). However, the pink salmon captured in east Greenland was indicating signs of gonad maturation by developing a dorsal “hump” and darkening color in 2012, an even year. Also, prevailing Atlantic currents would have moved the pink salmon eastward away from the capture location, making it an unlikely origin. Pink salmon were also introduced into Norway from the 1960s to the late 1970s (Bjerknes and Vaag 1980), which produced self-sustaining populations in 11 rivers in Finnmark, northern Norway (Hesthagen and Sandlund 2007), and pink salmon are also caught occasionally in Finland (ICES 2013). However, the prevailing Atlantic currents moving eastward again reduce the likelihood of a Scandinavian origin for the pink salmon caught in east Greenland. Pink salmon also have been caught annually in low numbers (5 to 30 per year) in Icelandic rivers since the 1960s (ICES 2013); however, these fish are likely strays from northern Russian populations (Icelandic Ministry of Fisheries and Agriculture 2013). There are also pink salmon in the Great Lakes following a single introduction of fry into Lake Superior in 1956, but it is thought that these pink salmon are not anadromous (Kwain 1982) and hence are an unlikely origin for the pink salmon caught in east Greenland. Several attempts have been made to stock pink salmon in the western North Atlantic, with little long-term success (Dempson 1980, Randall 1984). However, Dempson (1980) suggests that small naturally occurring populations of pink salmon in Newfoundland remain a possibility. Pink salmon were artificially maintained in Maine from 1906 to 1925, but returns dimin-

ished by 1927 (as reviewed in Dempson 1980) and pink salmon were planted in Maine once again in 1982 (Randall 1984). Pink salmon from British Columbia were transplanted to Newfoundland starting in 1959 (Lear 1975), but returns had diminished by 1976 (Dempson 1980). Pink salmon have been captured on the east coast of Canada in northern Labrador and in Newfoundland up to the late 1970s (Dempson 1980), and in New Brunswick in 1983 (Randall 1984) and also in Nova Scotia (Crossman 1991). However, no reports of pink salmon have been found in the western North Atlantic for 30 years (ICES 2013) and therefore it is an unlikely source for the pink salmon captured on the east coast of Greenland. If the pink salmon captured in east Greenland originated on the west coast of North America, estimated travel distance following the prevailing currents moving east and north is approximately 3750 nm from Point Hope, Alaska, and it would take the pink salmon approximately 157 days to reach the capture location. A routing through the McClure Strait is likely more feasible than via the Davis Strait because of reduced ice-cover and evidence that the Northwest Passage (via McClure Strait) has already been used as an ice-free corridor to connect individuals from two populations of bowhead whales originating in the Atlantic and Pacific Oceans (Heide-Jørgensen et al. 2012). Although pink salmon are unlikely to overwinter in the Arctic due to their shallow vertical distribution, they can eat a variety of prey items (Karpenko et al. 2007), suggesting this possibility cannot be ruled out. We hope that additional specimens will be captured in future years, allowing more thorough analyses and discussion of possible origins and migration routes.

The 2005 capture of a second kokanee in the Mackenzie River watershed, 14 years after the capture of the first kokanee in 1991, suggests the pathways facilitating dispersal of this species to the Mackenzie River drainage remain open. Babaluk et al. (2000a) summarize possible origins for the kokanee captured in 1991, including stocking efforts in Saskatchewan, Alberta, and British Columbia, as well as native populations in the Arctic and Thutade Lakes at the headwaters of the Peace River system. Babaluk et al. (2000a) concluded that the most likely origin of the kokanee captured in 1991 was the nearest known native populations in the Peace River system. Although stocking efforts for kokanee continue in British Columbia, as the kokanee captured in 2005 was age 4+ (i.e., hatched in 2001) and provincial stocking reports show that only 100 kokanee total were stocked in 2001, it is unlikely to have originated from this stocking program. No other stocking efforts for kokanee from any province into this system are known. Therefore, the kokanee captured in the Mackenzie River drainage in 2005 likely originated from the native populations in the Peace River system, similar to the kokanee captured in 1991.

There are many opportunities in researching dynamic Pacific salmon; however, the challenges of working with these rare species in

the vast geographic area of the Arctic must be addressed. Relying on voluntary reporting of Pacific salmon is necessary due to their relative low abundance in the vast geographic area. However, identifying the distribution of Pacific salmon using this method is a reflection of the locations of subsistence fisheries or other research projects and our ability to access information from these harvests. Therefore, this information can be used to identify trends in abundance and to document harvest locations, but is not a reflection of the actual number of Pacific salmon in the Arctic or the overall extent of their geographic distribution. Often, there are issues with correctly identifying species because of the rarity of Pacific salmon in subsistence fisheries. Increased communication with local communities and other research projects operating in the Arctic may increase reporting. An additional challenge in using this method is that the only certainty is the harvest location; the possible origins of vagrant salmon and routes of colonization are largely inferred from information regarding oceanographic conditions, ecology of the species, and locations of other self-sustaining populations. Compounding this, the arctic marine ecosystem is undergoing substantial changes, and the overall effect of these changes on aquatic species is largely unknown. Also, vagrants to the Arctic may be escapees from aquaculture efforts. As records of aquaculture for Pacific salmon species have not been found for Norway, Iceland, or eastern Canada, and Russian efforts are little known, we assume that, if present, escapees would originate from western North American or Japanese aquaculture efforts and therefore follow similar marine pathways to the Arctic as vagrants from natal populations in these areas.

The future of Pacific salmon in the Arctic looks promising; geographic distribution is increasing and trends suggest higher abundances. However, in order for vagrant salmon to become self-sustaining populations, viable freshwater habitat must be found, the timing of spawning and emergence must be correct to allow for survival of the juvenile fish, and the juvenile salmon must survive the harsh marine environment and return as adults. Future work using genetic analyses to more clearly identify the origin of Pacific salmon harvested, similar to mixed-stock fishery analyses (e.g., Beacham et al. 2009, Flannery et al. 2010), would provide information on the origin and source populations of salmon in the Canadian Arctic. Verifying successful spawning in the Arctic is necessary to identify potential sources for vagrants and the habitat conditions necessary for successful spawning and egg incubation for salmon at the northern extent of their range. Clearly, Pacific salmon provide an opportunity to monitor significant changes to the Arctic perhaps as a result of climate warming, and may be indicating pathways used by other similar opportunistic marine species. The challenges of researching such rare and colonizing species are matched by the opportunities they present.

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References

- Abdul-Aziz, O.I., N.J. Mantua, and K.W. Myers. 2011. Potential climate change impacts on thermal habitats of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean and adjacent seas. *Can. J. Fish. Aquat. Sci.* 68:1660-1680. <http://dx.doi.org/10.1139/f2011-079>
- Arrigo, K.R., D.K. Perovich, R.S. Pickart, Z.W. Brown, G.L. van Dijken, K.E. Lowry, M.M. Mills, M.A. Palmer, W.M. Balch, F. Bahr, N.R. Bates, C. Benitez-Nelson, B. Bowler, E. Brownlee, J.K. Ehn, K.E. Frey, R. Garley, S.R. Laney, L. Lubelczyk, J. Mathis, A. Matsuoka, B.G. Mitchell, G.W.K. Moore, E. Ortega-Retuerta, S. Pal, C.M. Polashenski, R.A. Reynolds, B. Schieber, H.M. Sosik, M. Stephens, and J.H. Swift. 2012. Massive phytoplankton blooms under arctic sea ice. *Science* 336:1408. <http://dx.doi.org/10.1126/science.1215065>

- Ashjian, C.J., S.R. Braund, R.G. Campbell, J.C. George, J. Kruse, W. Maslowski, S.E. Moore, C.R. Nicolson, S.R. Okkonen, B.F. Sherr, E.B. Sherr, and Y.H. Spitz. 2010. Climate variability, oceanography, bowhead whale distribution, and Inupiat subsistence whaling near Barrow, Alaska. *Arctic* 63:179-194.
- Azumaya, T., and Y. Ishida. 2005. Mechanism of body cavity temperature regulation of chum salmon (*Oncorhynchus keta*) during homing migration in the North Pacific Ocean. *Fish. Oceanogr.* 14:81-96. <http://dx.doi.org/10.1111/j.1365-2419.2004.00323.x>
- Babaluk, J.A., J.D. Reist, and G. Low. 2000a. First record of kokanee salmon, *Oncorhynchus nerka*, in Great Slave Lake, Northwest Territories. *Can. Field Nat.* 114:680-684.
- Babaluk, J.A., J.D. Reist, J.D. Johnson, and L. Johnson. 2000b. 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* 53:161-164.
- Beacham, T.D., K. Le, M. Wetklo, B. McIntosh, T. Ming, and K.M. Miller. 2009. Population structure and stock identification of chum salmon from western Alaska determined with microsatellite DNA and major histocompatibility complex variation. In: C.C. Krueger and C.E. Zimmerman (eds.), *Pacific salmon: Ecology and management of western Alaska's populations*. *Am. Fish. Soc. Symp.* 70:141-160.
- Bjerknes, V., and A.B. Vaag. 1980. Migration and capture of pink salmon, *Oncorhynchus gorbuscha* Walbaum in Finnmark, North Norway. *J. Fish. Biol.* 16(3):291-297. <http://dx.doi.org/10.1111/j.1095-8649.1980.tb03706.x>
- 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. <http://dx.doi.org/10.1029/JC094iC12p18043>
- Craig, P., and L. Haldorson. 1986. Pacific salmon in the North American Arctic. *Arctic* 39:2-7.
- Crawford, R.E., S. Vagle, and E.C. Carmack. 2012. Water mass and bathymetric characteristics of arctic cod habitat along the continental shelf and slope of the Beaufort and Chukchi Seas. *Polar Biol.* 35(2):179-190. <http://dx.doi.org/10.1007/s00300-011-1051-9>
- Crossman, E.J. 1991. Introduced freshwater fishes: A review of the North American perspective with emphasis on Canada. *Can. J. Fish. Aquat. Sci.* 48(Suppl. 1):46-57. <http://dx.doi.org/10.1139/f91-303>
- Dempson, J.B. 1980. Present status of pink salmon (*Oncorhynchus gorbuscha*) in the Newfoundland region. *ICES C.M.* 1980/M:27.
- Drenner, S.M., T.D. Clark, C.K. Whitney, E.G. Martins, S.J. Cooke, and S.G. Hinch. 2012. A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. *PLoS One* 7(3):e31311. <http://dx.doi.org/10.1371/journal.pone.0031311>

- Drinkwater, K.F., G. Beaugrand, M. Kaeriyama, S. Kim, G. Ottersen, R.I. Perry, H. Pörtner, J.J. Polovina, and A. Takasuka. 2010. On the processes linking climate to ecosystem changes. *J. Marine Syst.* 79:374-388. <http://dx.doi.org/10.1016/j.jmarsys.2008.12.014>
- Eisner, L., N. Hillgruber, E. Martinson, and J. Maselko. 2013. Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi Seas. *Polar Biol.* 36:87-113. <http://dx.doi.org/10.1007/s00300-012-1241-0>
- Fechhelm, R.G., A.M. Baker, B.E. Haley, and M.R. Link. 2009. Year 27 of the long-term monitoring of nearshore Beaufort Sea fishes in the Prudhoe Bay region: 2009 annual report. Report for BP Exploration (Alaska) Inc. by LGL Alaska Research Associates, Inc., Anchorage, Alaska. 84 pp.
- Flannery, B.G., T.D. Beacham, J.R. Candy, R.R. Holder, G.F. Maschmann, E.J. Kretschmer, and J.K. Wenburg. 2010. Mixed-stock analysis of Yukon River chum salmon: Application and validation in a complex fishery. *N. Am. J. Fish. Manag.* 30:1324-1338. <http://dx.doi.org/10.1577/M10-014.1>
- Friedland, K.D., R.V. Walker, N.D. Davis, K.W. Myers, G.W. Boehlert, S. Urawa, and Y. Ueno. 2001. Open-ocean orientation and return migration routes of chum salmon based on temperature data from data storage tags. *Mar. Ecol. Prog. Ser.* 216:235-252. <http://dx.doi.org/10.3354/meps216235>
- George, C., L. Moulton, and M. Johnson. 2009. A field guide to the common fishes of the North Slope of Alaska. Published by the North Slope Borough, Department of Wildlife Management, P.O. Box 69, Barrow, Alaska, USA.
- Gordeeva, N.V., and E.A. Salmenkova. 2011. Experimental microevolution: Transplantation of pink salmon into the European North. *Evol. Ecol.* 25:657-679. <http://dx.doi.org/10.1007/s10682-011-9466-x>
- Grebmeier, J.M., J.E. Overland, S.E. Moore, E.V. Farley, E.C. Carmack, L.W. Cooper, K.E. Frey, J.H. Helle, F.A. McLaughlin, and S.L. McNutt. 2006. A major ecosystem shift in the northern Bering Sea. *Science* 311:1461-1464. <http://dx.doi.org/10.1126/science.1121365>
- Gritsenko, O.F., N.V. Klovach, and L.F. Urusova. 2000. A new epoch for salmon stocks in the north-western Pacific. *N. Pac. Anadr. Fish Comm. Doc.* 503. 9 pp.
- Heide-Jørgensen, M.P., K.L. Laidre, L.T. Quakenbush, and J.J. Citta. 2012. The Northwest Passage opens for bowhead whales. *Biol. Lett.* 8:270-273. <http://dx.doi.org/10.1098/rsbl.2011.0731>
- Hendry, A.P., V. Castaic, M.T. Kinnison, and T.P. Quinn. 2004. The evolution of philopatry and dispersal: Homing versus straying in salmonids. In: A.P. Hendry and S.C. Stearns (eds.), *Evolution illuminated salmon and their relatives*. Oxford University Press, Toronto, pp. 52-91.
- Hesthagen, T., and O.T. Sandlund. 2007. Non-native freshwater fishes in Norway: History, perspectives and consequences. *J. Fish Biol.* 71(Suppl. D):173-183. <http://dx.doi.org/10.1111/j.1095-8649.2007.01676.x>

- Hunt, G.L., P. Stabeno, G. Walters, E. Sinclair, R.D. Brodeur, J.M. Napp, and N.A. Bond. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Res. Pt. II* 49:5821-5853. [http://dx.doi.org/10.1016/S0967-0645\(02\)00321-1](http://dx.doi.org/10.1016/S0967-0645(02)00321-1)
- Icelandic Ministry of Fisheries and Agriculture. 2013. Diadromous fish. Accessed May 2013: <http://www.fisheries.is/main-species/diadromous-fish/>
- ICES. 2013. Report of the Working Group on North Atlantic Salmon (WGNAS), 3-12 April 2012, Copenhagen, Denmark. ICES CM 2013/ACOM:09. 380 pp.
- Irvine, J.R., and B.E. Riddell. 2007. Salmon as status indicators for North Pacific ecosystems. *N. Pac. Anadr. Fish Comm. Bull.* 4:285-287.
- Irvine, J.R., R.W. Macdonald, R.J. Brown, L. Godbout, J.D. Reist, and E.C. Carmack. 2009. Salmon in the Arctic and how they avoid lethal low temperatures. *N. Pac. Anadr. Fish Comm. Bull.* 5:39-50.
- Johnson, J., and P. Blanche. 2011. Catalog of waters important for spawning, rearing or migration of anadromous fishes—Arctic Region, effective June 1, 2011. Alaska Department of Fish and Game, Special Publication No. 11-04, Anchorage.
- Kaeriyama, M. 2008. Ecosystem-based sustainable conservation and management of Pacific salmon. In: K. Tsukamoto, T. Kawamura, T. Takeuchi, T.D. Beard Jr., and M.J. Kaiser (eds.), *Fisheries for global welfare and environment*. Proceedings of 5th World Fisheries Congress. TerraPub, Japan, pp. 371-380.
- Karpenko, V.I., A.F. Volkov, and M.V. Koval. 2007. Diets of Pacific salmon in the Sea of Okhotsk, Bering Sea, and northwest Pacific Ocean. *N. Pac. Anadr. Fish Comm. Bull.* 4:105-116.
- Kwain, W. 1982. Spawning behavior and early life history of pink salmon (*Oncorhynchus gorbuscha*) in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 39:1353-1360. <http://dx.doi.org/10.1139/f82-182>
- Lear, W.H. 1975. Evaluation of the transplant of Pacific pink salmon (*Oncorhynchus gorbuscha*) from British Columbia to Newfoundland. *J. Fish. Res. Board Can.* 32:2343-2356.
- McLaughlin, F.A., E.C. Carmack, R.G. Ingram, W.J. Williams, and C. Michel. 2004. Oceanography of the Northwest Passage. In: A.R. Robinson and K.H. Brink (eds.), *The sea*, vol. 14: The global and coastal ocean. *Interdisciplinary Regional Studies and Syntheses*. Harvard University Press, pp. 1211-1242.
- Moore, S.E., and K.L. Laidre. 2006. Trends in sea ice cover within habitats used by bowhead whales in the western Arctic. *Ecol. Appl.* 16(3):932-944. [http://dx.doi.org/10.1890/1051-0761\(2006\)016\[0932:TISICW\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2006)016[0932:TISICW]2.0.CO;2)
- Moore, S.E., and H.P. Huntington. 2008. Arctic marine mammals and climate change: Impacts and resilience. *Ecol. Appl.* 18(2):S157-S165. <http://dx.doi.org/10.1890/06-0571.1>
- Moore, S.E., K.M. Stafford, D.K. Mellinger, and J.A. Hildebrand. 2006. Listening for large whales in the offshore waters of Alaska. *BioScience* 56:49-55. [http://dx.doi.org/10.1641/0006-3568\(2006\)056\[0049:LFLWIT\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2006)056[0049:LFLWIT]2.0.CO;2)

- Moore, S.E., J.C. George, G. Sheffield, J. Bacon, and C.J. Ashjian. 2010. Bowhead whale distribution and feeding near Barrow, Alaska, in late summer 2005-06. *Arctic* 63(2):195-205.
- Moss, J.H., J.M. Murphy, E.V. Farley, 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.
- 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.
- National Snow and Ice Data Center. 2012. Arctic sea ice breaks 2007 record low. Accessed April 9, 2013: <http://nsidc.org/arcticseaicenews/2012/08/>
- Nielsen, J.L., G.T. Ruggerone, and C.E. Zimmerman. 2013. Adaptive strategies and life history characteristics in a warming climate: Salmon in the Arctic? *Environ. Biol. Fish.* 96:1187-1226. <http://dx.doi.org/10.1007/s10641-012-0082-6>
- Perrette, M., A. Yool, G.D. Quartly, and E.E. Popova. 2011. Near-ubiquity of ice-edge blooms in the Arctic. *Biogeosciences* 8:515-524. <http://dx.doi.org/10.5194/bg-8-515-2011>
- Polyak, L., R.B. Alley, J.T. Andrews, J. Brigham-Grette, T.M. Cronin, D.A. Darby, A.S. Dyke, J.J. Fitzpatrick, S. Funder, M. Holland, A.E. Jennings, G.H. Miller, M. O'Regan, J. Savelle, M. Serreze, K. St. John, J.W.C. White, and E. Wolff. 2010. History of sea ice in the Arctic. *Quaternary Sci. Rev.* 29:1757-1778. <http://dx.doi.org/10.1016/j.quascirev.2010.02.010>
- Post, E., M.C. Forchhammer, M.S. Bret-Harte, T.V. Callaghan, T.R. Christensen, B. Elberling, A.D. Fox, O. Gilg, D.S. Hik, T.T. Høye, R.A. Ims, E. Jeppesen, D.R. Klein, J. Madsen, A.D. McGuire, S. Rysgaard, D.E. Schindler, I. Stirling, M.P. Tamstorf, N.J.C. Tyler, R. van der Wal, J. Welker, P.A. Wookey, N.M. Schmidt, and P. Aastrup. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325:1355-1358. <http://dx.doi.org/10.1126/science.1173113>
- Prowse, T.D., C. Furgal, F.J. Wrona, and J.D. Reist. 2009. Implications for climate change for northern Canada: Freshwater, marine and terrestrial ecosystems. *Ambio* 38(5):282-289. <http://dx.doi.org/10.1579/0044-7447-38.5.282>
- Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle. 378 pp.
- Randall, R.G. 1984. First record of a pink salmon (*Oncorhynchus gorbuscha*) in the Miramichi River, New Brunswick. *Nat. Can.* 111:455-457.
- Reist, J.D., F.J. Wrona, T.D. Prowse, M. Power, J.B. Dempson, R.J. Beamish, J.R. King, T.J. Carmichael, and C.D. Sawatsky. 2006. General effects of climate change on arctic fishes and fish populations. *Ambio* 35(7):370-380. [http://dx.doi.org/10.1579/0044-7447\(2006\)35\[370:GEOCCO\]2.0.CO;2](http://dx.doi.org/10.1579/0044-7447(2006)35[370:GEOCCO]2.0.CO;2)
- Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. *Bull. Fish. Res. Board Can.* 184. 966 pp.

- Stephenson, S.A. 2006. A review of the occurrence of Pacific salmon (*Oncorhynchus* spp.) in the Canadian western Arctic. *Arctic* 59(1):37-46.
- Swanson, H.K., K.A. Kidd, J.A. Babaluk, R.J. Wastle, P.P. Yang, N.M. Halden, and J.D. Reist. 2010. Anadromy in arctic populations of lake trout (*Salvelinus namaycush*): Otolith microchemistry, stable isotopes, and comparisons with arctic char (*Salvelinus alpinus*). *Can. J. Fish. Aquat. Sci.* 67:842-853. <http://dx.doi.org/10.1139/F10-022>
- Tanaka, H., Y. Takagi, and Y. Naito. 2000. Behavioural thermoregulation of chum salmon during homing migration in coastal waters. *J. Exp. Biol.* 203:1825-1833.
- Walker, R.J., V.V. Sviridov, S. Urawa, and T. Azumaya. 2007. Spatio-temporal variation in vertical distributions of Pacific salmon in the ocean. *N. Pac. Anadr. Fish Comm. Bull.* 4:193-201.
- 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(2):171-186. <http://dx.doi.org/10.1046/j.1365-2419.2000.00131.x>
- Welch, D.W., A.I. Chigirinsky, and Y. Ishida. 1995. Upper thermal limits on the oceanic distribution of Pacific salmon (*Oncorhynchus* spp.) in the spring. *Can. J. Fish. Aquat. Sci.* 52:489-503. <http://dx.doi.org/10.1139/f95-050>
- Welch, D.W., Y. Ishida, and K. Nagasawa. 1998. Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): Long-term consequences of global warming. *Can. J. Fish. Aquat. Sci.* 55:937-948. <http://dx.doi.org/10.1139/f98-023>
- Woods, S., and C. Carothers. 2011. Annotated bibliography: Subsistence use and knowledge of Beaufort salmon populations. Report for the US Department of the Interior Bureau of Ocean Energy Management, Regulation and Enforcement, Alaska OCS Region, 3801 Centerpoint Dr., Suite 500, Anchorage, AK 99503. 98 pp.
- Vermeij, G.J., and P.D. Roopnarine. 2008. The coming arctic invasion. *Science* 321:780-781. <http://dx.doi.org/10.1126/science.1160852>