James D. Reist, Frederick J. Wrona, Terry D. Prowse, Michael Power, J. Brian Dempson, Jacquelynne R. King and Richard J. Beamish

An Overview of Effects of Climate Change on Selected Arctic Freshwater and Anadromous Fishes

Arctic freshwater and diadromous fish species will respond to the various effects of climate change in many ways. For wide-ranging species, many of which are key components of northern aquatic ecosystems and fisheries, there is a large range of possible responses due to inter- and intra-specific variation, differences in the effects of climate drivers within ACIA regions, and differences in drivers among regions. All this diversity, coupled with limited understanding of fish responses to climate parameters generally, permits enumeration only of a range of possible responses which are developed here for selected important fishes. Accordingly, in-depth examination is required of possible effects within species within ACIA regions, as well as comparative studies across regions. Two particularly important species (Arctic char and Atlantic salmon) are examined as case studies to provide background for such studies.

INTRODUCTION

As noted elsewhere (1), freshwater ecosystems of the Arctic are complex and highly diverse with respect to size, connectivity, and structure and function. These factors and the wide geographic distribution of freshwaters in the Arctic as defined by ACIA and used here from sub-arctic, low to high Arctic will result in a wide range of climate change effects on those freshwaters and biota present in them (2). A number of important groups of northern fishes are present in these waters (3). These fishes consist of those which conduct their entire life history within freshwater habitats, and those which move between freshwater and marine areas (i.e., diadromous forms consisting of both anadromous fishes such as many salmonids which spawn in freshwater and feed in the sea, and catadromous fishes such as anguillid eels which do the converse). Presenting the potential responses to climate change for all freshwater and anadromous fish species present in the Arctic (i.e., n~99) (3) is beyond the scope of this contribution. Rather, the approach adopted here is to provide a series of examples of effects upon species that represent a range of possible responses. Species chosen are those which are particularly important for northern fisheries and/or pivotal in ecosystems. Accordingly, this contribution summarizes many of the potential responses of arctic freshwater and diadromous fishes to climate change. Although treated somewhat distinctly here, many of the effects noted separately for each of these groups of fishes in ACIA regions are also applicable to similar species elsewhere in the Arctic.

CLIMATE CHANGE EFFECTS ON ARCTIC FRESHWATER FISH POPULATIONS

The ability of fish to adapt to changing environments is species-specific. In the case of rapid temperature increases associated with climate change, there are three possible outcomes for any species: local extinction due to thermal stress, a northward shift in geographic range where dispersive pathways and other biotic and abiotic conditions allow, and genetic change within the limits of heredity through rapid natural selection. All three are likely to occur, depending on the species (4). Local extinctions are typically difficult to project without detailed knowledge of critical population parameters (e.g., fecundity, growth, mortality, population age structure, etc.). Dispersal and subsequent colonization are very likely to occur, but will very probably be constrained by watershed drainage characteristics, and ecological and historical filters (5). In watershed systems draining to the north, increases in temperature are very likely to allow some species to shift their geographic distribution northward (3). In watershed systems draining to the east or west, increases in temperature will possibly be compensated for by altitudinal shifts in riverine populations where barriers to movements into headwaters do not exist. Lake populations needing to avoid temperature extremes are very likely to be confined to the hypolimnion during the warmest months provided anoxic conditions do not develop. Patterns of seasonal occurrence in shallower littoral zones are very likely to change, with consequent effects on trophic dynamics. Changes in species dominance will very probably also occur because species are adapted to specific spatial, thermal, and temporal characteristics that are very likely to be altered by climate-induced shifts in precipitation and temperature.

Before successful range extensions can occur, habitat suitability, food supply, predators, and pathogens must be within the limits of the niche boundaries of the species.

In addition, routes to dispersal must exist. Physiological barriers to movement such as salinity tolerances or velocity barriers (i.e., currents) will possibly restrict range extensions where physical barriers to migration (e.g., waterfalls, non-connected drainage basins) do not exist. Against this background of dynamic physical and biotic changes in the environment, some regional and species-specific climate change

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projections for freshwater and diadromous fishes of the Arctic are outlined below for the different regions defined by ACIA (2): Region 1 Arctic Europe, East Greenland and Russian European North; Region 2 Siberia; Region 3 Chukotka, Bering Sea, Alaska and western Canada; and, Region 4 Northeast Canada, Labrador Sea, Davis Strait and West Greenland.

Region 1: European Percids

Under scenarios of climate change, spawning and hatching of spring and summer spawning populations are likely to occur earlier in the year. For example, European perch (*Perca fluviatilis*) are very likely to advance spring spawning by as much as a month (4) and juveniles will very probably experience longer growth periods and reach larger sizes at the end of the first summer. The potential benefits of increased size, however, may not be realized if higher egg incubation temperatures are associated with smaller larvae having smaller yolk sacs and increased metabolic rates (6, 7). Small larvae are more susceptible to predation, have higher mortality rates, and are confronted with a shorter period during which they must adapt to external feeding to survive (6). In addition, increased overwinter survival is very likely to be associated with increased demand for prey resources and will possibly lead directly to population stunting (i.e., smaller fish sizes).

The zander (*Sander lucioperca*) is a eurythermal species distributed widely in Europe whose growth and recruitment success is correlated with temperature (8). The present northern distribution coincides with the July 15 °C isotherm and is likely to shift northward with climate change. Successive year-class strengths and growth rates in northern environments are also likely to increase as temperatures increase. Increases in both abundance and size are very likely to have consequences for the competitiveness of resident coldwater-guild fishes if concomitant increases in lake productivity fail to yield sufficient ration to meet the needs of expanding populations of zander and other percids.

Evidence that northward colonization is already occurring comes from the Russian portion of Region 1. Over the last 10 to 15 years, northern pike (*Esox lucius*), ide (*Leuciscus idus*), and roach (*Rutilus rutilus lacustris*) have become much more numerous in the Pechora River Delta and the estuary Sredinnaya Guba (~68° N) of the Barents Sea.(9).

Region 2: Fishes in Siberian Rivers

Many species of fish in the large northward flowing rivers of Siberia have the potential for significant northward range extensions and/or responses to climate change. Several species in the Yenisey and Lena rivers that prefer warmer boreal-plain habitats (e.g., roach, ide, common dace *Leuciscus leuciscus baicalensis*, European perch, and ruffe *Gymnocephalus cernus*) are likely to move into the northern mouth areas of these rivers that are currently dominated by whitefishes and chars. Overall, fish species diversity is likely to increase, but this probably will be at the expense of the coldwater salmonids. The speed at which this process might occur is uncertain, however, it may already be occurring and is likely to be within approximately the next 10 years. In addition, as environments change, other species (e.g., carp bream *Abramis brama* and zander) are likely to be intentionally stocked in the area, which is likely to result in additional pressures upon native arctic fish populations.

Region 3: Alaskan Game Fish

Food availability and lotic productivity are often determined by nutrient availability, and are believed to be a major controlling factor in riverine fish production. Several studies have found that fish density and growth correlate with nutrient status and food availability in streams, with larger standing crops in nutrient-rich streams (10, 11, 12). In particular, salmonid biomass in nutrient-poor environments varies with nutrient levels, habitat type, and discharge (13). The bottom-up propagation of nutrients through algal and invertebrate production to fish has been projected to be a possible result of climate-induced increases in nutrient additions associated with permafrost degradation. However, this premise has rarely been tested, and the relationship between nutrient loading and fish production is poorly understood (14). Shifts in stable carbon and nitrogen isotope distributions have demonstrated a coupling between the stimulation of benthic algal photosynthesis and accelerated growth in stream-resident insect and fish populations (15). In addition, experimental fertilization of Alaskan tundra rivers has demonstrated increased growth rates for adult and young-of-the-year Arctic grayling (*Thymallus arcticus*), with the strongest response observed in the latter (16).

Temperature increases associated with climate change are also likely to be associated with lower flows, with which growth of adult Arctic grayling is also highly correlated. At low flows, adult growth is low, whereas young-of-the-year continue to grow well (16). As Arctic grayling in many Alaskan systems are already food-limited, the associated increases in metabolic costs are likely to be associated with decreased survival unless nutrient loading associated with permafrost degradation offsets the increased metabolic costs of low-flow conditions (17).

Lake trout (*Salvelinus namaycush*) are a keystone predator in many Alaskan lakes. Low food supply and temperatures, however, keep the species near physiological limits for survival with the result that lake trout will possibly be particularly sensitive to changes in either temperature or food supply initiated by climate change (18). Increases in temperature are very likely to increase metabolic demands, which will very probably lead to lower realized growth rates unless met by sufficient increases in ration.

Many populations are already food-limited, which suggests that further increases in temperature are very likely to have significant effects on population abundance. Bio-energetic modeling of juvenile populations of lake trout in the epilimnion of Toolik Lake suggests that they will not survive a 3 °C increase in mean July epilimnetic temperatures given existing ration, and would require a greater than eight-fold increase in food to achieve historical end-of-year sizes (18). Documented increases in epilimnetic temperatures, however, have not been associated with increased food availability. If recent changes in the lake foreshadow long-term trends, these modeling results suggest that young lake trout will not overwinter successfully, and the associated changes in mortality patterns may lead to local extinction and the disruption of lake-trout control of the trophic structure in many arctic lakes (18).

Region 4: Northern Québec and Labrador Salmonid and Pike Populations

Among the salmonids of northern Québec and Labrador, the response to temperature changes is very likely to track physiological preferences for warmer waters.

Several species present in southern areas, such as native Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) and introduced brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*), are very likely to extend their ranges northward.

While the warmer-water percid and cyprinid species are restricted to the southwest and unlikely to extend their range to the north (unless moved by humans) because of dispersal

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barriers (19), the euryhaline salmonids are able to move from estuary to estuary as conditions allow. For example, the successful movement of rainbow and brown trout and exotic salmon species (*Oncorhynchus* spp.) in the estuary of the Gulf of St. Lawrence has been documented (20), and there is some indication that brown trout dispersal in Newfoundland may be temperature-limited (21). As a result of probable range extensions, Arctic char (*Salvelinus alpinus*) are very likely to be reduced or replaced by anadromous Atlantic salmon and/or anadromous brook trout throughout much of the southern portion of the region and brook trout are very likely to become a more important component of native subsistence fisheries in rivers now lying within the tundra zone (19). Lake trout are likely to disappear from rivers and the shallow margins of many northern lakes and behave as currently observed in temperate regions (22).

Effects on Widespread Freshwater Species

Northern pike habitats in much of subarctic North America and Europe are projected to sustain some of the most severe consequences of global climate change.

Adult northern pike actively avoid surface temperatures in excess of 25 °C, which are very likely to become more frequent as air temperatures increase throughout much of the distributional range. In shallower lakes, lake-chemistry changes associated with temperature increases will possibly result in cooler bottom waters becoming anoxic and a restriction of suitable habitat (23). Studies in Ohio impoundments have shown that although northern pike show summer growth, there is an associated weight loss during the periods of habitat restriction (24). Accordingly, northern pike throughout much of their current range are expected to be restricted in both numbers and size as a result of climate change.

Attempts to relate fish yields and mean annual air temperatures have been coupled with geographic information techniques to project shifts in both distribution and yields of important freshwater fishes in this region (25). In general throughout sub-arctic Québec, yields for lake whitefish (*Coregonus clupeaformis*) are projected to increase by 0.30 to >1.0 kg/ha/y. Northern pike yields in southern portions of the Hudson Bay drainage are projected to increase by 0.03 to 0.10 kg/ha/y, and those in northern portions to increase marginally (0.01 to 0.03 kg/ha/y). Walleye (*Sander vitreus*) yields in the southern drainage basin of Hudson Bay are projected to increase by 0.01 to 0.10 kg/ha/y. These changes are projected to result from occupancy of new, presently unsuitable areas in the north, and increased overall productivity throughout the entire area. The total overall productivity will possibly be offset due to declining production in southern areas that become unsuitable due to suboptimal thermal regimes for these species or to local population extirpation.

Although many projected effects of climate change on arctic freshwater fishes seem to be generally positive (e.g., increased growth resulting from ameliorating thermal conditions), a common finding is that commensurate favorable changes must also occur in other factors (e.g., increased nutrient loading and productivity of lower trophic levels).

A central issue is whether arctic freshwater systems have the capacity for suitable change in all relevant parameters underpinning fish survival and productivity, and will do so at the rate driven by concomitant changes in climate, or whether disconnects among key freshwater ecosystem processes and/or components will result from differential responses to climate change (e.g., rate, direction, and nature of climate-induced changes) (3).

Effects of Climate Change on Arctic Diadromous Fish

About 30 of the approximately 99 species of fishes within the Arctic regions belonging to the families Petromyzontidae, Acipenseridae, Anguillidae, Clupeidae, Osmeridae, Salmonidae, and Gasterosteidae (3) exhibit diadromous behavior (i.e., spend part of their lives in the marine environment and migrate to freshwater to spawn, or the converse). Most arctic diadromous species are actually anadromous (i.e., use estuarine and/or marine environments for feeding and rearing; and freshwater environments for spawning, early life-history, and, in the case of most arctic species, overwintering); only freshwater eels (Anguillidae) and some lampreys (Petromyzontidae) are catadromous (i.e., breed at sea and rear in freshwater). Most anadromous species in the Arctic are facultatively anadromous (26) in that many individuals in a population do not necessarily migrate to sea even though it is accessible. Typically, anadromous behavior is most prevalent at northern latitudes (27) because the ocean is more productive than adjacent freshwater habitats in temperate and arctic zones (28). For a number of facultative anadromous species (e.g., Arctic char, Dolly Varden *Salvelinus malma*, brook trout, brown trout, and threespine stickleback *Gasterosteus aculeatus*), anadromous behavior declines in frequency or ceases toward the southern portion of the distributional range of the species (several references in 27). Anadromy in Arctic char also declines or ceases towards the extreme northern geographic limits, probably because access to and time at sea, hence benefits, are limited (29). Facultative anadromous species exhibit anadromy in polar regions to take advantage of marine coastal productivity and escape extreme oligotrophic conditions that typify arctic lake systems. Generally, individuals of a population that exhibit anadromous behavior have a larger maximum size and higher maximum age, indicating some benefit to seaward migration and feeding.

Diadromous fishes will integrate climate change effects on freshwater, estuarine, and marine areas, hence the total impact on these fishes is very likely to be significant (3, 30, 31). This has major resulting impacts since these fishes support important fisheries in all arctic regions (32, 33). The following paragraphs discuss the consequences of climate change for diadromous fishes.

The projected impacts of climate change on arctic lakes suggest that, overall, productivity of these limited systems will very probably increase due to a longer ice-free growing season and higher nutrient loads. Anadromous fish populations will probably benefit initially with increases in survival, abundance, and size of young freshwater life-history stages, which will possibly cascade to older, normally anadromous stages. Thus, facultatively anadromous species will possibly exhibit progressively less anadromous behavior if the benefits of remaining in freshwater systems outweigh the benefits of migrating to coastal areas for summer feeding over time. When the freshwater food supply was experimentally increased, the incidence of anadromous migration by Arctic char decreased (34). However, the increased estuarine production discussed elsewhere (35) will possibly offset any tendency to reduce facultative anadromy in response to increased freshwater production. The exact balance and circumstances of how such scenarios unfold will be ecosystem-specific and will depend on the details of present productivity, accessibility, and ease of migration by fish, as well as the nature and degree of any climate-related effects.

The variability associated with projected changes in productivity is uncertain. The anadromous species present in the Arctic (3) are typically long-lived (15–50 years) compared to other fish species. Longevity benefits species living in variable environments by ensuring a relatively long reproductive cycle, thus

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Box 1
Effects of environmental change on life-history and population characteristics of Labrador Arctic char.

Present-day relationships between environmental and biological parameters must be understood to provide the foundation for assessing future climate change effects on fish populations. The general lack of such understanding for most arctic fishes currently precludes in-depth development of comprehensive and accurate qualitative scenarios of impacts, and limits quantification of effects under those scenarios. Development of such understanding requires substantive long-term data that are relatively sparse for most arctic fish; a circumstance that demands redressing. A notable exception is the availability of data for Arctic char. The distribution and life-history patterns of Arctic char are complex, and few attempts have been made to relate fluctuations in abundance, catch rates, and stock characteristics to environmental variables such as temperature and precipitation. The table in this box lists associations between biology and variability in environmental parameters for Arctic char from northern Labrador, Canada.

Table. Environmental associations for Nain Arctic char.

Timing	Significant environmental parameters	Probable environmental effect	Observed biological effect on individual fish	Observed biological effect on fish population
Within year	Summer air temperature Sea-surface temperature	Increased marine productivity within limits	Increased weight Increased length Increased growth	Better condition
First summer of life	Winter precipitation	Increased snowpack Decreased seasonal freezing More overwintering habitat	Increased overwinter survival Decreased energetic costs for maintenance (increased growth)	More fish Earlier recruitment to the fishery (i.e., lower age-at-catch)
Fourth year of life (first year at sea)	Summer air temperature Summer precipitation	Increased nutrient loading to nearshore habitat Increased nearshore productivity	Increased growth Increased survival	Increased weight at catch Decreased age-at-catch

Long-term (1977–1997) monitoring of the char fishery at Nain, Labrador (56° 32’ N, 61° 41’ W) has produced data on both anadromous fish and environmental variables that have been applied in assessing long-term variability in catch biometrics (41). Climate variability, particularly annual and seasonal, was found to have effects at critical life-history stages, and to affect average stock age, weight, and length characteristics, thus determining the dynamics of exploited Arctic char populations several years later and their eventual spawning success (41). The table in this box also summarizes aspects of climate variability and the probable effects on the population.

Mean age-at-catch and weight of Arctic char from the Nain fishery declined significantly, with a lag of four years, in response to high summer precipitation.This precipitation-related change is probably due to fluctuations in river flow and nutrient dynamics during the initial migration of Arctic char to nearshore marine areas. First-time migrants tend to stay in the nearshore areas (42, 43) and are most likely to be immediately affected by changes in nutrient inputs resulting from variability in river flow. High-precipitation years increase nutrient and particulate organic carbon exports from river and lake catchments (44, 45), which increase nutrient inputs to nearshore marine feeding areas and probably increases productivity at all trophic levels.

The significance of increased winter precipitation is related to events occurring in the first critical winter of life for char. Heavier, more frequent snowfalls in Labrador maintain ice cover in an isothermal state and limit ice thickness (46). Deeper snowpack maintains taliks, or unfrozen areas, in lake and river beds (44, 47), improving winter refugia conducive to fish survival (44, 48, 49).

The possible effects of temperature on Arctic char are complex. Mean fish length increased with rising summer temperatures and the persistence of optimal growth temperatures (12–16 °C) over a longer period of time (50, 51). High spring temperatures and accelerated ice breakup, however, can have negative effects on populations migrating with ice breakup (52). In the Fraser River (Labrador), breakup typically occurs in late April or early May (53) and would be well advanced, as would seaward migration, in years experiencing above-normal May temperatures. Although temperature increases can advance preparatory adaptations for marine residency (i.e., smoltification), they also result in a more rapid loss of salinity tolerances and a shortening of the period for successful downstream migration (54). Rapid increases in temperatures are likely to impinge on the development of hypo-osmoregulatory capabilities in migrants and decrease growth due to the increased energetic costs of osmoregulatory stress, increase the probability of death during migrations to the sea, and decrease average growth by reducing the average duration of marine residence.

Several conclusions arise from this study:

- Long-term, comprehensive biological and environmental datasets are critical to assess and monitor climate change impacts on fish populations.
- Climate variables are very important in understanding year-to-year variability in stock characteristics.
- Causative relationships appear to exist between life history and environment but precise roles played, timing of the effect, and limits to the effect need more thorough investigation.
- For long-lived arctic fish, the effects of particular environmental conditions are often lagged by many years, with cascading effects on fishery production and management.
- Environmental effects are manifested in the fish population in the same way that other effects such as exploitation are (e.g., in terms of individual growth that translates into survival, fitness, reproduction, and ultimately into population-dynamic parameters such as abundance), thus distinguishing specific effects of climate change from other proximate drivers may be problematic.
- Particular environmental effects tended to reinforce each other with respect to their effect on the fish; although generally positive in this study, effects from several environmental parameters could presumably act antagonistically resulting in no net effect, or could synergistically act in a negative fashion to substantially impact the population.

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Box 2
Projecting stock-specific effects of climate change on Atlantic salmon.

Differences in stock characteristics, local geography, and interannual variations in spawning escapement of Atlantic salmon confound attempts to apply the results of specific field studies (55, 56, 57, 58) in projecting the effects of climate change (59). Further complications arise from the ongoing debate regarding whether environmental variation and population effects are greatest in fresh or marine waters (31), and how these act to determine survival of various life stages and population abundance. Knowledge of Atlantic salmon biology, however, is sufficient to describe the range of temperature conditions required for optimal growth and reproductive success, and thus to allow inferences of climate change effects. Atlantic salmon life-history stages all occur within optimal temperature ranges (19, 60, 61, 62). However, variation in the required range of optimal temperatures for salmon at different life stages makes projecting the effects of climate change difficult. To date, three approaches to tackling the problem have been proposed in the scientific literature (3).

In the first approach, regional climate scenarios and projections are coupled directly to knowledge of the physiological limits within which salmon operate. For example, winter discharges and associated overwintering habitat will respond to precipitation changes (63). Low summer discharge on the east coast of Newfoundland and in southern Québec, which limits parr (young salmonid with parr-marks before migration to the sea) territory and hampers upstream adult migration, is also very likely to change, affecting population abundances in many rivers (63). Problems with this approach include uncertainty in precipitation and extreme events forecasts, and coupling of regional climate models with ocean circulation models.

A second approach to understanding the possible impacts of climate change on Atlantic salmon is to apply what is known about relationships between weather and salmon population dynamics. For example, historical records from the salmon fisheries in the Ungava region of northern Québec show a correlation between ice conditions, the late arrival of salmon, and poor catches. This relationship suggests that an improvement in salmon abundances will possibly occur in the future associated with a climate-induced reduction in the extent and duration of sea-ice cover (64, 65).The correlation between stock characteristics and latitude (63) suggests that mean smolt (young salmonid which has developed silvery coloring on its sides, obscuring the parr marks, and which is about to migrate or has just migrated into the sea) ages are likely to decrease in association with increases in average temperatures and growing-season length. Modeling results project that temperature increases and decreases will have varying effects on populations at different latitudes (Table below) (59).Where present-day temperatures are at the upper end of the optimal temperature range for growth, increases in temperature reduced growth, increased average riverine residency and associated riverine mortalities, decreased smolt production, and increased parr densities. The reverse (increased smolt production and decreased parr densities) occurred when temperatures at the lower end of the temperature range optimal for growth were raised. Modest changes in precipitation, and thus available habitat, had no significant direct effect or interactive effect with changes in temperature on either smolt production or parr density under any of the considered temperature scenarios. Thus, depending upon the exact location and characteristics of the salmon population, the precise impact of a given environmental change under a future climate scenario may be positive or negative relative to present conditions. This makes regional differences in fish biology, present-day local climate, and climate change scenarios extremely important in projecting future situations.

Table. Results of modeling experiments projecting the possible effects of climate change on different populations of Atlantic salmon (59).

Population location	Temperature increase		Temperature decrease	
	Smolt production	Parr density	Smolt production	Parr density
47° 01' N, 65° 27' W	decrease	increase	no change	no change
50° 11' N, 61° 49' W	increase	decrease	decrease	increase
53° 42' N, 57° 02' W	increase	decrease	decrease	increase

A third approach to projecting the effects of climate change involves attempting to shift ecological zones into more appropriate geographic locations to reflect probable future climate regimes and the known physiology of potentially affected species. The present distribution of many fish is limited by the position of the summer isotherms that limit the fish either directly due to thermal relationships or indirectly through effects on critical resources such as food (66). Use of this approach suggests that Atlantic salmon will possibly disappear from much of their traditional southern range in both Europe and North America as temperatures rise, and find more suitable habitat in cold rivers that experience warming. In the eastern Atlantic, the overall area occupied by salmon is likely to shrink due to a lack of landmasses to the north with potentially suitable environments. In the western Atlantic, rivers in the Ungava Bay area will possibly become more productive and are likely to experience increases in the numbers of salmon (e.g., the Koroc and Arnaux rivers). Rivers that currently have large salmon runs are also likely to become more productive (e.g., the George, Koksoak, and Whale rivers) and experience associated increases in salmon abundances (19).There are also rivers on Baffin Island and Greenland that will possibly become warm enough for Atlantic salmon to colonize. Such colonization, however, is likely to come at the expense of Arctic char populations that currently inhabit the rivers because of competition between the two species. Constraints on redistribution northward with climate change include reductions in the availability of spawning substrate with increased sediment loading of rivers, changes in stream and river hydrology, and delay in the establishment of more diverse and abundant terrestrial vegetation and trees known to be important for the allochthonous inputs that provide important sources of carbon for salmon (67).

minimizing the risk that prolonged environmentally unfavorable periods (5–15 years) will result in the loss of a spawning stock (36). Anadromous forms of arctic fish species that are relatively long-lived (>10–15 years) are probably suited to cope with increased variability that will possibly accompany climate change. Initially, as environmental conditions improve, successful spawning episodes are very likely to increase in frequency. Anadromous fish that are short-lived (<10–15 years) are likely to exhibit more variability in abundance trends with increased variability in environmental conditions.

Anadromous species also inhabit streams or rivers when in freshwater in addition to lakes. Projected climate impacts on arctic hydrology (37) suggest that runoff is very likely to be driven by increased precipitation and will very probably not be as seasonally variable; winter flows are very likely to be enhanced and summer flows reduced. In addition, warmer conditions are projected to reduce the length of winter, shorten the ice season, and reduce ice-cover thickness. Thus, streams that were previously frozen solid will very probably retain water beneath the ice, benefiting anadromous species that utilize

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streams for winter habitat (e.g., Dolly Varden). Overwintering habitat is critical for arctic species and is typically limited in capacity (26). However, the shortened ice season and thinner ice are very likely to reduce ice-jam severity during spring. This will have implications for productive river deltas that require flooding. There are several anadromous species, such as Arctic cisco (*Coregonus autumnalis*), that rely on deltas as feeding areas, particularly in spring (26).

Anadromous fish are by definition highly migratory and tolerant of marine conditions. Thus, as limiting environmental factors ameliorate, a number of sub- or low-arctic anadromous species are likely to extend their northern limits of distribution to include areas within the Arctic. Pacific salmon species are likely to colonize northern areas of Region 3. Sockeye salmon (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) have already been incidentally recorded outside of their normal distribution range on Banks Island, Northwest Territories, Canada (38). Similarly, anadromous species such as Atlantic salmon, alewife (*Alosa* spp.), brown trout, and brook trout will possibly also extend their northern range of distribution in Regions 1 and 4. New anadromous species invading the Arctic are likely to have negative impacts on species already present. However, for many of these subarctic species, climate change is likely to have negative impacts on southern populations, offsetting any positive benefits that will possibly accrue in the north (39). Catadromous species such as European eel (*Anguilla anguilla*; Region 3) are primarily warm-water species limited by colder arctic temperatures (e.g., Nordkappe, northern Norway is the present limit) (40). Eastward colonization of Russian areas of Region 2, where the species does not now occur, is possible; additionally, increased abundances are likely in some areas where the European eel presently occurs but where populations are insufficient for fisheries (e.g., Iceland).

CASE STUDIES

Two Arctic Anadromous Species are Particularly Important in Northern Fisheries: Arctic char (all regions) and Atlantic salmon (Regions 1 and 4). To indicate the range of possible responses of these species to climate change, they are treated separately in Boxes 1 and 2, respectively.

CONCLUSIONS

Variation in life history among wholly freshwater and diadromous species has substantive consequences for the interpretation and projection of potential climate change effects on these fishes. Furthermore, many arctic diadromous, particularly anadromous, species of fishes are facultative in their life histories—that is, they exhibit life history variation within each species that parallels inter-specific variation in habitat use (e.g., Arctic char exhibits co-occurring anadromous and non-anadromous life history types).

Climate change effects will be quite different according to the type of aquatic habitat occupied (1, 2, 68) as well as with respect to the area of the Arctic in which those habitats occur. Thus, widely distributed wholly freshwater fishes (e.g., burbot, *Lota lota*) will experience geographic variation in shifting climate drivers both latitudinally within an ACIA region and also among regions. Similarly, for anadromous species such as Arctic char, variation in multiple climate drivers will be different even in the local context depending upon which life history type is examined—freshwater forms will integrate climate change effects on the local freshwater habitat(s) only, whereas anadromous forms will integrate effects for freshwater habitats (e.g., lakes used for early rearing, rivers used for migrations) and also for marine feeding areas (e.g., estuarine and nearshore areas). This increases the complexity of potential responses of such fishes and thus makes generalizing about climate change effects on arctic freshwater and anadromous fishes difficult. Facultative life histories, especially when present within populations, add another layer of complications. Moreover, the relatively large number of freshwater and diadromous species present in the Arctic (n~99) (3) results in even further complexity. Accordingly, to develop a manageable suite of possibilities regarding the responses of these species to climate change, the approach adopted here was to provide a series of examples of effects for key species that represent the range of fishes in this group. Species chosen were those particularly important for northern fisheries and/or pivotal in ecosystems, or which are likely to exhibit significant shifts due to climate change that can serve as useful illustrations of the range of possibilities. However, the range of possible responses of all arctic fish species is likely much greater than that enumerated here. In most cases, limited information prevents widespread comparisons for key fish species both within and among regions of the Arctic. That, and wide geographic diversity within species, suggests that in-depth examinations of climate change effects are required for each species as well as with regards to the comparisons among ACIA regions in order to best underpin projection of climate change effects and to aid preparedness to meet challenges affecting northern fish populations. Regardless, substantive effects of climate change, both positive and negative, will occur on arctic freshwater and anadromous fish species. This, in turn, will affect human uses of many of these species (32).

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James D. Reist, Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, Manitoba, R3T 2N6, Canada, Tel.: 204 983 5032, Fax: 204 984 2403.
reistj@dfo-mpo.gc.ca

Frederick J. Wrona, National Water Research Institute of Environment Canada, Department of Geography, University of Victoria, PO Box 1700 STN CSC, Victoria, BC, V8W 2Y2, Canada.
Fred.wrona@ec.gc.ca

Terry D. Prowse, Water and Climate Impacts Research Centre, National Water Research Institute of Environment Canada, Department of Geography, University of Victoria, PO Box 1700 STN CSC, Victoria, BC, V8W 2Y2, Canada.
Terry.Prowse@ec.gc.ca

Michael Power, Department of Biology, University of Waterloo, 200 University Avenue West, Waterloo, ON, N2L 3G1, Canada.
m3power@sciborg.uwaterloo.ca

J. Brian Dempson, Fisheries and Oceans Canada, 80 East White Hills Road, PO Box 5667, St. John's, NL, A1C 5X1, Canada.
dempsonb@dfo-mpo.gc.ca

Jackie R. King, Fisheries and Oceans Canada, 3190 Hammond Bay Road, Nanaimo, BC, V9T 6N7, Canada.
KingJac@dfo-mpo.gc.ca

Richard J. Beamish, Fisheries and Oceans Canada, 3190 Hammond Bay Road, Nanaimo, BC, V9T 6N7, Canada.
beamishr@dfo-mpo.gc.ca

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