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Fisheries: Effects of Climate Change on the Life Cycles of Salmon

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Changes in climate are likely to impact water temperature, quantity and quality and thus alter the biological composition, production and function of aquatic environments. Understanding the responses of aquatic life, such as fish, to these changes represents a fundamental ecological challenge.

Temperature affects all vital processes of cold-blooded aquatic organisms, including activity, feeding, growth and reproduction. Thus, it is widely believed that climate warming will affect the distributions of marine and freshwater species, resulting in a general shift polewards to reflect their thermal preferences. Moreover, the composition and relative abundance of species in local communities will shift towards those of warmer temperatures. It is also predicted that these effects may be more pronounced towards the poles where warming is expected to be greater than in the tropics. Evidence is growing that such changes are occurring in both marine and freshwater ecosystems in response to the warming of aquatic environments in recent decades.

Climate change will not only affect aquatic environments through the direct effects of temperature, but also through other environmental changes coincident with, or driven by, the changes in temperature. Ocean currents are predicted to change and with them so will circulation patterns and regions of nutrient upwelling that affect water quality and biological productivity. For example, the Eastern Pacific Ocean, which has undergone warming in recent decades, has experienced a concurrent decline in productivity, particularly in the near-surface zone. The cause, however, remains poorly understood, but the implications are far reaching for the ecological community. Climate change will also alter annual and seasonal precipitation patterns and increase variability within and among years, which are expected to have profound effects on freshwater environments, affecting lake levels and stream flows. Moreover, if changes in water quantity occur with changes in water temperature, then changes in water quality will likely follow, owing to changes in concentrations of ions, dissolved gases, and organic materials. Thus, the effects of climate change on aquatic environments, both marine and freshwater, are expected to be multifaceted.

SALMON AS AN INDICATOR

Fishes, such as salmon, which spend their lives both in freshwater and marine environments (i.e., diadromous; Figure 1) are ideal for the study of responses to climate change and may prove to be good biological indicators of it. Their life cycle, which takes them from freshwater through estuarine and out into open ocean habitats and then back again, exposes salmon to a diversity of potential effects resulting from climate change. The typical life cycle of anadromous salmon (*Oncorhynchus* and *Salmo* spp.) begins with the spawning of eggs into nests constructed in the gravel of freshwater rivers or streams during the fall (Figure 1). The eggs incubate through the winter and hatch in the spring, with the juveniles emerging from the gravel shortly thereafter. The juveniles remain in freshwater streams, rivers and/or lakes for as little as a couple of months or up to several years (five) before migrating through estuaries and out into the ocean. It is in the ocean where the vast majority of the salmon's growth occurs over a period ranging from a few months up to several years (four). During this oceanic period, salmon appear to be almost continuous travelers and may migrate distances in excess of 5000 km away from the oceanic outlet of their natal river. They then return to their natal river to breed and may migrate up to 4000 km in fresh water to reach their spawning grounds. Accurate homing to the natal river to breed facilitates the evolution of population-specific traits and the intra-specific variation that so characterizes salmon species.

Global warming is predicted to affect freshwater before it affects marine habitats because of the relatively rapid effects of changes in runoff and precipitation on freshwater systems, and the buffering capacity of the oceans. Moreover, rivers and streams are likely to be among the most

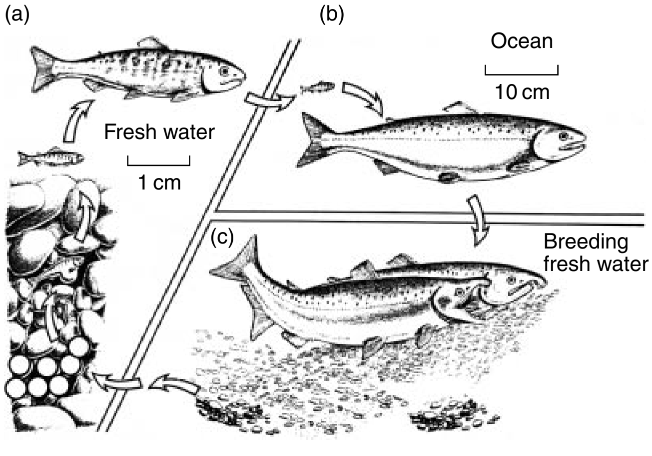

Figure 1 A generalized life cycle of anadromous salmon, involving (a) egg incubation and juvenile rearing in fresh water followed by (b) migration to the ocean for sub-adult growth and then (c) the return to fresh water for breeding

sensitive aquatic environments to warming because of their small volumes and sensitivity to changes in flow discharge. Thus salmon, with their early and adult life history stages occurring in these environments, will be exposed early on to such direct effects of climate change. In addition, it is generally thought that temperate species, such as salmon, will be more susceptible because warming is predicted to be greater at higher than lower latitudes. Salmon will also be subject to the indirect effects of climate change, such as changes in ocean currents, wind patterns and timing of river flows, that affect the productivity and availability of food, the costs of migration and mortality.

Generally, it is difficult to predict the responses of aquatic animals to climate change, partly because of lack of information about their environmental requirements and the dynamics of their life histories. Salmon, however, have been well studied and quantitative models exist for such things as growth, feeding, egg incubation, thermal tolerance and life history. In addition, a number of long time-series on salmon populations exist by which the responses to climate change may be identified. Finally, the large amount of among-population variation within salmon makes them well suited to study, because the first response of organisms to changing climate will involve changes at this level.

RESPONSES OF SALMON TO CLIMATE CHANGE

Climatic warming is likely to affect salmon species negatively, particularly those populations that rely extensively on freshwater habitats for juvenile rearing. They are likely to face altered water temperatures and precipitation related changes in flow regimes. It is predicted that there would be major alternations in river hydrology resulting from earlier snow melt and increases in the elevations at which freezing occurs. As the flows of many salmon rivers are dominated by snowmelt, summer runoff may decrease and winter runoff may increase.

Climate change may impact salmon at a variety of life stages, beginning at egg incubation (Figure 2). Changes in water temperatures and river flows during this life stage may cause sub-optimal juvenile emergence from the gravel nests and result in increased egg and early juvenile mortality. Egg development is largely temperature dependent, as is the period following hatching when juveniles remain in the gravel for several weeks surviving on the nutrients in their yolk sacs before beginning exogenous feeding and emerging. The timing of emergence from the gravel has likely evolved in response to selection for a presumably optimal time for survival (e.g., temperature and flow), food availability and competitive advantages. If winter temperatures increase following climate change, egg incubation will be shortened and result in earlier juvenile emergence from the gravel, in the future. Such a shift away from the

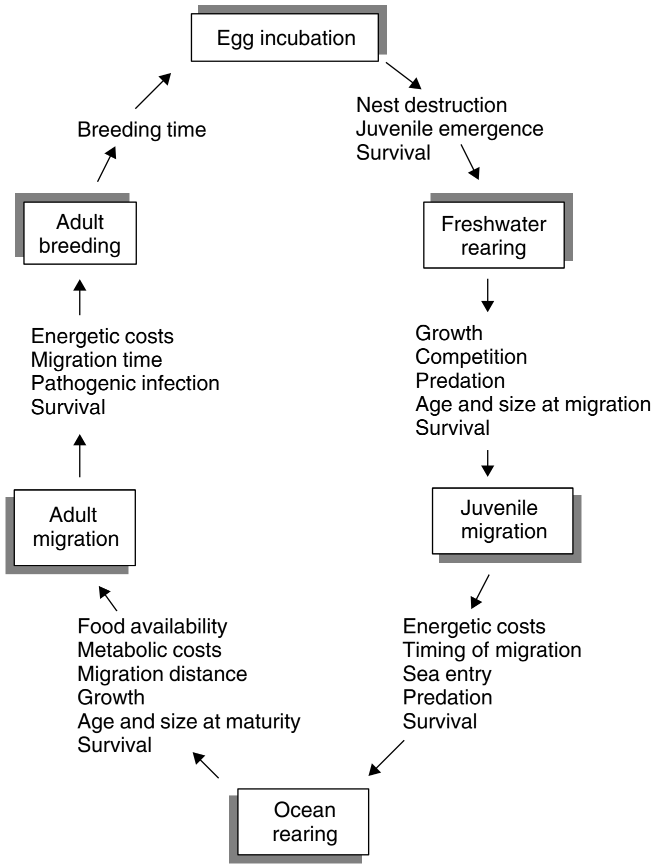

Figure 2 Potential impacts of climate change at various life stages of salmon

optimal timing for juvenile emergence is likely to result in increased mortality. Moreover, if climate change results in increased winter flows, as many models predict, gravel shifts caused by flooding may become more frequent and larger, increasing the susceptibility of incubating eggs to destruction. In addition, increased flows may occur during emergence, when the juveniles are highly susceptible to displacement.

The subsequent growth and survival of the juveniles in fresh water will be affected directly by temperature and flow regimes, and indirectly through changes in the aquatic community in response to the altered hydrology. Each salmon species has characteristic upper (usually below 30 °C) and lower (freezing) temperature limits for survival. Within these limits, there is an optimum temperature range over which feeding and growth occurs (e.g., 6–22.5 °C for Atlantic salmon), but this range declines as the availability of food declines. The effects of climate warming on growth of juvenile salmonids can thus be expected to differ with latitude.

At the southern edge of their distribution area, salmon growth may be retarded and mortality higher because of expanded periods with unfavorably high temperatures. This may be further compounded by the expected reductions in flow and thus habitat during summer months. Generally, stream flow is positively related to habitat space for, and thus abundance of stream fishes. Increased water temperatures may also alter the aquatic community structure, both in terms of the forage base for juvenile salmon and the competitor and predator communities. Expansion of the ranges of more southerly, warmer water communities is expected. Such potentially deleterious effects on growth may, in turn, influence over-winter survival and subsequent marine survival, both of which are size related.

In northern areas, on the other hand, growth rate will increase because of more favorable temperatures during summer and a longer growing season. However, droughts may be more frequent during summer than today, resulting in reduced habitat and food availability, and thus retarded growth. On the whole, however, freshwater growth is expected to be better and the age of migration to the ocean (smolting), which is growth related, lower than today. Moreover, because production of salmon smolts is inversely related to age of smolting due to annual freshwater mortality rates of 40–60%, the smolt production is expected to increase in northern rivers. Thus, losses in production of juvenile salmon in the south may well be overridden, at least initially, by gains in the north.

The spring photoperiod is considered the major environmental cue initiating the transformation from freshwater juvenile to seaward migrating smolt, whereas various river-specific stimuli (e.g., water temperature, water flow, and lunar cycle) regulate the timing of the seaward migration. Such river-specific stimuli likely reflect local adaptations that have evolved to insure an optimal timing of smolt migration in terms of survival and subsequent growth. For example, descending smolts are subject to heavy mortality from fish and birds in the river and estuary. To avoid such predation, smolts migrate down river in schools. If climate change results in reduced spring flows, as is predicted for many temperate rivers, the smolt run may be more dispersed over time and schools smaller in size, resulting in increased exposure to predation. Moreover, the energetic costs of migration may be higher and time taken to descend longer. Changes in river temperatures and flow regimes may also lead to sub-optimal timing of entry into the sea. Timing of sea entry is critical for the early sea survival of smolts because of physiological stress, metabolic costs, food availability and predation, all of which are influenced by sea temperatures.

Once in the ocean, salmon are likely to face further effects of climate change including altered sea surface temperatures, currents and areas of nutrient upwelling, all of which directly or indirectly affect their lives. It has been predicted that modest rises in sea surface temperatures, in line with predictions of global warming over the next half-century, could cause salmon to disappear from much of the North Pacific Ocean. During November–March, for instance, sockeye salmon are only found in regions where the sea surface temperature is below 7 °C and thus show remarkably low thermal limits which excludes vast areas of the North Pacific that are otherwise potentially habitable. It is speculated that this is driven by interactions between water temperature and metabolic rate when food supplies are low. The salmon may be avoiding warmer water because food supplies are insufficient to maintain high metabolic rates, which increase exponentially with temperature in cold-blooded animals such as fish. In addition to a reduction in their habitat, a northern shift in its distribution will force salmon to travel farther to reach their breeding rivers, resulting in smaller fish with fewer eggs.

In the Atlantic, where salmon survival, particularly that of out-migrating juveniles, appears related to the areal extent of 8–10 °C water during spring, the situation may be more complicated. Sea surface temperatures may interact with changing currents to either decrease or increase area of the 8–10 °C water during spring and thus, salmon survival. Warmer sea surface temperatures in the Atlantic may also lead to a northward expansion of the range of salmon, as apparently occurred during 1919–1938 when a strong inflow of warm Atlantic water into the Kara Sea, Northern Russia, led to the eastward expansion of salmon.

Warmer sea surface temperatures are also likely to interact with currents to alter the marine communities exploited by salmon, reducing food availability (zooplankton biomass). It has been speculated that this, coupled with higher metabolic costs in warmer water, will lead to smaller salmon, a prediction that is consistent with evidence that climate variation over the North Pacific Ocean is responsible for long-term (1925–1993) trends in the body size of sockeye salmon.

Upon return to fresh water during their breeding migration, adult salmon are likely to encounter increased water temperatures and decreased river flows associated with climate warming that may cause additional prebreeding mortality and reduced egg deposition. Increased water temperatures influence temperature-related metabolic processes, with energy expenditure during migration increasing exponentially with temperature. Moreover, because of a positive relation between temperature and pathogenic infection rate in salmonids for several bacterial pathogens, increased temperatures will likely increase the susceptibility of breeders to pathogens and parasites. Reduced water flows, in addition to affecting water temperatures, will also influence the ease of migration because it is a primary determinant of upstream fish passage. In general, lower flows create lower velocity conditions that enhance upstream fish passage. Many rivers, however, have obstacles (e.g., falls, barriers) that can only be passed during higher flow conditions. Thus delays in river ascent may occur, increasing the energetic expense for the adults, which do not feed during the breeding migration. Such low flows are also believed to select against large adult body size, which could result in reduced salmon size in many rivers.

Finally, breeding time in salmonid fishes appears adapted to present day thermal and flow regimes in such a way that conditions are favorable for breeding, egg incubation and juvenile emergence and subsequent feeding. Thus, climatic induced changes in thermal and flow regimes are likely to have deleterious consequences for one or more of these life history events that are intimately linked to breeding time.

Climate change is thus likely to impact the life cycle of salmon at a variety of stages (Figure 2). Salmon do have the ability to respond immediately to warming events, such as an El Niño, by altering migration patterns. However, this response is often either inappropriate, or insufficient to compensate for strong negative effects on growth and survival. Thus, while the response of salmon to climate change will, at least initially, involve environmentally mediated changes (i.e., phenotypic plasticity) in life history, it will likely require longer-term genetic change as well. The speed and ability of the life history to respond (through plasticity and genetic change) will be important in determining the extent to which salmon populations become compromised.

See also: **Life Cycles**, Volume 2; **Fisheries: Pacific Coast Salmon**, Volume 3.

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