Life Cycles

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Although no generally agreed definition of life exists, various processes associated with living organisms often help distinguish them from inert matter. These processes include growth, or its potential; reaction to stimuli in the immediate environment; passive or active movement; metabolism through which matter and energy are transformed into the organization of organic compounds unique to each individual; and reproduction.

As organisms grow and age, most go through various developmental stages in which some of these processes, or certain aspects of them, are particularly emphasized. For instance, a butterfly began life as an egg and later emerged as a larva, the eating for growth stage. The larva eventually pupated and underwent metamorphosis before emerging as a butterfly. Only as a butterfly can the insect mate, reproduce, and thus complete its life cycle. A species' life cycle is thus the sequence of developmental stages that individuals pass through, going from the start of one stage to the start of that same stage in the next generation.

Animals and many simple organisms complete their life cycle in a single generation. For instance, individuals of various species of protists (microorganisms which have both plant and animal characteristics) and bacteria originate from the fission of a single existing individual, grow to maturity, and then complete their life cycle by dividing into two new individuals. In more 'advanced' animal species, the individual originates from the fusion of male and female sex cells (gametes), grows to reproductive maturity, produces gametes, and then completes the life cycle through successful mating.

Most plants, and some fungi and protists, have life cycles with alternating generations. Individuals originate from germinating spores, which grow into gamete-producing organisms. Fertilized gametes can grow into spore-producing organisms. Spore germination completes the life cycle.

Life cycles provide frameworks for exploring how different species might cope with global change. Global change is occurring because the scale of human activities now exceeds that of all other species and affects biospheric fluxes of matter and energy. Global change encompasses the direct and indirect effects of changes in atmospheric composition, biological diversity, land use, and climate. Since different stages of a life cycle often have different functions (e.g., growth, reproduction), and requirements (e.g., temperature, habitat, food) to fulfil those functions, different aspects of global change will likely have different, possibly even compensatory, impacts over a complete life cycle. Thus, one needs to consider how each component of global change might affect each life stage in forecasting how a species might respond to global change as a whole. This approach is illustrated with three very different life forms: the spruce budworm, a naturally outbreaking forest insect; wild salmon, a group of fishes which spend parts of their life cycle in freshwater and parts in saltwater; and black spruce, a ubiquitous tree species of North America's boreal forest.

RESPONSES OF THE SPRUCE BUDWORM TO GLOBAL CHANGE

The spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), the dominant insect defoliator of North America's coniferous forests, has been outbreaking on a roughly 35 year cycle since before the first Europeans arrived on the continent. Its outbreaks last 10–15 years and during outbreaks spruce (*Picea* species) and balsam fir (*Abies balsamea*) are often killed over vast areas. In its life cycle (Figure 1), the spruce budworm has one generation a year. In mid-August, 2–3 weeks after the eggs are laid and most adult moths have died, the first instar (stage immediately prior to shedding the first skin) larvae hatch and move to overwintering sites on the branches. They overwinter as small, second instar larva and become active again in early May. Then they pass through four heavily feeding instars before pupating in late June. In July, emerged moths mate, disperse, and lay eggs. The spruce budworm's potential for causing tree mortality stems from its rapid growth and high fecundity (realized fertility) of 170–200 eggs per female. A mature sixth instar larva weighs approximately 100 mg (fresh weight) and is roughly 20–30 mm long. This is about 1500 times larger than it was as a second instar larva just 6–9 weeks earlier.

Global change, particularly climate change, may affect insect populations directly through their *per capita* growth rates or indirectly through interactions and feedbacks with other species and abiotic components of the environment. These interactions and feedbacks often depend on delicately tuned phenological relationships. For instance, the spruce budworm, like many other herbivores, has synchronized its greatest nutritional demand (the heavily feeding larval stages) with the time when developing, rather then mature, host plant foliage is most available. Developing is often better for herbivores than mature plant tissue because it is lower in fibre (which can limit digestibility), higher in nitrogen (nutritional value), and lower in secondary metabolites (defensive chemicals). In a warmer climate, foliage is generally expected to develop more quickly, thus diminishing the time interval when herbivores can find the best foliage. Since cold-blooded animals such as insects also

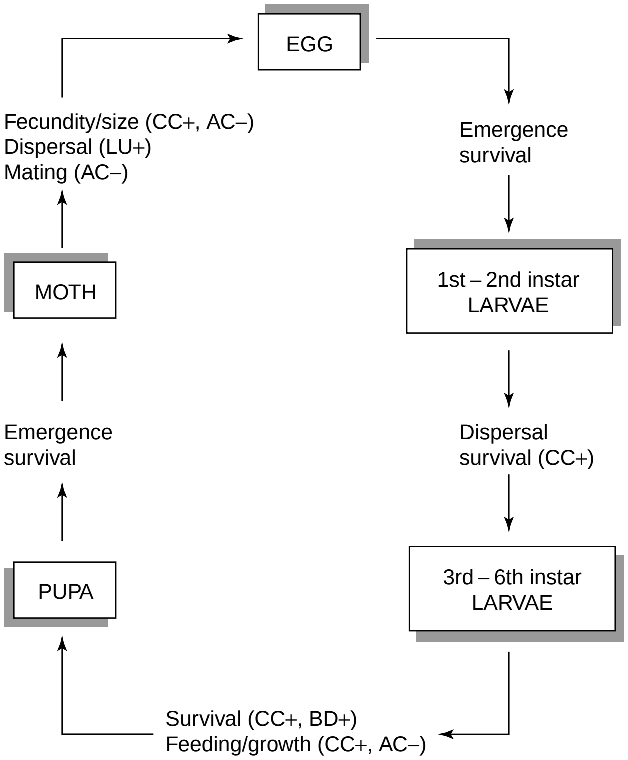

Figure 1 Generalized life cycle of the spruce budworm. Boxes enclose the major stages. The principal functions and processes needed to progress from stage to stage are designated by phrases interrupting the directing arrows. Letters in parentheses indicate components of global change: AC, atmospheric chemistry; BD, biodiversity; CC, climate change; or LU, land use), which the text describes as potentially influencing the function or process. A plus or minus indicates whether the influence is expected to be largely positive or negative for the insect

develop faster and feed more actively at higher temperatures, however, the net effect is uncertain. Many insect herbivores may remain well synchronized in phenological development with that of their host plants' foliage, even in changing climates. On the other hand, increased atmospheric CO_2 concentrations may allow host plant foliage to accumulate secondary metabolites fast enough that herbivory becomes inhibited relatively earlier in development, and this may work against some insects.

Under climate change, the southwestern part of the spruce budworm's range can expect drier conditions with the increasing likelihood of drought. Warmer, drier conditions directly increase spruce budworm reproductivity and larval survival. Indirect effects are also important. The vulnerable larval stages can escape many natural enemies (e.g., the fungal pathogen *Erynia (Zoophthora) radicans*) because larvae develop faster at high temperatures than at normal temperatures, and this reduces the length of their exposure. Furthermore, larvae develop more quickly at high temperatures than many of their natural enemies. As many of these natural enemies have alternate hosts, they are less closely synchronized phenologically with the spruce budworm than is the budworm with its host trees. Hence, some phenological de-synchronization of the spruce budworm with its natural enemies is expected as climate change progresses. In summary, warmer, drier conditions tend to weaken the regulating effects of natural enemies and simultaneously increase reproductivity and larval survival. Thus, the expectation for longer or more frequent outbreaks in warmer, drier climates.

Protracted trends toward warmer climates will allow many successive generations of directed natural selection, particularly for organisms like some insects (e.g., aphids) with many generations per year. (Increased climatic variability may disrupt this process frequently for short periods but seems unlikely to forestall it over the long term). Consequently, genotypes best suited to warmer environments are expected to become increasingly common, resulting in genetically adapted populations. Experimental and observational evidence suggests that such adaptations may produce increases in the rates of phenological development; increases in the number of generations per year; shifts in geographical and also possibly host range; changes in morphology, physiology, and reproductive strategy; and possibly even speciation or extinction.

Other aspects of global change could affect spruce budworm outbreak patterns but these are more speculative. For instance, biodiversity loss manifested as a lack of suitable plant habitat or lack of alternate hosts could have serious consequences for certain natural enemies. Up to a point, this loss may be compensated by other natural enemies so that there is little overall effect on the spruce budworm's outbreak cycle. In central parts of the range, land use changes, manifested as increased wildfire control and harvesting, allow the spruce budworm's host tree species to capture ever increasing proportions of the forest. The resulting increase in feeding and egg-laying sites lends itself toward larger scale, and possibly more intense, outbreaks. In contrast, experiments suggest that elevated atmospheric CO_2 concentrations can impede the chemical communication systems that many insects use for finding mates and food sources. The prevalence and importance of this impedance in the wild is unknown.

Figure 1 summarizes this discussion. climate change has a more pervasive influence throughout the life cycle of the spruce budworm than other components of global change, and will likely benefit spruce budworm populations. biodiversity loss and land use change are also represented as having net positive influences for the spruce budworm. The only negative aspects of global change diagrammed in Figure 1 are associated with elevated atmospheric CO_2 concentrations. The large scale consequences of other changes in atmospheric composition are even less certain.

RESPONSES OF SALMON TO GLOBAL CHANGE

Wild salmon populations, *Oncorhynchus* and *Salmo* species, are declining globally: populations of Atlantic salmon are declining or have been extirpated in two-thirds of their native range, hundreds of Pacific salmon populations have gone extinct during the past century and hundreds more are at risk. The cause of these declines is multifaceted, and the relative contributions of human-induced changes, natural climatic events and other abiotic and biotic factors have not been firmly established. Unquestionably, however, human impact has been substantial.

The spatial scale at which human-induced changes affect wild salmon varies through the course of their life history, with localized impacts predominating in fresh water and global impacts predominating in oceanic environments (Figure 2). In fresh water, habitat degradation, pollution and introductions of exotic species represent the main human-induced impacts. Logging, agricultural, urban and resource extraction activities may all degrade habitat (e.g., sedimentation, channelization, flow conditions, removal of bank vegetation and fragmentation) and water quality (e.g., temperature, dissolved oxygen, nutrients and pollution). The effects of pollution also occur at large scales: acid rain is blamed for losses of Atlantic salmon populations in Europe and North America. Introduction of cultured salmon, exotic fishes and other aquatic organisms generally have localized impacts in fresh water. Escape of aquacultured salmon and stocking of hatchery salmon pose ecological (e.g., resource competition), genetic (e.g., loss of diversity), and disease threats to wild populations. In Norway, such practices have introduced and spread the parasite *Gyrodactulus salaris* which has almost eradicated 40 salmon populations.

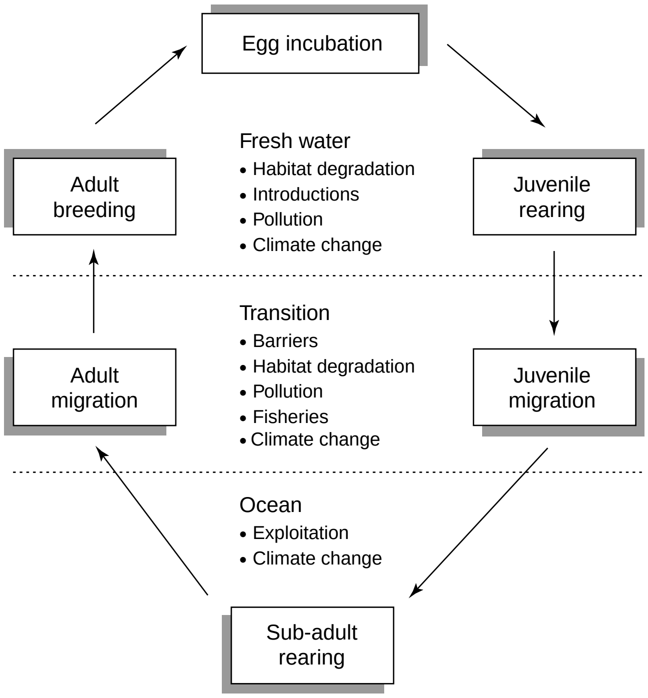

Figure 2 Principal impacts of global change during the life cycle of anadromous salmon, from egg incubation through juvenile freshwater and sub-adult oceanic rearing to adult freshwater breeding. Three critical stages are depicted: (1) fresh water; (2) the transition between fresh and salt water; and (3) ocean

The transition stage is also affected at predominately local scales. The major cause of salmon extirpations is blockage of their upstream migration routes, particularly by hydropower dams. Fortunately, the importance of this is declining. Effective fish passage mechanisms have been developed, inefficient dams removed, and with few hydropower opportunities remaining, dam construction is falling. Habitat degradation and pollution affect the energetic costs, susceptibility to predation, physiological state and ultimately, survival of salmon during migration. Over-fishing can also severely depress target populations and contribute to their risk of extirpation.

Oceanic impacts on wild salmon occur mainly at large scales, reflecting the vastness of this domain. Particularly important are climatic changes (see **Fisheries: Effects of Climate Change on the Life Cycles of Salmon**, Volume 3) and exploitation. It has been predicted that modest rises in sea surface temperatures due to climate change could result in salmon disappearing from large areas because of their narrow thermal limits during winter and early spring. Warmer sea surface temperatures may also interact with currents to alter the location and availability of food for salmon, which current evidence suggests will cause a reduction in salmon body size. Exploitation effects occur both directly (from salmon fisheries [discussed above] and incidental catches during other fisheries), and indirectly (e.g., industrial fisheries competition of salmon with forage fish such as capelin and sand lance).

This analysis shows that most human impacts on Atlantic salmon are intensifying throughout the lifecycle, that they are predominantly negative, and that they are interacting in complex ways. Sustainability of wild salmon thus depends on forecasting and minimizing these impacts. The latter depends on maintaining a diversity of gene pools and population structures to provide evolutionary flexibility for salmon in response to an uncertain future.

RESPONSES OF BLACK SPRUCE TO GLOBAL CHANGE

Trees are amongst the longest-lived organisms on earth; several decades are usually required to reach sexual maturity or full fecundity, and generation times are often 50–200 years. Adaptations and changes in forest tree composition in response to global change will largely reflect the competitive abilities and ecological tolerances of existing ecotypes rather than the rapid evolution of new ecotypes. As the main structural component of forested landscapes, trees are the primary providers of habitat for many terrestrial organisms, and changes in the overstory resulting from global change will have wide-ranging repercussions.

Black spruce, *Picea mariana*, is an abundant, evergreen conifer found throughout the North American boreal forest. It has the most northerly range of any tree species on the continent, extending to the tree line, and is commonly found as far south as the temperate forests of the Great Lakes region. This slow-growing tree reaches heights of 15–25 m and ages exceeding 200 years on productive sites, but assumes a more shrub-like stature on very poor sites or in extreme climates. Over much of its southern and central range, it forms dense stands of considerable standing biomass, either by itself on wetter sites, or in combination with other species on well-drained sites. In northern locations, stands are more open and growth is reduced; at its southern limits, this species is confined to cold, wet, or shallow-soiled sites.

Black spruce seed and pollen cones emerge in the spring, and fertilized seeds mature by fall of the same year. Cones continue to disperse seed for several years after ripening. Seed production occurs regularly in stands over 25 years old, and peaks in stands between 50 and 150 years of age. Seed fall is accelerated for 2–3 years after wildfire. Seeds are commonly dispersed 100–200 m from stand edges, but individual seeds can achieve much greater dispersal distances, particularly during high winds or on crusted snow. Black spruce also reproduces vegetatively from lower living branches, which become partially buried by organic debris. This form of reproduction is common in open-grown stands, particularly in the far north where successful pollination and subsequent seed germination are restricted.

Climate change could have large direct impacts on the range, abundance and vigour of virtually all forest trees, including black spruce. Warmer temperatures should improve seed production and germination at higher latitudes and may allow considerable extension of black spruce beyond the current tree line. In contrast, the forecasted northerly extension of the western Canadian prairies would greatly reduce the southern extent of the species' range in western Canada. The direct effects of changes in precipitation patterns are less predictable. Black spruce is well adapted to drier upland sites as well as wetter lowland sites, both in the colder continental climates of northwestern North America, and in the cool, more humid climates to the east. However, drier conditions combined with warmer temperatures may restrict germination, limit seedling establishment, and increase drought stress in established stands. Increased temperatures and CO_2 levels will improve tree growth, but may put black spruce at a competitive disadvantage on sites which provide suitable habitat for competitors such as white pine (*Pinus strobus*), jack pine (*Pinus banksiana*) and oak (*Quercus*) species which have greater temperature or CO_2 growth responses.

In the southeastern portion of its range, climate change effects on black spruce populations may be manifested largely through alterations in competitive relationships with other species. Longevity, conservative resource requirements and broad ecological tolerances suggest that established black spruce trees and stands may not be greatly affected by the forecasted changes in climate. Increased competition from faster growing and/or more shade tolerant competitors, however, is likely to reduce seedling establishment and sapling vigour.

Climate change influences on the frequency and intensity of rarely occurring, catastrophic events (e.g., wildfire, insect outbreaks, storms, severe frosts) are equally as important to forest trees as the direct effects of incremental changes in climate averages. Like most boreal species, black spruce is adapted to and dependent upon infrequent wildfires, which destroy existing stands but produce dense, vigorous new stands of the same species. Increased fire frequencies (i.e., within every 30–40 years) could reduce black spruce abundance by burning many stands before most trees reach full fecundity. In contrast, substantial reductions in fire frequency could permit the incursion of faster-growing or more shade-tolerant competitors which are less fire-adapted but better resource competitors than black spruce. Feedback between changes in stand composition and fire frequency are also likely. Large increases in broad-leaved species will reduce fuel availability and perhaps fire frequency.

Insect epidemics affect individual tree species directly through herbivory, and indirectly by altering competitive relationships with other plants. Outbreaks of the major insect pest of black spruce, the spruce budworm, reduce stand vigour and destroy current seed production, but cause little long-term damage to black spruce. This reflects the phenological development of feeding larvae, which is synchronized with vegetative bud flush and foliar development in balsam fir and white spruce, the spruce budworm's principal host species. Vegetative bud flush in black spruce usually occurs 10–14 days later. Differential effects of climate change on herbivore-host phenology could either reduce or greatly increase defoliation of black spruce by altering the synchrony of bud flush and budworm larval feeding. Climate-induced changes in the frequency and severity of insect outbreaks on associated species (e.g., forest tent caterpillar on trembling aspen and spruce budworm on balsam fir) could alter the competitive position of black spruce.

Other facets of global change which have widespread implications for forest trees include logging, deforestation and afforestation. Most of the land base currently occupied by black spruce has little agricultural value because of climate and soil limitations, and more land suitable for black spruce is currently reverting from agriculture to forests than *vice versa*. In contrast, logging activities have had large and sustained negative impacts on the representation of black spruce on the landscape. Black spruce is highly valued for pulpwood and saw timber, and has been logged extensively throughout the southern boreal. Typically, on peatland sites, black spruce remains the predominant species in second growth stands, although there may be regeneration delays and reductions in stand densities. Without planting and stand tending, many areas on upland sites revert from black spruce-dominated to mixed-wood forests with black spruce a minor component. The widespread establishment of black spruce plantations has maintained this species on other parts of the landscape, but often at reduced densities and with different stand compositions and structures than are found in stands of wildfire origin.

CONCLUSION

The life cycles of three very different species have provided analytic frameworks for developing a qualitative understanding of how each species is likely to react to global change. Global change will affect some stages of a life cycle more than others, and certain aspects of global change, either individually or interactively, are more important than others at these particularly vulnerable stages. To establish in a new area or persist in its current habitat, a species must be able to complete its life cycle. By identifying the most vulnerable stages, life cycle analyses can provide a focus for management efforts ranging from repelling invading species to protecting endangered ones (see **Integrated Pest Management in an Era of Global Environmental Change**, Volume 4).

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