

Climate warming and disease risks in temperate regions – *Argulus coregoni* and *Diplostomum spathaceum* as case studies

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Abstract

The link between climate changes and disease risks from various pathogens has been increasingly recognized. The effect of climatic factors on host–parasite population dynamics is particularly evident in northern latitudes where the occurrence and transmission of parasites are strongly regulated by seasonality-driven changes in environmental temperatures. Shortened winter periods would increase growth potential of many parasite populations. The ways in which climate warming could affect life history dynamics of the directly transmitted crustacean ectoparasite *Argulus coregoni* and complex life cycle trematode *Diplostomum spathaceum*, which frequently cause problems in northern fish farming, are discussed. Increased problems for fish farming are predicted in terms of increased infection pressure from these parasites in future. This would increase problems associated with infections and increase the use of expensive management protocols with high environmental impact.

Introduction

Climate warming (Houghton *et al.*, 2001) is undoubtedly among the most evident threats facing the environment on the global scale (e.g. Walther *et al.*, 2002; Thomas *et al.*, 2004). In addition to consequences directly affecting the function of ecosystems, climate warming may also have indirect effects, e.g. by changing the incidence of disease threats from parasitic infections (Harvell *et al.*, 1999, 2002). This is particularly evident in northern temperate regions where the occurrence and transmission of parasites are characterized by strong seasonality driven by temperature changes in the ambient environment. For instance, a large proportion of each year is unsuitable for parasite transmission, growth and reproduction, and therefore parasite life cycles are completed within narrow temporal limits. Parasites are well adapted to their environment and may quickly respond to factors influencing their transmission opportunities and growth by displaying adaptive phenotypic plasticity (Thomas *et al.*, 2002; Poulin, 2003; Fenton &

Rands, 2004; Hakalahti *et al.*, 2005). However, rapid environmental changes in relation to evolutionary time may interfere with host–parasite interactions that have evolved under specific environmental conditions. Although this may be detrimental for parasites as well as for their free-living hosts, changes such as elevated ambient temperatures may also be beneficial for parasites if they extend the period of transmission and reproduction or provide grounds for rapid evolution of new life history characteristics.

In the present paper, we focus on two harmful metazoan parasite species found in fish culture, a directly transmitted ectoparasite *Argulus coregoni* and a complex life cycle endoparasite *Diplostomum spathaceum* (Stables & Chappell, 1986; Field & Irwin, 1994; Hakalahti & Valtonen, 2003; Hakalahti *et al.*, 2004c) (figs 1 and 2). *Argulus coregoni* is a parasitic crustacean, which attaches to the fish and feeds on its blood and tissues, causing skin damage and predisposing the fish to various secondary microbial infections (Lester & Roubal, 1995). *Diplostomum spathaceum* is a trematode with a life cycle including passage through birds, snails and fish (fig. 2). Free-living stages (cercariae) are released from snails in high numbers to infect the lens of the fish eye (Karvonen *et al.*, 2004a), where the parasites may cause cataracts

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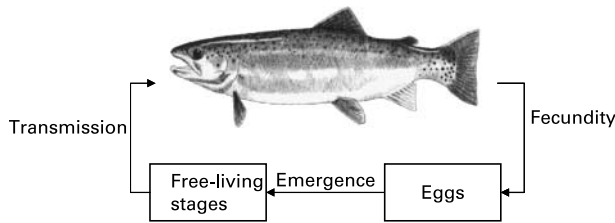


Fig. 1. The life cycle of *Argulus coregoni*. Free-living metanauplii hatch from over-wintered eggs and actively search for a fish host relying on finite energy resources obtained from the egg. Following attachment, *A. coregoni* undergoes several developmental stages before the life cycle is completed.

and blindness (Shariff *et al.*, 1980, Karvonen *et al.*, 2004b). This results in problems at farms through impaired feeding, stunted growth and reduced survival of the fish (Crowden & Broom, 1980; Owen *et al.*, 1993; Buchmann & Uldal, 1994; Seppälä *et al.*, 2004). The transmission of both parasite species to fish is strongly temperature dependent and takes place during the open water period in summer. However, in Finnish conditions the pattern of parasite transmission is different as *A. coregoni* has a strict cohort-type transmission with one annual generation (Hakalahti & Valtonen, 2003) whereas the cercarial release of *D. spathaceum* from snails is continuous and may include overlapping parasite 'generations'. Thus, these species provide us with essentially different frameworks for a comparative life history study. In the following sections, we review the results from long-term studies conducted on the life histories of these parasites and discuss (i) how increasing environmental temperature could affect their short- and long-term life history options and (ii) how this would reflect on the commercial problems caused by the parasites and the preventative protocols designed against them.

Effects of temperature on the population dynamics of *A. coregoni*

Field surveys undertaken in Finland (Hakalahti & Valtonen, 2003) and in Japan (Shimura, 1983) indicate strong seasonality in the infection patterns of *A. coregoni* on fish in terms of recruitment and population abundance. Parasite populations over-winter only as dormant eggs, and their hatching and subsequent recruitment to fish are limited to water temperatures exceeding 10°C (Shimura, 1983; Mikheev *et al.* 2001; Hakalahti & Valtonen, 2003; fig. 3A). In Central Finland, highest population abundance of *A. coregoni* on fish are typically recorded between May and July (Hakalahti & Valtonen, 2003) and from early July onwards, parasites start to detach from fish to lay their eggs and then die (Hakalahti *et al.*, 2004a). Consequently, the number of parasites on fish declines towards the end of the open water period (Hakalahti & Valtonen, 2003; fig. 3A). The egg-laying period of *A. coregoni* is extended up to September (Hakalahti *et al.*, 2004b). This variability in timing of maturation is caused by the preceding recruitment pattern on fish, which is characterized by peak hatching in May followed by a slower hatching rate

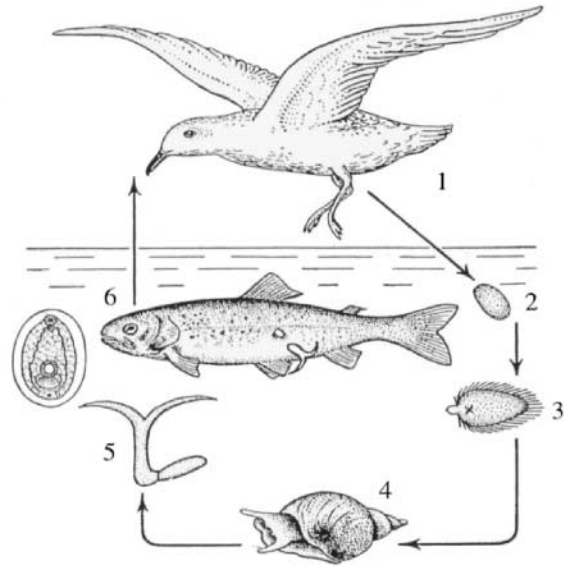


Fig. 2. The life cycle of *Diplostomum spathaceum*. Parasites reproduce sexually in the intestine of fish-eating birds such as gulls (1), and release eggs (2), which then hatch to free-swimming miracidia (3). Miracidia infect freshwater snails (4) and commence asexual reproduction giving rise to thousands of cercariae (5). Cercariae penetrate fish, establish in the eye lens and develop to metacercariae (6). The life cycle is completed after an infected fish is eaten by a bird. (Modified from Dogiel *et al.*, 1961.)

until September (Mikheev *et al.*, 2001; Hakalahti & Valtonen, 2003). Such an extended hatching pattern can be interpreted as an adaptive bet-hedging strategy (see Fenton & Hudson, 2002; Hakalahti *et al.*, 2004a), rather than as emergence of multiple annual parasite generations. Assuming an incubation time of 600 day-degrees determined for eggs of *A. coregoni* (Shimura, 1983), first eggs in early July could not hatch before early August. At that time, the parasite population consists mainly of adult individuals, and parasite numbers on fish are markedly lower than earlier in the summer (Hakalahti & Valtonen, 2003; fig. 3A). Thus, we conclude that the parasite population exhibits a one-generation cycle with the emergence of offspring not taking place until the following spring (Hakalahti & Valtonen, 2003). At higher water temperatures in Japan, however, *A. coregoni* undergoes two generations per year (Shimura, 1983).

In northern temperate regions, average temperatures are expected to increase due to anthropogenic climate change (Houghton *et al.*, 2001). Consequently, the periods of active growth in *A. coregoni* are likely to be further extended in future, and this may affect parasite life history dynamics in two ways. Firstly, since thermal conditions directly affect the incubation time of *Argulus* spp. eggs (Shafir & van As, 1986) and developmental rates of both juveniles and adults (Hakalahti & Valtonen, 2003), higher water temperatures may facilitate more rapid population cycles. Secondly, clear potential for the shift from a one-generation to a two-generation *A. coregoni* population cycle exists in Finland. Calculations based on

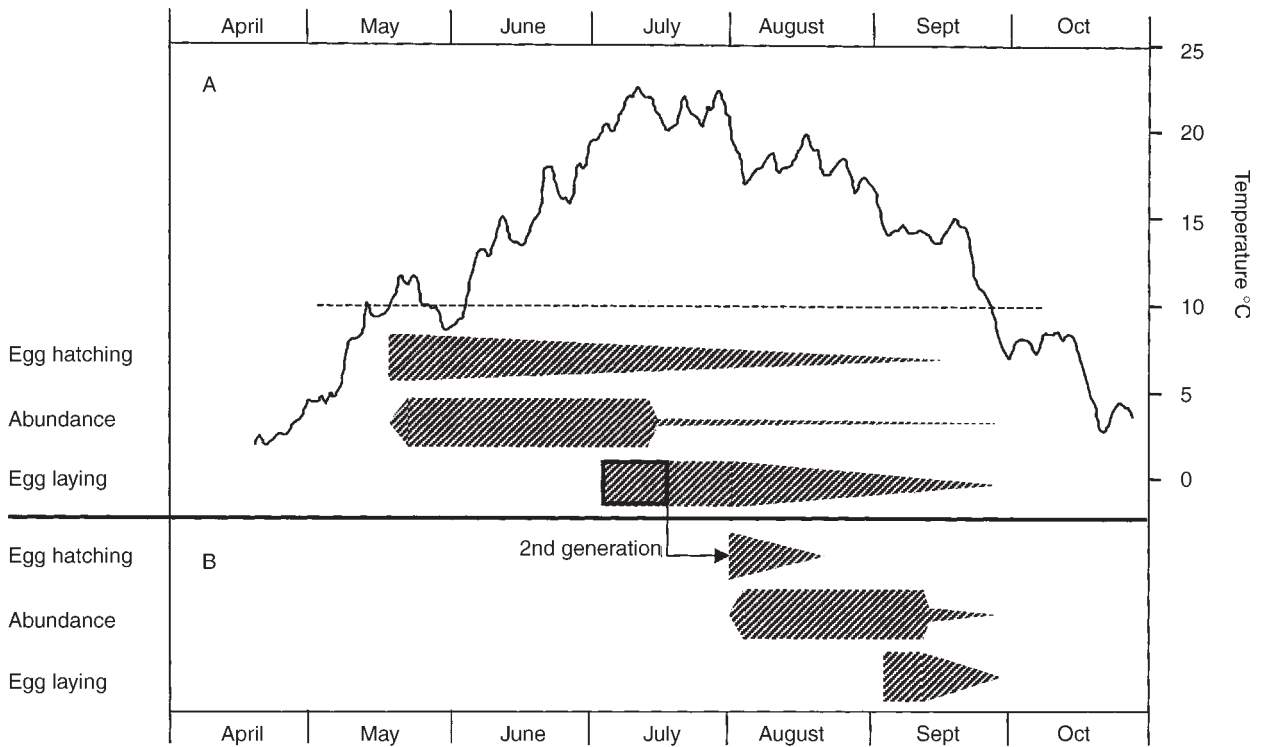


Fig. 3. Annual population cycle of *Argulus coregoni* in a fish farm in Central Finland in 2001. A) observed population cycle and ambient daily water temperatures; B) hypothetical emergence of the second annual parasite generation from eggs laid between 3 and 18 July, which, based on day-degree sums from ambient water temperatures, would have had sufficient time to reproduce in September (see Hakalahti & Valtonen, 2003). Dotted line indicates the critical minimum temperature of 10°C for population growth.

day-degree sums of ambient water temperatures in 2001 show that emergence and maturation of the second generation would have been possible (fig. 3B), although this was not supported by the field data. It must be emphasized that female *A. coregoni* produce two types of eggs depending on ambient environmental conditions: a proportion of eggs laid during the early reproductive season hatch immediately after the obligatory incubation period (about 600 day-degrees), whereas diapausing eggs, which show a delayed hatching pattern, are produced later in the season (Shimura, 1983; Hakalahti *et al.*, 2004a, 2004b; fig. 4). Such a facultative diapause is usually a maternally-controlled trait (Mousseau & Fox, 1998), and is common strategy among organisms living in environments with unpredictable season length (e.g. Mousseau & Roff, 1989; Bradford & Roff, 1993). It allows additional generations to emerge when conditions are favourable, or enter diapause if they are not. Therefore, we suggest that *A. coregoni* has the potential to respond to longer-lasting growth seasons and to shift from a one-generation to a two-generation population cycle. This will result in more rapid population growth and inevitably leads to increased parasite problems at fish farms.

Extended periods of the occurrence of *A. coregoni* during the open-water periods would be harmful for farmed fish. The parasite rarely causes fish mortality when it occurs in low numbers, but its feeding activities

cause skin damage and stress reactions, which make fish prone to a range of secondary infections (Lester & Roubal, 1995). For instance, we have recorded significantly higher and faster mortality rates among fish with concomitant *A. coregoni* and *Flavobacterium columnare* infections compared to single infections (M. Bandilla, E.T. Valtonen, L.-R. Suomalainen & T. Hakalahti, unpublished data). Management of *A. coregoni* populations in Finnish farms is generally conducted by destroying eggs in ponds and treating fish with an in-feed medication (emamectin benzoate) in early spring, before the parasite recruitment to fish has started (see Hakalahti *et al.*, 2004c). The medication prevents parasite settlement and has an extended duration of efficacy to up to 9 weeks (Hakalahti *et al.*, 2004c). However, emergence of the second parasite generation would create late outbreaks of *A. coregoni* in autumn when the efficacy of the medication has already ceased (fig. 3). These late outbreaks would make it necessary to administer medication twice a year, which inevitably leads to increased management costs for fish farmers and more harmful management practice in terms of environmental impact.

Effects of temperature on transmission of *D. spathaceum*

Transmission and development of *D. spathaceum* is controlled by surrounding environmental temperature at

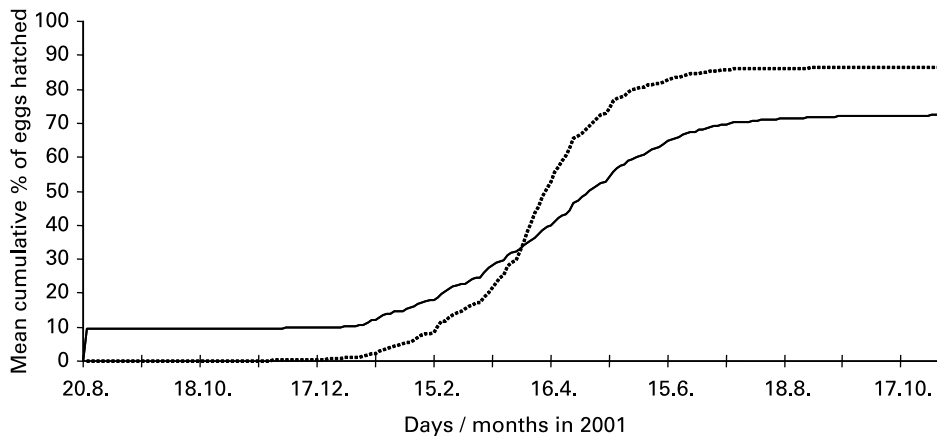


Fig. 4. Mean cumulative hatching of *Argulus coregoni* egg batches laid between 4 and 22 July (continuous line) and between 3 and 19 August (dotted line) in 2001. During the breeding, parasites were maintained under ambient photoperiodicity and water temperature conditions; egg hatching was monitored at constant room temperature; the proportion of eggs laid in July hatched in August immediately after the required incubation period potentially allowing emergence of the second annual generation; all eggs laid in August were diapausing eggs, which would not have hatched in nature until the following spring. (Data obtained from Hakalahti *et al.*, 2004a.)

all stages of the life cycle except for sexual reproduction in the endothermic avian definitive host. Development of the parasite eggs in water, infection of the snail first intermediate hosts and the cercarial release from the snails are all continuous processes, but are restricted to summer water temperatures above 10°C (Waadu & Chappell, 1991; Chappell *et al.*, 1994; Karvonen *et al.*, 2004c). In Central Finland, a large proportion of cercarial output and transmission to fish by *D. spathaceum* takes place during the period between June and August followed by a marked decrease from September onwards (Karvonen *et al.*, 2004c). Metacercarial development in fish is also temperature dependent and rapid cooling of the water in autumn inhibits the development of metacercariae established in late summer (A. Karvonen, personal observation).

Climatic change which extends the period of summer water temperatures may change this pattern in two ways. Firstly, it may directly affect the parasite by prolonging the period suitable for development in snails, cercarial release, transmission to fish and metacercarial development (fig. 5). Secondly, temperature also controls the population dynamics of the hosts, especially snails, which reproduce continuously when conditions are favourable for egg laying and development. Increased water temperatures in late summer and autumn may affect snail life history dynamics in such a way that new generations are produced. In fact, intensive reproduction of snails and subsequent recruitment of large numbers of young individuals has been observed at Finnish fish farms in August–September when water temperature has remained high towards autumn (A. Karvonen *et al.*, unpublished data). This could affect parasite dynamics indirectly by providing new hosts which would otherwise be absent and unavailable for infection. Thus, parasite dynamics are closely connected to the host population structure and may be enhanced significantly if both direct and indirect effects occur in concert.

Extended patterns of *D. spathaceum* transmission can be problematic for fish farmers in several ways. Essentially, the parasite can induce cataracts in fish (Shariff *et al.*, 1980; Karvonen *et al.*, 2004b), which may lead to blindness and a range of secondary effects (e.g. Crowden & Broom, 1980; Owen *et al.*, 1993; Seppälä *et al.*, 2004, 2005a). Since cataract formation is dependent on the infection intensity (Karvonen *et al.*, 2004b), continued cercarial production in late summer and autumn could be detrimental by elevating parasite numbers in fish. Furthermore, cataract formation is induced mainly by fully-developed metacercariae (Seppälä *et al.*, 2005b) and higher temperatures in autumn could allow continued metacercarial development and cataract formation. Indications of these effects have already been observed at some Finnish fish farms, where losses of heavily infected fish have occurred in late autumn (A. Karvonen *et al.*, unpublished data; fig. 5). Prevention of parasite occurrence in Finnish fish farms is generally effected by disinfecting the ponds in spring to eradicate over-wintered adult snails. These procedures can be relatively effective, but also laborious and expensive, and are therefore usually conducted once a year. However, possible emergence of new snail generations and enhanced parasite development within the snails may produce late outbreaks of *D. spathaceum* in autumn and could make the eradication of the snails in spring inadequate for parasite prevention (fig. 5). Thus, prolonged parasite transmission following an increase in temperature would make it necessary to perform preventative actions twice a year, which unavoidably result not only in high financial costs to farmers but also increase environmental pollution.

Conclusions

Transmission and reproduction of parasites in northern latitudes is controlled strongly by temperature. The

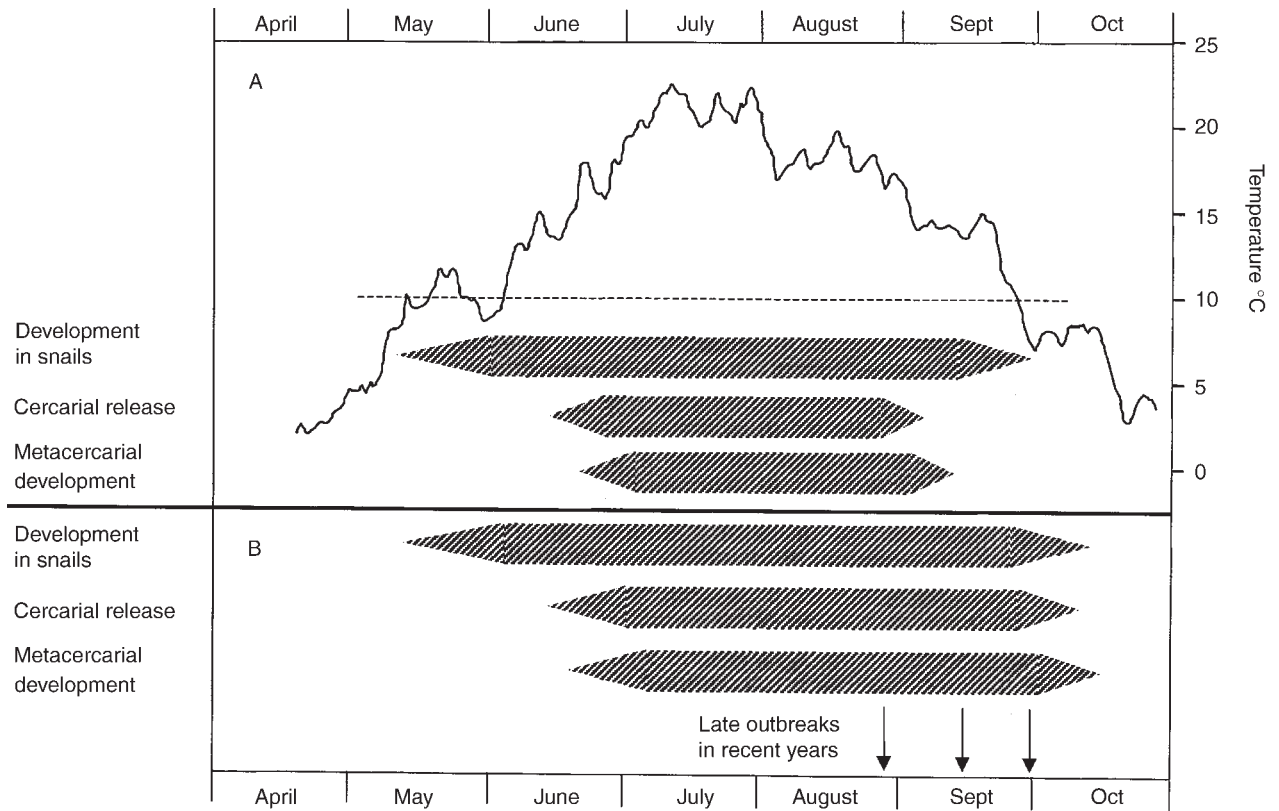


Fig. 5. Timing of development of *Diplostomum spathaceum* infections in snails and fish in Central Finland. A) normal situation; B) hypothetical situation where parasite development and transmission are continued because of elevated water temperatures. Arrows indicate *D. spathaceum* outbreaks in fish farms in Central Finland in 2001, 2002 and 2004; dotted line indicates water temperature 10°C.

present results on the life histories of two disease-causing parasites in fish farming, the crustacean *A. coregoni* and the digenean *D. spathaceum*, suggest that climate warming may impose a serious risk for fish farming through increased infection pressure from these parasites. *Argulus coregoni* typically undergoes one generation per year in Finland, but the clear potential for the shift to a two-generation cycle exists and this may be triggered by increasing temperature. Prolonged summer temperatures may also continue the cercarial output from *D. spathaceum* and extend the period of high-level transmission. Proposed changes in the transmission of *A. coregoni* and *D. spathaceum* would probably lead to disease outbreaks at fish farms and increase problems associated with infections and the use of expensive and harmful preventative protocols.

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