Climate change effects on trematodiases, with emphasis on zoonotic fascioliasis and schistosomiasis

Santiago Mas-Coma *, Maria Adela Valero, Maria Dolores Bargues

Departamento de Parasitologia, Facultad de Farmacia, Universidad de Valencia, Av. Vicent Andrés Estellés s/n, 46100 Burjassot, Valencia, Spain

ARTICLE INFO	ABSTRACT
	The capacity of climatic conditions to modulate the extent and intensity of parasitism is well known since long ago. Concerning helminths, among the numerous environmental modifications giving rise to changes in infections, climate variables appear as those showing a greater influence, so that climate change may be expected to have an important impact on the diseases they cause. However, the confirmation of the impact of climate change on helminthiases has been reached very recently. Only shortly before, helminthiases were still noted as infectious diseases scarcely affected by climate change, when compared to diseases caused by microorganisms in general (viruses, bacteriae, protozoans). The aim of the present paper is to review the impact of climate change on helminthiases transmitted by snails, invertebrates which are pronouncedly affected by meteorological factors, by focusing on trematodiases. First, the knowledge on the effects of climate change on trematodiases in general is reviewed, including aspects such as influence of temperature on cercarial output, cercarial production variability in trematode species, influences of magnitude of cercarial production and snail host size, cercarial quality, duration of cercarial production increase and host mortality, influence of latitude, and global-warming-induced impact of trematodes. Secondly, important zoonotic diseases such as fascioliasis, schistosomiasis and cercarial dermatitis are analysed from the point of view of their relationships with meteorological factors. Emphasis is given to data which indicate that climate change influences the characteristics of these trematodiases in concrete areas where these diseases are emerging in recent years. The present review shows that trematodes, similarly as other helminths presenting larval stages living freely in the environment and/or larval stages parasitic in invertebrates easily affected by climate change as arthropods and molluscs as intermediate hosts, may be largely more susceptible to climate change impact than those helminths in whose life cycle such phases are absent or reduced to a minimum. Although helminths also appear to be affected by climate change, their main difference with microparasites lies on the usually longer life cycles of helminths, with longer generation times, slower population growth rates and longer time period needed for the response in the definitive host to become evident. Consequently, after a pronounced climate change in a local area, modifications in helminth populations need more time to be obvious or detectable than modifications in microparasite populations. Similarly, the relation of changes in a helminthiasis with climatic factor changes, as extreme events elapsed relatively long time ago, may be overlooked if not concretely searched for. All indicates that this phenomenon has been the reason for previous analyses to conclude that helminthiases do not constitute priority targets in climate change impact studies.

* Corresponding author. Tel.: +34 96 3544905; fax: +34 96 3544769.
  E-mail address: S.Mas-Coma@uv.es (S. Mas-Coma).

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1. Introduction

Climate change and global warming are now accepted facts. Changes in air and sea surface temperatures, as well as changes in precipitation, sea level, and ocean salinity and circulation patterns, are predicted for the future. Natural ecosystems will be impacted in one way or another by these environmental changes. Climatic factors affect several ecological processes at different levels, from the performance of individual organisms, to the dynamics of populations and community interactions, up to the distribution of species, because of the link between changes in ecosystem properties and functions with large-scale climate fluctuations (Poulin and Mouritsen, 2006). The ecological consequences of climate change in terrestrial and marine ecosystems are expected to be determined by complex cascading effects arising from modified trophic interactions and competitive relationships. The synergistic effect of climate change and parasitism on host population dynamics and community structure has recently been emphasized (Mouritsen et al., 2005).

The capacity of climatic conditions to modulate the extent and intensity of parasitism is well known since long ago. The development and transmission rates of parasitic organisms are particularly sensitive to weather conditions. The current climate change (global warming) will affect the distribution and survival rate of parasite vectors and intermediate hosts and also directly influence the reproduction and maturation rate of parasites carried by them

(McCarthy et al., 2001). As early as 1990, the Intergovernmental Panel on Climate Change (IPCC) had warned that the climate change could affect the prevalence of vector-borne parasitic diseases (Houghton et al., 1990).

The potential importance of parasites and pathogens as mediators of host population dynamics under changing climatic conditions in general and global warming in particular has been recently reviewed (Harvell et al., 2002; Mouritsen and Poulin, 2002a). Any influence of climate on parasitism is potentially important for natural communities and ecosystems. Many recent studies have emphasized the causal relationship between climate change and parasitic diseases, whether emerging (new infections) or re-emerging (diseases rapidly increasing in either local prevalence and intensities or expanding their geographical distribution) (Harvell et al., 1999, 2002; Patz et al., 2000; Marcogliese, 2001; Lafferty et al., 2004). In recent years, the problem of emerging diseases has been a significant concern (Molyneux, 2007). There is also evidence that climate can act to synchronize cycles of host population abundance by directly affecting the survival and transmission of parasite infective stages (Cattadori et al., 2005). Thus, the many direct and indirect effects of temperature and other climatic variables on parasite transmission are bound to have community-wide impacts. For the interest of both human and domestic animal health, as well as of the preservation of natural communities and ecosystems, it becomes crucial to understand how parasites may respond to the climatic changes expected in next decades, according to results obtained with forecasting climatic models.

Unfortunately, climate change overlaps other anthropogenic and environmental modifications (included in the broad term of 'global change') which are able to give rise to outbreaks of parasitic diseases by their own, so that establishing the causality of disease emergence by climate change is usually not an easy task. There are several complete analyses of global change factors which have been identified as primary drivers of these changes (Bradley, 1993; Molyneux, 1997, 2003; Childs et al., 1998; Gubler, 1998; Fayer, 2000; Gajadhar and Allen, 2004; Patz et al., 2000, 2004; Chomel et al., 2007). Moreover, predicting how climate change may impact on any given parasites or their hosts is proving difficult, because of the many direct and indirect effects of temperature and other climatic variables on parasite transmission (Poulin, 2006).

2. Expected environmental changes and their effects on disease transmission

2.1. Changes in key climate parameters

It shall be noted that there is no perfect model of the climate system. This means that all predictions are inherently uncertain, with the sources and importance of that uncertainty depending on the relation between weather (what we get) and climate (what we expect). Anyway, predictions for the next few decades are considered to be reasonably robust, which is not the case for later time periods. All in all, at present meaningful interpretation of regional features can only be made at spatial scales that are considerably larger than those required for sound estimates of future climate change effects on human and animal health. This gap between the spatial resolution of climate model output and the more local spatial scale appropriate for health assessments remains a major problem. The microclimate environment of a host or disease agent may not be identical to the overall climate of the area. Moreover, the vulnerability to climatic change is highly variable in the different ecozones of the world, due to the differential capacity to adapt and respond. So, current climate change predictions should be considered indicative rather than accurate (Stone, 2008). Additionally, it shall be taken into account that the nature of the climate system is chaotic, which means that a slight difference can alter the future climate for many decades (Delecluse, 2008).

The Fourth Assessment Report of the IPCC published at the end of 2007 summarizes the results of thousands of research projects around the world. According to this IPCC Report, temperature and precipitation will modify present regional climates. The observations show a clear increase in the temperature of the Earth's surface and the oceans. The global air temperature from the preindustrial era (1850–1899) to the present time has increased by 0.76 °C and the growth rate has progressively accelerated: the linear rate in the last 50 years is double the centennial rate, and 11 of the last 12 years rank among the warmest years since 1850. Among predictions for the 2020s, warming is not guaranteed at any one location, although in all locations the odds are high that warming will occur. The regional distribution of this warming shows the greatest amount of warming to be expected over land and a moderate but significant warming signal in the Southern Hemisphere (Stone, 2008). The higher warming at high latitudes is expected to be strongest during the winter and early spring seasons. One direct consequence of this warming is the reduction of areas covered by snow and the retreat of the major glaciers of the world in both high and low latitudes. Satellite observations show a marked decrease of the snow covered area in the Northern Hemisphere. The sea ice is also observed to be rapidly melting in the summer season. The year 2007 showed a record decrease in the sea ice extent (Delecluse, 2008).

In terms of precipitation, maps of projected changes only really indicate that the largest potential changes and the highest uncertainties coincide with areas with low base precipitation amounts, particularly deserts and polar regions. There is a trend of increased precipitation in already wet regions and a trend of reduced precipitation in already dry regions (Delecluse, 2008). At the regional scale, projected changes may depend on the season (Stone, 2008).

Additionally, this evolution in climate change will be marked by extreme events, such as storms, heat waves, flash floods and droughts (Delecluse, 2008). Changes in the frequency or intensity of extreme weather events may not directly follow changes in the average. Changes in the frequency of extreme weather events may change for more physical reasons too. The probability of an extremely hot day will have increased by more than a factor of 2, even with just a half standard deviation shift in the average temperature. The converse would of course follow for extremely cold days (Stone, 2008). There may be no obvious effect on the average temperature if rainfall decreases over a given area. On the other hand, heat waves may become much more common, because of a lack of moisture to cool the ground through evaporation during more frequent dry periods. As for rainfall, projected changes in the frequency of extreme hourly and daily events are in fact expected to be unrelated to changes in the average rainfall (Allen and Ingram, 2002). The average rainfall amount depends mostly on the vertical temperature gradient of the atmosphere, in other words on how quickly the top of the atmosphere can radiate energy into space, which will change only slightly with increased carbon dioxide concentrations. Moreover, short extreme rainfall events depend on how much water the air can hold, which increases exponentially with temperature. So, in a future warmer world, short extreme rainfall events should become much stronger and more frequent, possibly in areas that become drier on average (Stone, 2008).

2.2. Effects of climate changes on infectious diseases

Climate restricts the range of infectious diseases, whereas weather affects the timing and intensity of outbreaks (Epstein, 2004). So, changes in climate factors may affect the distribution or ecological range of infectious diseases, whereas the frequency and magnitude of disease

outbreaks change with weather extremes such as flooding and droughts. Evidence-based biological effects of climate change on living organisms, including pathogens and their vectors, comprise (Hughes, 2000): (i) effects on physiology, metabolism or development rate; (ii) effects on distribution; (iii) effects on the timing of life cycle or life history events; and (iv) adaptation, particularly of the so-called r-strategist organisms. According to theory on ecological strategies, r strategists are species with short generation times and rapid population growth rates and consequently they are the most responsive to climate change (for a review on the r and K selection concepts, r and K parameters and theoretical model, r/K dichotomy and continuum, and applications of the r/K model to parasitism, see Mas-Coma et al., 1987b). This is in the background of microparasites, including viruses, bacteriae and protozoans, which have been the pathogens more related to infectious disease emergence (Taylor et al., 2001).

Concerning effects on population dynamics, life cycle and disease transmission, climate factors can have a direct impact on infectious diseases that have a development stage in the environment and/or in an invertebrate intermediate host or vector (De La Rocque et al., 2008; Mas-Coma et al., 2008). Thus, most infectious agents do not replicate below a certain temperature threshold, and their growth rate is strongly modulated at temperatures above this level. Within an invertebrate vector, pathogen replication rate and dynamics may be affected by the invertebrate body temperature and, as a result, the infection process in the different organs of the invertebrate and the duration of the cycle will also be affected (Reiter, 2001). Temperature increase is expected to bring a relaxation of the restricting effects of low temperatures on vector survival, dispersal and disease transmission in colder climates. A priori, this would make temperate environments more receptive to more tropical, mainly vector-borne, diseases. The effect may be more pronounced in areas where the abiotic conditions are near to the threshold prohibiting the disease development cycle, i.e., often around 14–18 °C at the lower end of the temperature scale and 35–40 °C for the maximum limit (Githeko et al., 2000).

Where the development period of a pathogen would exceed the life span of the invertebrate, its vector role becomes impossible and transmission does not occur. Moreover, vector competence, including capacity to attract infection, enable pathogen multiplication and ensure subsequent excretion, may be enhanced by higher temperatures (Purse et al., 2008). Temperature directly impacts on the ecology, life cycle, behaviour and survival of invertebrate vectors (Rodhain, 2000), and therefore on vector population dynamics and disease transmission (Rogers, 1988). Higher temperatures increase the invertebrate metabolic rate, egg production amount, and feeding frequency, reducing the duration of the development periods and impacting on the number of generations per year and population abundance (De La Rocque et al., 2008). Disease transmission is modulated by the survival, reproduction rates and daily activity of the vector, as well as by the pathogen development rate inside the vector. To quantify how these parameters increase or reduce pathogen transmission, a quantitative modelling approach based on the basic reproductive number (R_0) may be applied (Rogers and Randolph, 2006). R_0 defines the number of new cases of disease that arise from a single case and, except for the host recovery rate, all components in the R_0 equation appear to be sensitive to abiotic factors, mainly temperature. With two variables changing at an exponential scale, even a small change in temperature may cause significant changes in disease incidence, seasonal patterns and geographical distribution (De La Rocque et al., 2008).

In relation to effects on distribution and ecological range, climate may be a good pathogen distribution predictor at the continental scale, whereas other environmental factors are likely to be more important at a local scale (Hendrickx et al., 2001). The geographic distribution of diseases can be determined by isotherms or isohyets. Climate change alters the latitudinal and/or altitudinal distribution of both vector and disease, although it shall be considered that an expanded vector range does not necessarily lead to a wider disease transmission. It is the complex interplay of various factors that determines the overall effect of climate on the incidence and distribution of the disease and its causative agent and vector (De La Rocque et al., 2008). For instance, changes in rainfall in (sub)tropical zones may render habitats more, or less, suitable for vectors. Moreover, the mosaic of local microclimates is also crucial for the distributions of vector and reservoir, similarly as for the potential impact of climatic parameter changes. This particularly concerns diseases transmitted by water-borne vectors as freshwater snails which present patchy distributions among the endemic areas (Doumenge et al., 1987; Mas-Coma et al., 1999). The microgeographical fragmentation of such diseases may be locally modified by climate change, several transmission foci disappearing, moving or altering their transmission efficiency and new transmission foci appearing. Changes in precipitation and evapotranspiration rates may give rise to more standing water collections representing new habitats for vector hosts as mosquitoes and snails, while desiccation may reduce vector populations.

Climate change may also be in the background of an ecological invasion, giving rise to disease agents or pathogen-vector/host complexes emerging in a newly colonised area. Steps may include from an unusual flare-up of a disease, to outbreak recurrence, range expansion, or invasion into novel territories and ecosystems, concomitantly with vector or host range shifts. Progressive invasion stages are host niche encroachment, entry, initial pathogen establishment, colonisations, secondary spread and, finally, sustained occupancy (Sakai et al., 2001). The introduction of a new pathogen or vector into areas with more favourable climatic conditions can have a devastating effect on the affected host populations and, where the pathogen is able to establish, may also produce durable colonisation of new ecosystems and new disease transmission modes and patterns.

When analysing the effects on timing of life cycle events, seasonality appears as the key climate component. Summer temperatures are, in many temperate regions, as high as much of the tropics, so that the crucial

difference is represented by the cold winter. Thus, when tropical vector-borne pathogen complexes become introduced during the right season, in most cases the disease is eliminated when the winter arrives (Reiter, 2001). An increase in winter temperatures, especially nighttime temperature, with a reduction in the number of frost days and an earlier spring, would change such a scenario. Profound changes in temperature are predicted to occur precisely during the springs and end of summers, according to the IPCC Report. So, the number of parasites or vector generations per year will increase. Moreover, changes in seasonal rainfall profiles may also have a clear impact. An increased inter-annual variability and more frequent alterations between drought and flooding may enhance various disease epidemics, and relatively discrete changes in the distribution of rains may also have a huge impact on the dynamic of diseases (De La Rocque et al., 2008). Moreover, volatile weather and heat waves can disrupt long-term established ecological equilibria between species, including pathogens, vectors and hosts.

3. Climate change and helminthiases

Among the different infectious diseases affecting man, domestic animals and sylvatic animals, helminthiases have a tremendous importance because of their large impact on human health whether directly in helminth species specific of humans or indirectly in helminth species proper of animals but able to infect humans (zoonoses). They also have veterinary interest because of production losses in livestock and diseases of pets, and because of the capacity of many helminth species to regulate the abundance of free living animal populations (Mas-Coma et al., 1987a; Scott, 1987; Hudson et al., 1998; Albon et al., 2002) and communities (Minchella and Scott, 1991; Mouritsen and Poulin, 2002b) and hence affect the functioning of ecosystems.

These metazoan parasites present very different transmission patterns, ecological requirements and spreading strategies according to the different helminth groups (Mas-Coma et al., 2008). Their dependence on abiotic and biotic factors is related to the host specificity they show at the different levels of their life cycles, to the viability range characteristics of their free living stages, and also to the interactions of the environmental conditions with their host populations, in both terrestrial (including freshwater) and marine environments. Accordingly, there are helminth species which show a marked and wide dependence from external environmental characteristics, whereas the environmental interactions with others appear to be very scarce and almost negligible. The differences in environmental dependence are evident when comparing helminths presenting life cycles with only one host (monoxeny), with two or more hosts involved in the transmission (heteroxeny), with or without an invertebrate (insects, mites, snails) as intermediate host or vector, with or without free living stages, and with or without reservoir host species (less specific helminths able to infect different domestic and/or sylvatic animal species and humans) (Mas-Coma et al., 2008).

The literature on the interactions of helminths with abiotic and biotic factors is very broad, including both experimental and field studies. In helminthology, the traditional use of experimental models has pronouncedly helped in understanding helminth ecology, epidemiology and transmission in the nature. Among the numerous environmental modifications giving rise to changes in helminth infections, climate variables appear as those showing a greater influence (Ollerenshaw and Smith, 1969). Thus, climate change may be expected to have an important impact on helminthiases. However, a very few years ago, helminthiases were noted as infectious diseases scarcely affected by climate change, when compared to diseases caused by microorganisms in general (viruses, bacteriae, rickettsiae, protozoans). A quantitative analysis of the risk of infectious disease emergence allied to the nature of the organisms, their mode of transmission and source, showed that viruses, bacteriae and protozoans are more likely to emerge than macroparasites (e.g., helminths), that around 75% of emergent organisms are from zoonotic sources, and that emergences are independent of the mode of transmission (Taylor et al., 2001).

The confirmation about the impact of climate change on helminthiases has been reached only very recently (Mas-Coma et al., 2008). The aim of the present paper is to review climate change impact on helminthiases transmitted by snails, invertebrates which are pronouncedly affected by meteorological factors, by focusing on trematodiases.

4. Effects of climate change on trematodiases

4.1. Influence of temperature on cercarial output

Cercarial production may enhance at higher temperatures as a simple consequence of increased host metabolic activity and the greater energy available to the parasite. The rate of physiological processes increases markedly with increasing temperatures in the case of ectothermic animals, such as snails. A simple formula to obtain the Q_{10} value, which measures the change in physiological rates per 10 °C increase (Schmidt-Nielsen, 1997), proved to be useful to analyse the influence of temperature by computing the difference of cercarial output rates at two different temperatures (a Q_{10} value of 1 indicates no change in cercarial output rate, a value lower than 1 indicates a reduction in output rate, a value of 2 indicates a 2-fold increase, etc.) (Poulin, 2006). For most physiological processes which rely on enzymatic reactions, Q_{10} values range between 2 and 3, implying a doubling or tripling of physiological rates per 10 °C increase in temperature. However, Q_{10} values are not constant for different parts of the temperature range. In the vicinity of 20 °C, Q_{10} values are normally closer to 2 than 3 in aquatic invertebrates. This typical range of Q_{10} values provides a rough null hypothesis for investigations of temperature-dependent cercarial production by trematodes in snail hosts (Poulin, 2006).

In flukes, temperature has a direct and pronounced effect on a crucial step of their life cycles, such as the production of cercariae in the first (or unique) intermediate molluscan host in both aquatic life cycles (Kendall

and McCullough, 1951; Dinnik and Dinnik, 1964; Boray, 1969; Ollerenshaw, 1971; Nice and Wilson, 1974; Tang et al., 1979; Rim, 1982; Shostack and Esch, 1990; Lo and Lee, 1996; Umadevi and Madhavi, 1997; Mouritsen, 2002) and terrestrial life cycles (Krull and Mapes, 1952; Mas-Coma et al., 1987c). Cercarial output by snails is a key component of the trematode's transmission success (Erasmus, 1972; Galaktionov and Dovrovolskij, 2003). An analysis of experimental data available about temperature's influence on cercarial emergence from their snail hosts indicated that Q_{10} values reported for temperatures around 20 °C are markedly higher than those for physiological processes at the same temperature. This suggests that cercarial output is not simply directly related to host metabolism, and that other factors act in synergy with it to determine how many cercariae are produced per time unit (Poulin, 2006). Moreover, Q_{10} values for cercarial production in the 25–30 °C range were computed because they are not constant throughout the temperature range, and showed a decrease from 20 to 25–30 °C.

Changes in cercarial output mediated by temperature show to vary widely among fluke species, from small reductions to 2000-fold increases in response to a 10 °C rise in temperature, with a geometric mean suggesting an almost 8-fold increase. The observed temperature-mediated increases in cercarial output are much more substantial than those expected from basic physiological processes, for which 2–3-fold increases are normally seen (Poulin, 2006).

4.2. Cercarial production variability in trematodes

The cercarial production process shows different biological characteristics depending on trematode species. Constraints on cercarial output are not the same accross all species. There are digeneean species in which a single miracidium produces a finite number of cercariae per snail (total output genetically predermined by its number of totipotent cells), whereas in other species it gives rise to a virtually infinite succession of cercariae marked by energy availability (Erasmus, 1972; Galaktionov and Dovrovolskij, 2003). Constraints on the total number of cercariae generated from a single miracidium might affect how long increased cercarial output rates can be maintained. In species with finite total output, elevated cercarial emergence at high temperature will last only until all totipotent cells are exhausted. In trematodes with no predermined limit to cercarial numbers, the increased rate of cercarial emergence can be sustained as long as the snail provides sufficient resources.

Development patterns of the cercariogenous larval stages appear crucial in the production of cercariae. In *Fasciola*, more or less long, finite cercarial production appears related to the number of generations of cercariogenous rediae and independent of the different lymnaeid vector species involved (Dinnik and Dinnik, 1956, 1964; Rondelaud and Barthe, 1987; Rondelaud, 1994; Rondelaud et al., 2004). In schistosomes, the infinite cercarial production capacity is related to replication processes of different generations of sporocysts which appear to be bipotential, first cercariogenous and finally sporocysto-genous to give rise to the following bipotential sporocyst generation (Jourdane and Theron, 1987).

In some digeneans, although cercarial production is inhibited below a certain temperature, the production of rediae or sporocysts continues and the generative stages accumulate inside the snail (Galaktionov and Dovrovolskij, 2003). Infected snails may be stored at such low temperatures prior to their use in cercarial release experiments. When they are exposed to temperatures of 20 °C or higher, their parasites switch from redial to cercarial production and the large accumulated redial population causes a disproportionate emergence of cercariae, not as a direct effect of temperature on rate of production but as a clearance of the large population of cercarial progenitors. This could, at least in part, account for the very high Q_{10} values in some species (Poulin, 2006).

4.3. Influences of magnitude of cercarial production, cercarial size and snail host size

Constraints on maximal cercarial output vary among trematode species and families (Galaktionov and Dovrovolskij, 2003), determining how cercarial output responds to temperature. However, it might be expected that, in similar snail hosts, a digenean producing 100 cercariae per day at a given temperature would have more host resources available to expand its production than one that already produces 5000 cercariae of similar size daily at the same temperature. The magnitude of cercarial production may thus interact with temperature changes to determine how production rates will respond. Moreover, cercarial size is another component to be also taken into consideration besides the quantity of cercariae produced, although no obvious trade-off between numbers and size of cercariae appears. However, despite the wide variation in the magnitude of cercarial output at 20 °C, this variable does not appear to covary with Q_{10} in cercarial production among trematode species (Poulin, 2006).

Similarly, snail host size must also be taken into account. If one trematode uses a snail species that is twice as large as that used by an other related trematode which produces the same number of cercariae per day at a given temperature, the former has access to more host resources to increase its production of cercariae than the latter. Cercarial output with increasing host shell length is a phenomenon already documented in Schistosomatidae (Loker, 1983), and suggests that resource limitation may constrain cercarial output, and that trematodes exploiting larger hosts have acccess to more resources. In schistosomes, cercarial size also increases with increasing host shell length (Loker, 1983). However, the study showed that snail host has little impact on the potential of a trematode to increase its cercarial production, since different trematode species using the same snail species can have widely different Q_{10} values (Poulin, 2006).

Across both species values and phylogenetically independent contrasts, neither the initial cercarial output magnitude nor the snail shell size correlated with the relative increase in cercarial production mediated by rising temperature (Poulin, 2006).

4.4. Cercarial quality

An increase in the quantity being produced may not lead to increased per capita transmission success if the cercariae are of lower survivorship and infectivity. Although with exceptions (e.g., Lo and Lee, 1996), cercarial survival generally decreases with increasing temperature (e.g., Evans, 1985; McCarthy, 1999; Mouritsen, 2002), as a direct result of the increased activity of cercariae at higher temperatures accelerating the depletion of their finite energy reserves (Pechenik and Fried, 1995; McCarthy, 1999). In its turn, cercarial infectivity generally increases with temperature before dropping off at high temperatures (e.g., Evans, 1985; McCarthy, 1999). However, cercarial transmission efficiency is not negatively affected by increasing temperatures, when survival and infectivity of cercariae are combined (Evans, 1985; McCarthy, 1999). Low cercarial infectivity at lower temperatures is offset by low mortality, whereas improved infectivity at higher temperatures is counter-balanced by high mortality. In that way, transmission efficiency remains roughly constant within the 15–30 °C range (Evans, 1985; McCarthy, 1999). Under these conditions, a temperature-mediated increase in cercarial output would lead to a greater infection levels in the next hosts of trematodes, even if cercarial survival is lower at higher temperatures (Poulin, 2006).

4.5. Duration of cercarial production increase and host mortality

Although a rise in temperature will trigger an increase in cercarial output, this may be short-lived. It is quite likely, for instance, that at higher temperatures, and with cercarial production greatly enhanced, the snail host would not live as long as it would normally. A short-lived peak in cercarial emergence, however, may be sufficient to cause extensive mortality in the next host of the trematode (Poulin, 2006). For example, consecutive days of unseasonably hot weather resulted in increased cercarial production by microphallid trematodes on intertidal mudflats in Denmark; the consequence was the mass mortality and local extinction of the parasites' second intermediate hosts (Jensen and Mouritsen, 1992). Laboratory studies have shown that the exposure of second intermediate hosts to many cercariae simultaneously induces higher mortalities than the gradual exposure to low numbers typical of field conditions (e.g., Fredensborg et al., 2004). Consequently, there is no need for the increased cercarial output to be maintained over many weeks or months, for the temperature-mediated effects of parasites to have a substantial ecological impact (Poulin, 2006).

4.6. Influence of latitude

The latitude from which parasites and snails originated proved to be the only variable that appeared to influence Q_{10} values (Poulin, 2006). At high latitudes, cercarial production will only be allowed by summer temperatures exceeding 20 °C, and stopped by the too-low winter temperatures. Consequently, at environmental temperature around 20 °C, high-latitude trematodes would respond differently to a slight rise in temperature than trematodes from the tropics. This explains why the latitude from which the snail–trematode association originated correlated negatively with temperature-mediated increases in cercarial production. Within the 20–55° latitude range, trematodes from lower latitudes showed more pronounced temperature-driven increases in cercarial output than those from higher latitudes. This correlation persisted after correcting for trematode phylogeny, and thus indicates the importance of the natural thermal regime in shaping the responses of parasites to increasing temperatures. The lowest latitude included in the dataset was 21°N, and the low latitudes in the dataset therefore correspond to subtropical or mild temperate areas. The present results suggest that a small increase in environmental temperatures at those latitudes would have the greatest repercussions on trematode transmission (Poulin, 2006).

4.7. Global-warming-induced impact of trematodes

An increase of a few degrees in environmental temperatures should lead to marked increases in cercarial emergence from snail first intermediate hosts, with little if any reduction in their transmission efficiency. This may be taken into account as a common scenario for most host–trematode associations. Within the range of temperatures in which host and parasite can live, an increase in temperature is almost invariably coupled with an increase in cercarial output. This phenomenon results from two independent processes: higher temperatures not only trigger the emergence of cercariae from snails, but they also accelerate the production of cercariae within snails. The net outcome of increasing temperature will thus be a greater number of cercarial infective stages. This consequence of climate warming is not trivial: trematode parasitism is not only a major veterinary and health problem worldwide, but trematodes also play major roles in the structuring of animal communities. Any temperature-mediated increase in the extent of trematode infections may have measurable repercussions. Thus, global warming may also enhance the local impact of trematodes (Poulin, 2006).

The increase in cercarial output may take the form of brief pulses rather than a continuous release, but the effects of the former are known to be severe, at least for the small invertebrates commonly acting as second intermediate hosts for trematodes. A good example of such an impact in a natural ecosystem is the one caused by trematodes on the amphipod *Corophium volutator* in coastal soft-bottom habitats of the temperate North Atlantic (Mouritsen et al., 2005). Microphallid trematodes, mainly *Maritrema subdolum*, are common parasites that cause intensity-dependent and temperature-dependent mortality in the population of this amphipod. A simulation model parameterised with experimental and field data demonstrated that a 3.8 °C increase in ambient temperature (predicted for the year 2075) will likely result in a parasite-induced collapse of the amphipod population,

which in its turn may impact the coastal ecosystem as a whole, because of the amphipods' importance both as prey for benthic invertebrates, fish and birds, and to their stabilising effect on non-cohesive sediments. The disappearance of such amphipod beds will result in significant sea-bed erosion and, in turn, structural changes to the benthic animal and microflora community. In light of the expected sea-level rise (also as a consequence of global climate warming), and its predicted negative impact on salt marshes and anthropogenic coastal constructions, reduced sea-bed stability due to the absence of dense assemblages of amphipods will only serve to exacerbate problems (Mouritsen et al., 2005).

5. Fascioliasis

5.1. Environment, transmission and geographical distribution

Fascioliasis is an important disease caused by *Fasciola hepatica* and *Fasciola gigantica*. Whereas in Europe, the Americas and Oceania only *F. hepatica* is concerned, the distributions of both species overlap in many areas of Africa and Asia. Two hosts are needed for these species to complete their life cycle. The definitive host range is very broad and includes many herbivorous mammals, among which humans. Intermediate hosts are freshwater snail species of the family Lymnaeidae (Mas-Coma and Bargues, 1997).

The spreading power of fascioliasis is related to the large capacities of fasciolids to colonise and adapt to new environments, even of extreme characteristics (i.e., the inhospitality of the very high altitude), as well as to new intermediate and definitive hosts. The expansion of *F. hepatica* from the European original geographical area to other continents is also related to (i) the geographical expansion of its original European lymnaeid intermediate host species *Galba truncatula* and (ii) secondarily of the American species *Pseudosuccinea columella*, and (iii) its adaptation to other lymnaeid species authochthonous in the newly colonised areas. The smaller geographical distribution of *F. gigantica* seems to be related to the lesser diffusion capacity of their intermediate snail hosts, the African *Radix natalensis* and the Eurasian *Radix auricularia* (Mas-Coma, 2004; Mas-Coma et al., 2005).

At present, fascioliasis is emerging or re-emerging in many regions of Latin America, Africa, Europe and Asia, both at animal and human levels (Mas-Coma, 2004). The major human health problems are known in Andean countries (Bolivia, Peru, Chile, Ecuador), the Caribbean area (Cuba), northern Africa (Egypt), western Europe (Portugal, France and Spain) and the Caspian area (Iran and neighbouring countries) (Mas-Coma, 2004). Human fascioliasis is also showing the capacity to emerge in Southeast Asia, according to the high number of cases diagnosed in Vietnam since the beginning of the 21st century (De et al., 2006). The highest human prevalence and intensities appear in high altitude areas of Andean countries, where the fluke is able to develop strategies to favour the transmission, including a longer cercarial shedding period, a greater cercarial production per snail and a longer survival of infected snails (Mas-Coma et al., 2001).

Liver fluke development is very dependent of the environmental characteristics according to the nature of free living life cycle phases, which take place fully in the external freshwater milieu, and the vector phase, which develops completely within a freshwater lymnaeid snail, in its turn also very dependent from the environment. Despite of these restrictions, fascioliasis has become the vector-borne disease presenting the widest latitudinal, longitudinal and altitudinal distribution known (Mas-Coma, 2004). Fascioliasis is unique in being capable to give rise to human endemic areas from below sea level (as besides the Caspian Sea) up to the very high altitude (as in Bolivia, Peru, Ecuador and Venezuela). No other vector-borne disease presents such a wide altitudinal range (Mas-Coma et al., 2003).

5.2. Climatics and fascioliasis forecast indices

The yearly definitive host infection incidence of fascioliasis has been related to air temperature, rainfall and/or potential evapotranspiration. These factors affect the intermediate snail host population dynamics and the parasite population at the level of both the free living larval stages of egg and metacercaria and the intramolluscan parasitic larval stages of sporocyst, rediae and cercariae.

There are climatic fascioliasis forecast indices which are calculated with different equations which take into account variations in these climatic factors (Ollerenshaw and Rowlands, 1959; Ollerenshaw, 1971, 1973, 1974; Ollerenshaw and Smith, 1969; Malone et al., 1987, 1998; Bossaert et al., 1999). Several have been successfully applied to animal fascioliasis in different areas of Europe, Africa and the USA (see review in Fuentes et al., 1999). Until the study of Fuentes et al. (1999), climatic fascioliasis forecast indices had been applied neither to human fascioliasis nor to the extreme environmental conditions of the very high altitude endemic areas. Climatic factors taken into account by these indices markedly vary with both altitude and latitude. The analyses showed that the very high altitude climatic characteristics of the Northern Bolivian Altiplano human endemic region markedly differ from those of fascioliasis endemic lowland areas, such as those of the original European geographical distribution of *G. truncatula*. The Northern Altiplano presents the following climatic characteristics: the temperature has no marked seasonal character; there are large variations in temperature within a daily 24-h period; the rainfall distribution is seasonal, with a long dry season coinciding with the lowest minimum temperatures and a long wet season in which rainfall is concentrated; the evapotranspiration is very high, temporary water bodies being of very short duration, mainly in the arid period; and the solar radiation is high not only because of altitude, but also because of the lack of trees and shrubs.

Climate diagrams initially furnished results on the duration of the wet and dry seasons which did not fit the real conditions of the endemic area. Results became appropriate when introducing the modification of Schreiber (1981) in the aridity calculation. Consequently, modifications for high altitude and low latitude were proposed by Fuentes et al. (1999) in the two most useful indices: the Mt

index (proposed by Ollerenshaw and Rowlands, 1959, and modified by Ollerenshaw, 1971, 1973) and the Water budget-based system index (Wb-bs index) (proposed by Malone et al., 1987 and modified by Malone et al., 1998 for large scale regional use). Values of both modified Mt index and Wb-bs index reflected the possibility of optimum transmission during the December–March period. The results were statistically significant for the Wb-bs index when a meteorological station in which no lymnaeids were found was excluded. The modified Mt index was not sufficiently accurate. The modified Wb-bs index values allowed to classify the degree of transmission of human and animal fascioliasis in the Altiplanic zones studied into low, moderate and high risk areas.

After introducing modifications for high altitude and low latitude deduced from climate diagrams, the indices indicated that the contamination risk mainly concentrates in the November–April wet period. However, the only Altiplanic lymnaeid vector snail species G. truncatula appears to be almost exclusively linked to permanent water bodies, because of the high altitudinal evapotranspiration leading temporal water bodies to quickly disappear thus unabling lymnaeids to adapt and develop. This explains why the transmission on the Altiplano takes place throughout the year, opposite to the typical fascioliasis seasonality in Northern Hemisphere countries (Fuentes et al., 1999).

5.3. Remote sensing and geographic information systems

For application to infectious diseases, a complex suite of detectable environmental factors are important, all of which can be observed to a greater or lesser degree from space-borne platforms (Huh and Malone, 2001). Concerning fascioliasis, the following may be useful: (i) temperature, air, soil and surface water (diurnal temperature maximum and minimum, diurnal temperature difference, sea/water/land surface temperature), (ii) water, including soil moisture, standing water and atmospheric water vapor; (iii) condition of vegetation canopy over the earth; (iv) structure and dynamics of the lower atmosphere plus composition and dimensions of airborne particulates (aerosols) contained; and (v) topography and mineralogy, i.e., terrain relief and bedrock/soil types.

Remote sensing (RS) and geographic information systems (GIS) had already been used for animal fascioliasis (Malone and Yilma, 1999), but never for human endemic areas. In GIS for animal fascioliasis (Malone and Zukowski, 1992; Zukowski et al., 1992; Malone et al., 1992, 1998), surface hydrology, vegetation indices and temperature data based on previous knowledge have proved to be very useful. This is why the development of GIS for human fascioliasis was encouraged by several specialists (WHO, 1995; Hillyer and Apt, 1997).

The first attempt to apply these technologies to a human fascioliasis endemic area was that of Fuentes and Malone (1999) in Chile. Annual normalized difference vegetation index (NDVI) values were calculated for each region, using specialised computer software to extract values from advanced very high-resolution radiometer (AVHRR) 10-day (dekade) composite satellite images.

Based on different NDVI classes, a map of risk of fascioliasis transmission was made for each of the administrative zones, with the differentiation of four risk levels (zero, low, moderate and high). A model was proposed for forecasting fascioliasis transmission in Chile based on: (a) evaluation of prevalence at a local scale; (b) the compilation of the largest body of seasonal data possible; (c) the introduction of a modified monthly climatic index; (d) the use of higher resolution images (Landsat TM, Spot, Radarsat, etc.); (e) consideration of the influence of other, non-environmental factors in endemic zones.

More recently, studies were undertaken to analyse whether a GIS predicting model would be viable and useful in the Northern Bolivian Altiplano endemic zone (Mas-Coma et al., 1999). The prediction capacity of the remote sensing map based on NDVI data extracted from 10-day (dekade) composite images from the 1-km AVHRR, acquired by the National Oceanic and Atmospheric Administration's (NOAA) Television Infrared Observation Satellite (TIROS) (Fuentes et al., 2001), appeared to be higher than that from forecast indices based only on climatic data (Fuentes et al., 1999). A total overlapping between real ranges of human fascioliasis prevalence and predicted ranges of fascioliasis prevalence (transmission risk through NDVI) is worth mentioning. NDVI data maps represent a step further in the way to reach a GIS based on various parameters which could accurately fit real epidemiological and transmission situations of fascioliasis in high altitude endemic areas in Andean countries (Fuentes, 2004).

A GIS forecast model to conduct an epidemiological analysis of human and animal fasciolosis in the central part of the Andes has recently been proposed (Fuentes et al., 2005). This model allows, through the classification of the transmission degree into low, moderate and high risk areas, to identify those areas requiring the implementation of control activities. The analysis of the results of studies performed in many endemic areas of Bolivia, Peru and Ecuador demonstrate the validity and approximation of this forecast model combining the use of climatic data by means of calculation of forecast indices and remote sensing data, through the reclassification of NDVI values.

5.4. Effects of climate change and global warming on fascioliasis

The strong dependence of fascioliasis from weather factors indicate that climate change may have a marked influence on the future evolution of this disease. In human and animal hyperendemic high altitude areas of the Andean countries, warming and the El Niño-Southern Oscillation (ENSO) phenomenon are expected to have epidemiological consequences. Warming in tropical Andes appears obvious according to the observed general glacier retreat significantly increased in recent decades (Rosenzweig et al., 2007). The Chacaltaya Glacier in Bolivia is a typical example of a disappearing small glacier, its fast shrinkage being consistent with an ascent of the 0 °C isotherm of about 50 m/decade in the tropical Andes since 1980 (Rosenzweig et al., 2007). Chacaltaya is part of the Eastern Andean chain which just constitutes the

septentrional boundary of the Northern Bolivian Altiplano, the fascioliasis endemic area presenting the highest human prevalence and intensities known (Mas-Coma et al., 1999). This very high endemicity is related to the capacity of the Altiplanic lymnaeid G. truncatula to inhabit different types of permanent water bodies, most of which (subsoil effluences from shallow phreatic layers, large and small rivers, flooding areas called "bofedales", etc.) are linked to waters coming from the perpetual snow amounts of the Eastern Andean chain (Mas-Coma et al., 1999). Consequently, it becomes evident that the short-term increase of runoff because of glacier retreat and subsequent long-term reduction in water supply will greatly influence the epidemiology of the disease in that hyperendemic area. Unfortunately, the possibility of constructing artificial irrigations to palliate water restrictions is very risky in that region, as has been observed in the Peruvian Altiplano where the quick lymnaeid colonisation of an artificial irrigation area has given rise to a high human hyperdemic area (Esteban et al., 2002).

The warming trend will also directly enhance fluke transmission. On the Northern Altiplano, mean monthly temperature oscillates very scarcely (Fuentes et al., 1999), and high fascioliasis transmission rates surprisingly occur even if the mean environmental temperature is below the larval stage development minimum threshold of 10 °C throughout the year (Mas-Coma and Bargues, 1997), high daily temperatures compensating low night temperatures. The temperature mildering influence of Lake Titicaca in such very high altitude zone as the Northern Altiplano explains why the disease has remained restricted around the lake in both Bolivian and Peruvian surrounding areas (Mas-Coma et al., 1999; Esteban et al., 2002). A future small increase of temperature may lead to higher transmission and infection rates, and additionally modify the present low, moderate and high risk areas distinguished within the hyperendemic area by means of both climatic and RS–GIS mapping (Fuentes et al., 1999, 2001). A geographical spreading of these Altiplanic endemic areas to zones more far away from the lake should also be expected. Similar conclusions may be extrapolated to other tropical Andean endemic areas of countries as Peru, Ecuador and Venezuela, where human fascioliasis follows the so-called "valley pattern" of transmission and epidemiology (Mas-Coma, 2005).

Human and animal fascioliasis endemic areas of all these Andean countries may also be affected by modifications in precipitation and the ENSO phenomenon. Thus, an increase of rainfall may extend the contamination risk window presently linked to the November–April wet period (Fuentes et al., 1999). Increasing drought and floods associated with El Niño (Githeko et al., 2000; Magrin et al., 2007) may also influence fascioliasis epidemiology. Drought may modify the spatial, typical patchy fragmentation of fascioliasis foci, and floods may facilitate lymnaeid survival and geographicallly expand their populations. In fact, animal fascioliasis outbreaks were already detected in Ecuador after the great climatic irregularities taken place after the 1997/98 ENSO phenomenon. Consequently, fascioliasis shall be added to the list of diseases in specific geographical areas showing strong epidemiological evidence of increased risk associated to climate anomalies linked to the ENSO cycle (Kovats et al., 2003; Magrin et al., 2007).

Human and animal fascioliasis endemics in low altitude areas may also be affected by climate change. Global warming has been noted as the cause of increased animal fascioliasis in UK (Mitchell, 2002; Mitchell and Somerville, 2005; Pritchbard et al., 2005) and France (Thomas et al., 2007). However, the future scenario of the human and animal fascioliasis hyperendemic area of the Nile Delta, Egypt (Esteban et al., 2003), appears more complicated owing to the combination of increases of temperature and drought, reduction of precipitation, and consequent water stress and agricultural impact (Boko et al., 2007). The present epidemiological situation due to an overlapping of both causal agents F. hepatica and F. gigantica (Periago et al., 2008) may be pronouncedly altered because of climate change owing to both the different development characteristics of their respective larval stages (e.g., minimum temperature thresholds of 10 °C for F. hepatica and 16 °C for F. gigantica; Malone et al., 1998; Yilma and Malone, 1998) and the different ecological requierements of their respective, specific, small Galba/Fossaria and large Radix lymnaeid vectors (Bargues et al., 2001). The lymnaeids transmitting F. hepatica are species showing marked amphibious trends, more adapted to colder conditions and which use to inhabit small or very small water bodies, as those temporal collections depending from cultured field irrigation management (i.e., rice) or seasonal rain. Lymnaeids responsible for F. gigantica transmission are species more adapted to warmer conditions and preferring large and deeper water bodies rich in aquatic vegetation, as those more typical for permanent collections and main, wide canals for irrigation and water supply. Thus, transmission foci of both fasciolids are usually different and appear separate, even in the same endemic locality, and fascioliasis by F. hepatica is more related to seasonality than fascioliasis by F. gigantica (Mas-Coma, 2004).

6. Schistosomiasis

6.1. Meteorological factors, snail hosts and transmission

It seems clear that climate change and global warming will result in changes in aquatic environments. The expansion of suitable habitats for invertebrate hosts of waterborne parasites could result in risk of waterborne infections in humans and animals and increased distribution of the disease. There are different environmental factors that impact on the distribution of schistosomiasis. Temperature, water body type, rainfall, water velocity and altitude can all have a significant effect on the schistosome life cycle and survival of the intermediate snail host (Fenwick et al., 2007). Climatic changes are likely to affect the known geographical distribution of freshwater snails, such as Biomphalaria spp., the invertebrate hosts of Schistosoma spp. transmissible to humans, livestock and other animals (Morgan et al., 2001). For example, high temperatures may explain the absence of Biomphalaria spp. from coastal East Africa and the consequent absence of

Schistosoma mansoni transmission (Sturrock, 1966). Similarly, high mortality of *Biomphalaria pfeifferi* in South Africa is associated with periods of continuous high temperatures (Appleton, 1977). Thus, schistosomiasis is among the diseases able to increase both its local infection and geographic expansion with climate change, mainly with global warming (Githeko et al., 2000; Bergquist, 2001a,b).

6.2. Modelling and mapping

RS and GIS have shown to be very valuable for the analysis of the distribution of schistosomes on both reduced and large spatial scales (Brooker et al., 2000; Huh and Malone, 2001). A global network of collaborating health workers and earth scientists dedicated to the development of computer-based models that can be used to improve control programmes for schistosomiasis and other snail-borne diseases of medical and veterinary importance has been created (Malone et al., 2001; see www.gnosisGIS.org). The idea is for models to be assembled using GIS methods, global climate model data, sensor data from earth observing satellites, disease prevalence data, the distribution and abundance of snail hosts, and digital maps of key environmental factors that affect development and propagation of snail-borne disease agents. A work plan has been developed and agreement has been reached on the use of compatible GIS formats, software, methods and data resources, including the definition of a 'minimum medical database' to enable seamless incorporation of results from each regional GIS project into a global model. GNOSIS will point users to a toolbox of common resources resident on computers at member organisations, provide assistance on routine use of GIS health maps in selected national disease control programmes and provide a forum for development of GIS models to predict the health impacts of water development projects and climate variation (Malone et al., 2001).

The mapping of schistosomiasis has been a priority since long ago (Doumenge et al., 1987). In Africa, computer modelling has been applied to schistosomiasis in different countries, such as Egypt (Malone et al., 1997) and South Africa (Moodley et al., 2003), although focused on the geographical characterization rather than on the prevalence or intensity of infections. Only few attempts have been made thus far to predict changes in the frequency and transmission dynamics of schistosomiasis due to climate change (Martens et al., 1995, 1997; Zhou et al., 1998, 2008; Yang et al., 2005, 2006). The lack of long-term, high-quality datasets may, among other reasons, explain the discrepancy reported in given studies which did even came to different conclusions regarding the extent of schistosomiasis transmission under the scenario of a warmer climate (Martens et al., 1995, 1997). In Uganda, GIS coupled with satellite and climatic data has been used to map the distribution of infection and to overlay parasitological data with interpolated environmental surfaces (Kabatereine et al., 2004). Infection was shown to be widespread, with prevalence typically highest near the lakeshore and along rivers. Limits to transmission were identified as altitudes greater than 1400 m and areas where total annual rainfall was less than 850 mm. Hence,

as well as excluding areas where *S. mansoni* is unlikely to be a problem, the results also identify those areas where the problem of *S. mansoni* is greatest. In Cote d'Ivoire, remotely sensed environmental data from satellite imagery and digitalised ground maps were combined with data sets of prevalence and intensity of *S. mansoni* to establish a comprehensive GIS. Bayesian variogram models were applied for spatial risk modelling and prediction. Interestingly, the goodness of fit of different spatial models revealed that age, sex and socio-economic status has a tronger influence on schistosomiasis prevalence than environmental covariates (Raso et al., 2005).

6.3. Climate change and schistosomiasis control

Special efforts in analysing the potential impact of climate change on schistosomiasis have been recently made in China. The resurgence of *Schistosoma japonicum* infection in the past few years is taking place despite 50-year intensive control activities targeted against the amphibious intermediate snail host, *Oncomelania hupensis*, and large-scale chemotherapy campaigns using praziquantel. Explanations appear to be multifactorial, including the construction of the Three Gorges dam, the recovery of the Dongting Lake, and major flooding events. Additionally, a possible impact of climate change was also considered (Zhou et al., 2005). Remote sensing data were used to measure the impact of a flood on the dispersal of the intermediate snail host in the Lower Yangtze River basin (Zhou et al., 2002a). Predictive models of the spatial distribution of schistosomiasis appear to be hampered by the existence of different regional *O. hupensis* host subspecies. The habitats associated with these different subspecies vary considerably, with mountainous habitats in the west, and flood plain habitats in the east (Seto et al., 2002a). Environmental changes resulting from the Three Gorges dam and global warming are likely to result in an increase of the snail habitat. Prediction of schistosomiasis risk using Landsat TM imagery to identify snail habitats in mountainous regions was complicated by the occurrence of seasonal flooding, and it was suggested that soil maps may help to solve this complication (Seto et al., 2002b).

The current hypothesis is that an increase in annual growing degree-day (AGDD) will alter the extent and level of schistosomiasis transmission (Yang et al., 2006). In other terms, the number of parasite generations will increase by speeding up their development in longer growing seasons and extending the current area where parasite larvae and intermediate host snail can proliferate (Brooker et al., 2000). AGDD is a unit expressing the amount of heat energy an organism accumulates over an entire year and which correlates with the spatial distribution of living organisms (GDD can be articulated as the average daily temperature minus the developing temperature threshold of an organism). The heat units an organism requires to complete its development are fairly constant, given by the temperature above a critical threshold summed over the time period this lower temperature threshold is exceeded. It follows that organisms with high unit requirements are more likely to develop into mature stages in areas where AGDD is high. Employing a previously determined lower

temperature threshold for schistosome larvae development in the snail, the predicted temperatures were then transformed to a measure of AGDD, to forecast the transmission of schistosomiasis japonica, in the way to evaluate the effects of climate change on the frequency and transmission dynamics of this disease in China (Zhou et al., 2002b).

The time-series from 1972 to 2002 for 39 counties of eastern China, where *S. japonicum* is endemic, was analysed by using a modelling approach to estimate AGDD and employing a lower temperature threshold of 15.3 °C. The final model included both components, temporal (second order polynomials in time plus a seasonality component) and spatial (second order polynomials of the coordinates plus the thin-plate smoothing splines). Results showed that temperature increased over the past 30 years in all observing stations. There were distinct temporal trends with seasonality and periodicities of 12, 6, and 3 months, whereas only marginal spatial variation was observed. The predicted AGDDs for 2006 and 2003 showed increases for the entire area studied, with the AGDDs difference between these two time points exhibiting an increase from north to south. Results obtained suggest that temperature changes will alter the frequency and transmission dynamics of schistosomiasis japonica (Yang et al., 2006). This in turn might jeopardize progress made for transmission control or even interruption since the launch of China's national schistosomiasis control program in the mid-1950s (Utzinger et al., 2005; Zhou et al., 2005).

Unfortunately, average monthly temperatures were used in that study, because daily nighttime minimum or daily daytime maximum temperatures were not available. This may add a bias to the results obtained, since the development of parasite larvae in the snail could cease when the nighttime minimum temperature drops below a critical threshold or the daytime maximum temperature exceeds an upper threshold (Yang et al., 2006). It has been reported that natural temperature fluctuations aid the development of parasite larvae in the snail (Zhou et al., 2002a,b). Other sources of potential biases in predicting temperature changes are that nighttime minimum temperatures are expected to increase more than daytime maximum temperatures and, winter temperatures are predicted to increase more pronouncedly than summer temperatures (Easterling et al., 1997; Murphy et al., 2004).

7. Cercarial dermatitis

7.1. Cold climate lakes and transmision

This inflammatory skin reaction is caused by bird schistosome cercariae released by intermediate water snail hosts which penetrate and develop in human and mammal skin after repeated contacts with the cercariae in fresh- or salt-water bodies, depending on the species/genus of the parasite. Whereas these trematodes mature in birds, their development in mammals is restricted and schistosome death occurs at various intervals postinfection (Horak et al., 2000).

Swimmer's itch occurs globally and is recently showing an emerging trend, becoming an increasing problem in several lake regions both in Europe and North America (De Gentile et al., 1996). This disease is, in Europe, caused by cercariae of the genera *Trichobilharzia*, *Bilharziella* and *Gigantobilharzia*, all of them parasites of birds. *Trichobilharzia* is the genus which includes more species involved in human dermatitis (Simon-Martin and Simon-Vicente, 1999; Bargues et al., 2001). Human outbreaks have been recently reported, including up to high numbers of swimmers affected, as in France (Caumes et al., 2003), and up to numerous lakes being involved, as in Sweden (125 out of 248 municipalities with lakes had problems with dermatitis) (Thors and Linder, 2001). Cercarial dermatitis has even been reported from relatively cold climate areas such as lakes of Iceland (Kolarova et al., 1999), or French Alpine lakes (Annecy and Le Bourget) in the Savoy district (Dubois et al., 2001), suggesting that lower water temperature may prolong the life of the intermediate snail hosts.

Bird schistosomes show a rather narrow intermediate host specificity, parasitizing either one or several closely related snail species. *Trichobilharzia* spp. larval development takes place in snails of the families Lymnaeidae and Physidae, findings in other snail families needing confirmation (Bargues et al., 2001).

7.2. Climate change and increase of summer outbreaks

Reports of cercarial dermatitis usually refer to outbreaks, as the population affected (mainly vacationers) is generally very mobile (Lindblade, 1998). The disease is mostly associated with swimming or wading in recreational lakes. There is a tremendous variation in the water bodies involved, ranging from small garden ponds to very large lakes. Water bodies may be continuous or individual small lakes. Their surroundings may be densely populated, as in many central European regions, or in the wilderness, as in the north. Moreover, local differences within a water body may exist with respect to snail and bird populations and also sites for water related activities. However, human infection associated with the cultivation of rice in Thailand, Japan and China (Li et al., 1998; Kullavanijaya and Wongwaisayawan, 1993) and other occupational hazard (Pirila and Wikgren, 1957; Folster-Holst et al., 2001) have been reported, illustrating the diversity of situations related to fresh water. Cases related to sea water are infrequent, cercariae of *Austrobilharzia* being involved in South Africa, Australia and North America, and non-classified schistosomatid cercariae in dermatitis of people collecting marine molluscs in Venice lagoon, Italy (Canestri-Trotti et al., 2001).

Swimmer's itch is usually seasonal, warmer months being most prevalent because both the release of cercariae from snail hosts and the number of people that have contact with water reach peak levels in that year period (Chamot et al., 1998). It is known that temperature affects the rate at which schistosomatids develop within snails (Lodge et al., 1987). Observations suggested that higher temperatures accelerate trematode development within the snail, resulting in an earlier and more severe situation than in colder lakes. Additionally, higher populations of snails may correlate with higher levels of algae, leading to a

higher level of cercarial density in the water (Lindblade, 1998). Although the total number of the cercariae released from the snails can be inversely proportional to the temperature of the lakes (Zbikowska, 2001), it is the temperature increase which might induce an increase of cercarial shedding.

Climate change has been related to another phenomenon giving rise to an increase of summer outbreaks of cercarial dermatitis. Global warming in recent years have had a mildering effect on areas presenting lakes used by migratory birds, as for instance anatids. As a consequence, those birds do not further need to migrate southward for more appropriate warmer conditions, stay in central European lakes and become sedentary (Cotton, 2003). This opens the possibility for the life cycle of the bird schistosomatids to expand their transmission in these lakes during months in which transmission was stopped in cold years. This larger seasonal window may originate higher infection prevalence in snails, whose population activity is in its turn also seasonally enlarged, as well as a higher number of schistosomatid generations per year and higher prevalence in the birds of the lake. All in all, when the human swimming summer period arrives, the water may have a pronouncedly higher density of cercariae able to give rise to a higher human infection both in space and time.

8. Concluding remarks

The confirmation of the conclusion about an important climate change impact on helminthiases has been reached only very recently (see review in Mas-Coma et al., 2008). Only shortly before, helminthiases were still noted as infectious diseases scarcely affected by climate change, when compared to diseases caused by viruses, bacteriae and protozoans. These microparasites were noted as more likely to emerge than macroparasites as helminths on the base of a quantitative analysis of the risk of infectious disease emergence allied to the nature of the organisms, their mode of transmission and source (Taylor et al., 2001). Although helminths also appear to be affected by climate change, their main difference with microparasites lies on the usually longer life cycles of helminths, with longer generation times, slower population growth rates and longer time period needed for the response in the definitive host to become evident. Within the r–K continuum, helminths may evidently be catalogued as r-strategists too, including trematodes as the most r when compared to cestodes, nematodes and acanthocephalans (Esch et al., 1977; Combes, 1980; Wharton, 1986; Mas-Coma et al., 1987b). However, helminths appear to be less r than viruses, bacteriae and protozoans (see, for instance, Villareal et al., 2000). Consequently, after a pronounced climate change in a local area, modifications in helminth populations need more time to be obvious or detectable than modifications in microparasite populations. Similarly, the relation of changes in a helminthiasis with climatic factor changes, as extreme events elapsed relatively long time ago, may be overlooked if not concretely searched for. All indicates that this phenomenon has been the reason for previous analyses to conclude that helminthiases do not constitute priority targets in climate change impact studies.

The present review shows that trematodes, similarly as other helminths presenting larval stages living freely in the environment and/or larval stages parasitic in invertebrates easily affected by climate change as arthropods and molluscs, but also those using small vertebrates (e.g., rodents) as intermediate hosts (Mas-Coma et al., 2008), may be largely more susceptible to climate change impact than those helminths in whose life cycle such phases are absent or reduced to a minimum (two large-mammal-host life cycles as in taenids; ageohelminths as pinworms). Thus, trematodes in general and nematodes of several groups are clear candidates to suffer pronounced population modifications because of climate change. The cercarial stage of trematodes is affected to such a level that digeneans have even been proposed as potentially very useful markers to monitor climate change impact (Poulin and Mouritsen, 2006), and may even induce invertebrate host population collapses with cascade effects giving rise up to very large impacts on broad ecosystems, as shown by simulation models (Mouritsen et al., 2005). On the contrary, a previous review suggests that cestodes and acanthocephalans may also be affected, but at a lower level and mainly indirectly through effects on their exothermic invertebrate or small endothermic vertebrate hosts (Mas-Coma et al., 2008).

Two other aspects of helminths, also crucial concerning their susceptibility to climate change modifications, shall finally be emphasized too: (i) helminth capacity to induce more or less acquired immunological host response, and (ii) host (or vector) specificity characteristics of each helminth species. Thus, helminth species inducing a strong acquired immunological response will be able to buffer climate change effects leading to higher host individual infection rates, whereas those helminth species not able to do so may be more affected by climate changes because of being unable to control helminth intensity (Hudson et al., 2006). In its turn, helminths showing a strict host specificity, that is, only able to develop within a concrete host species, or even concrete host geographical strain, will be very dependent on the influences of climate change on the host population. On the contrary, helminths showing a less marked host specificity, that is, able to develop within different host species, or even phylogenetically distant species, have the possibility to buffer the influence of climate change more or less depending from the different adaptative capacities of the different host species to a given climate modification (Mas-Coma et al., 2008).

Conflict of interest statement

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