

Arctic parasitology: why should we care?

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The significant impact on human and animal health from parasitic infections in tropical regions is well known, but parasites of medical and veterinary importance are also found in the Arctic. Subsistence hunting and inadequate food inspection can expose people of the Arctic to foodborne parasites. Parasitic infections can influence the health of wildlife populations and thereby food security. The low ecological diversity that characterizes the Arctic imparts vulnerability. In addition, parasitic invasions and altered transmission of endemic parasites are evident and anticipated to continue under current climate changes, manifesting as pathogen range expansion, host switching, and/or disease emergence or reduction. However, Arctic ecosystems can provide useful models for understanding climate-induced shifts in host-parasite ecology in other regions.

Out in the cold: vulnerable societies and sensitive Arctic ecosystems

The Arctic, which encompasses northern regions of Alaska, Canada, Greenland, Iceland, Norway, Sweden, Finland, and Russia, has an estimated human population of four million, of which 10% are indigenous [1]. When considering the impact of parasites on human and animal health, this sparsely populated region is easily overlooked in comparison with temperate and sub-tropical regions, and especially the fecund, active tropical regions, where the majority of parasitic infections of human medical importance occur.

Nevertheless, parasitism in the Arctic significantly influences the health of people and domestic and wild animals. The challenges to investigating this are many, from the vast distances between remote, isolated communities, limited infrastructure and human capital, as well as restricted access to medical and veterinary care [2,3]. The limited medical infrastructure in the Arctic, serving a widely dispersed population, provides similar public health challenges to those of many tropical countries, even as sanitation obstacles and limited water treatment leaves populations vulnerable to waterborne parasites [4]. The paucity of meat inspection services, together with traditional subsistence

and hunter-based lifestyles, exacerbates the potential for zoonotic infections in people [5]. In addition, certain traditional meat preparation methods are not sufficient to inactivate parasites (e.g. *Trichinella nativa* in seal meat [6]). Direct effects of parasites on wildlife hosts can have population level impacts that reduce availability of subsistence game and quality of meat.

Generally, both host and parasite diversity in the Arctic is lower than in the tropics [7], increasing the sensitivity of the Arctic ecosystem to invasions and other environmental changes [3,8]. One prominent perturbation is climate change. In recent decades, the annual mean temperature in the Arctic has increased at almost twice the rate as that of the rest of the world and has already resulted in vegetation changes and invasion of new species [1]. The selective advantages that favoured survival of cold-adapted animals might be reduced, and new species can out compete them, either through direct competition for food and/or by introduction of new pathogens, including parasites [5,6]. Comparably, the transmission and epidemiology of endemic parasites might also change through shifts in parasite development and survival rates, and/or shifts in timing and patterns of migration, thereby altering infection pressures on hosts [6]. For example, global warming could alter the geographical distribution of *Trichinella* species with different tolerances to cold. However, identifying these trends and shifts can be particularly challenging when baseline data for many hosts and their parasites are incomplete [3.11].

Other changes, either directly or indirectly associated with climate change, are also having profound effects on the Arctic, including vegetation shifts, rising river flows, and expansion in marine shipping and tourism because of retreating sea ice [1,12]. Some of these changes will lead to the influx of novel species of parasites and their vectors, either transiently or permanently. Likewise, hosts (including *Homo sapiens*) spreading north might be naïve to parasites present in their new environment. Tourism is a key factor in northern economies and visitor numbers are predicted to increase; eating traditional foods in the quest for an 'authentic' experience means that some visitors could bite off more than they can chew [13].

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In this paper three 'hot topics' in Arctic Parasitology are presented: the impact of climate change on waterborne transmission of parasites, parasites and food security issues in the Arctic, and emerging parasitological threats for Arctic wildlife. The intention is to give an outline on why Arctic parasitology is relevant and to stimulate readers to explore other facets of this important field.

Climate change in the Arctic and waterborne parasites

According to the Intergovernmental Panel on Climate Change (IPCC), the burden of water-related diseases will be affected by climate change-related alterations in rainfall, surface water availability, and water quality [14]. As polar regions are subject to the earliest and most profound climate-induced changes [15], the Arctic, with its huge diversity of water sources, is expected to be particularly vulnerable (Figure 1).

Projected changes indicate that Arctic regions will become generally warmer and wetter. Indeed, the Arctic climate is already warming, and most models predict larger changes [1,16]. Greatest warming is predicted for the winter months, whereas precipitation is projected to increase by approximately 20%. Decreased reflection of solar radiation resulting from a decline in sea ice will also cause regional warming. Snow cover in the Arctic is expected to decrease by 10–20%. Additionally, the

frequency and severity of extreme weather events are predicted to increase [1,16].

From a global public health perspective, the most important waterborne parasites are Cryptosporidium spp. and Giardia duodenalis. Although human population studies suggest Giardia infection could be relatively common towards Arctic regions, [17], there are few reports of these parasites in Arctic wildlife [18,19]. This might indicate real absence, perhaps because of climatic conditions inactivating environmental stages [20,21], but probably also reflects limited survey and inventory for Giardia across the wide range of potential hosts. Higher temperatures and reduced snow cover could lead to expansion of the northerly range of different wild and domestic animals and consequent invasion of Giardia with these hosts. Milder climatic conditions might also facilitate survival of cysts and oocysts in the environment, thereby increasing their chances of transmission. Areas previously considered pristine could be substantially diminished. A potential risk of giardiasis from drinking untreated water for residents and tourists on Banks Island, Canada, has been postulated following detection of Giardia of assemblage A in muskoxen [19]. Elevated run-off from snowmelt and increased precipitation could exacerbate contamination of water supplies (Figure 1). The association between waterborne parasitic infection and increased precipitation

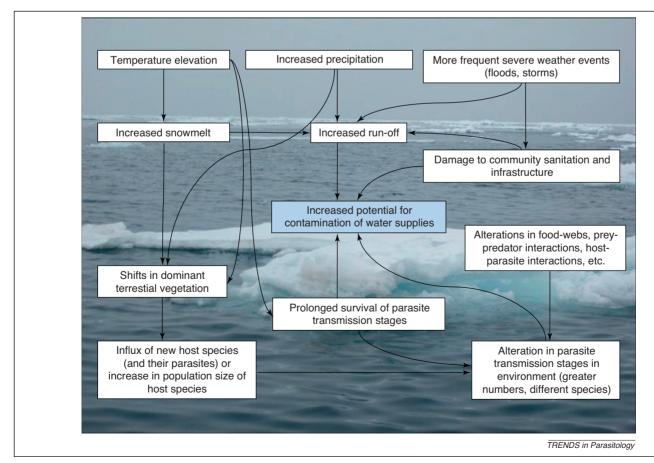


Figure 1. Flowchart of climate change effects on water contamination by parasites.

Predicted and current climate changes can affect the potential for contamination of water supplies with parasite transmission stages in the Arctic. Only changes that could increase contamination potential are included in the figure; some potential changes could reduce contamination potential (e.g. temperature changes can decrease survival of parasite transmission stages).

is well recognized [22,23], and outbreaks of waterborne cryptosporidiosis and giardiasis have been associated with snowmelt [24,25].

The complex interactions between hosts, parasites, and environment provide a challenge for predicting changes. This can be illustrated by the hypothesis that climate change could exacerbate the potential for waterborne transmission of Toxoplasma gondii in the Arctic [25]. Relatively high seroprevalences have been reported from various Arctic species, including polar bears and canids [26-28]. The supposition is that transmission is generally vertical or through consumption of infected prev animals by intermediate hosts, as felids, the only known definitive hosts for Toxoplasma, are rare or absent from the Arctic. Lynx (Lynx) canadensis, and possibly Lynx lynx) are the only relatively widespread wild felids of the Arctic; domestic cats are uncommon, and feral cat populations cannot survive outside established communities [29]. However, warmer temperatures could result in the expansion of the distribution range of lynx and other felids (e.g. cougar, bobcats) [30]; survival of domestic or feral cats will also probably increase. The potential for lifecycle completion and environmental contamination with Toxoplasma oocysts might therefore increase northwards, thus increasing the possibility for waterborne transmission and waterborne outbreaks of toxoplasmosis in the human population [25].

Parasites and food security in the Arctic

Food security encompasses a range of parameters including accessibility, availability, quality (nutritional value), sustainability of food production systems, and safety (absence of toxins, pesticides, microorganisms, etc.). Food security is generally low in Arctic communities [31]; among some isolated indigenous communities, food insecurity as high as 40–83% has been reported and among some 30% of Alaskan Native households [31].

Although Arctic wildlife provides a nutritious and economical food source, which also serves to maintain cultural traditions [32] (e.g. use of permafrost for food storage, food-sharing traditions, and use of traditional recipes), minimal meat inspection and absence of sufficient data for appropriate risk assessments [33] can increase the risk of communitywide outbreaks of foodborne parasitic infection. Several parasites of key importance are listed in the Table 1, along with potential effects of predicted climate changes on their transmission.

Table 1. Possible impacts of climate change on Arctic foodborne parasites

Parasite	Associated food ^a matrix	Impacts on lifecycle	Impacts on zoonotic transmission (food safety)
Diphyllobothrium latum and other Diphyllobothrium spp.	Fish	Faster embryonation of eggs in water, faster hatching and development of coracidia, increased abundance of crustacean intermediate hosts, but more rapid die-off in each case; faster development of procercoid larvae in crustaceans [34].	Higher numbers of parasites in crustaceans; more infections in fish and definitive terrestrial hosts.
Anisakis simplex, Pseudoterranova decipiens and other anisakid nematodes.	Fish	Faster embryonation of eggs in water, faster hatching and development of L2 larvae, increased abundance of crustacean intermediate hosts, but more rapid die-off in each case; faster development of L3 larvae in crustaceans; migration north of paratenic (fish, squid) and definitive final hosts [35].	Enhanced ice melts and water run-off affect embryonation, hatching, and maturation of stages in aquatic environment.
Trichinella spp. (especially T. nativa and T6 genotype)	Meat (especially bear, walrus)	Changes in snow/sea-ice cover could alter migration routes, and loss of ice platforms, resulting in more interspecies and intraspecies interactions, including greater intraspecies predation and scavenging of dead carcasses [36].	More/different species/genotypes of Trichinella establish with varying levels of infectivity to man.
Toxoplasma gondii	Meat (marine mammals; also birds and ungulates)	More definitive hosts (felid) establishing in the Arctic, leading to completion of sexual lifecycle. Increased intra/inter species predation and altered migration routes. New strains of <i>Toxoplasma</i> introduced to vulnerable Arctic populations.	Waterborne/foodborne transmission becomes possible with completion of lifecycle [25].
Echinococcus multilocularis and Echinococcus granulosus	Berries, mushrooms etc. Can also be dustborne, waterborne, etc.	Altered winter survival of intermediate hosts. Translocation or introduction of infected final or intermediate hosts could allow establishment of lifecycles [37]. Increasing temperature can facilitate survival of eggs in the environment (e.g. [38]).	Increased globalization/tourism with dogs could lead to introduction into new regions (such as <i>E. multilocularis</i> into mainland Fennoscandia) increasing risk of human infection and impacting harvesting of natural resources. ^b

^aCountry foods are particularly important; predominant country foods include fish (Arctic char, trout, salmon, cod, turbot etc.), marine mammals (beluga, narwhal, ringed seal, walrus, bowhead whale), birds (marine ducks, goose, ptarmigan), and terrestrial mammals (caribou, muskox, hares, bears), along with berries and shellfish. These are often prepared by traditional recipes relying on fermentation, spicing, salting, smoking, and air-drying, rather than cooking (e.g. Inuit specialities such as igunaq, iqluppik, misira, natsiminiq, nikku, pagqut, pitti, and tuktu).

bSuch as the recent identification of E. multilocularis in a red fox in Sweden (http://web.oie.int/wahis/public.php?page=single_report&pop=1&reportid=10263).

Diphyllobothrium spp. and nematodes of the family Anisakidae (Anisakis simplex and Pseudoterranova decipiens) are important zoonotic parasites in Arctic fish. Transmission is influenced by changes in temperature, pH, salinity, turbidity, etc. (Table 1). Seroepidemiological surveys of Inuit in Greenland for anisakid infection suggest an age-related effect, with an overall 4.7% prevalence in Ammasaalik district, but prevalences of 7.7–17.6% in people over 40 years of age [39]. No comparable data exist for Diphyllobothrium spp., but basic prevalence data on zoonotic D. latum versus non-zoonotic D. dendriticum in Arctic fish appear crucial for risk assessment and implementation of appropriate prevention measures. However, other Diphyllobothrium species could also infect humans, and until our knowledge on diversity and infection within this genus improves, it will be difficult to make wellfounded decisions.

The most important meathorne parasites of the Arctic are *Trichinella nativa*, *Trichinella T6*, and *Toxoplasma gondii*. The geographical distribution of cold-tolerant versus freeze-tolerant *Trichinella* species follow January isothermal lines, circa -5 °C for *T. nativa* [40], but the underlying cold tolerance of the muscle larvae depends on several factors, including temperature fluctuations around freezing point [41], host species [42], and infection duration [43]. Thus, shifts in host diversity and environmental temperature could lead to altered distribution.

The epidemiology of toxoplasmosis in the Arctic is intriguing. Presently, consumption of undercooked meat, particularly from marine mammals, seems a much more important risk factor for human infection than drinking untreated water. Serological surveys suggest widespread *Toxoplasma* infection in marine mammals [44], and high human occurrence was recorded in Kuujjuaraapik, North Quebec, where 80% of Inuit (with dietary preference for raw, dried meat from sea mammals) were found seropositive, compared with 10% in the ethnic Cree population in the same community (with dietary preference for cooked terrestrial mammals) [45,46].

Emerging parasitological threats for Arctic wildlife

Several examples of climate correlated shifts in host-parasite interactions in Arctic and sub-Arctic environments are already evident. For example, in response to elevated temperatures, (1978–2003) the lifecycle of muskox lungworm, Umingmakstrongylus pallikuukensis, has shifted from being predominantly two year to being predominantly one year [47], presumably related to cumulative changes and long-term global dynamics. Another emergence, because of short-term ephemeral extremes, are epidemics of severe disease associated with enhanced transmission of the filarioid nematode, Setaria tundrae, that occurred in reindeer following two consecutive warm summers; in Finland, the northern range of this parasite has now expanded [48]. Similarly, the northern limits of the moose winter tick, Dermacentor albipictus, have expanded in Northwest Territories, Canada [10]. Further relaxation of climatic constraints on more temperate parasites, vectors, or hosts, allowing such expansion, is a significant concern regarding invasive parasites around the Arctic and can have important consequences for existing host populations. Direct impacts of parasites on naïve host populations could lead to epidemic disease outbreaks (e.g. *Elaphostrongylus rangiferi* in caribou in Newfoundland [49]), whereas more subtle, but nevertheless important, parasite-mediated competition between invasive and endemic hosts, or cumulative impacts of enhanced parasite diversity, could affect host populations [9]. Wildlife translocations and introduction of agricultural and companion animals are of heightened concern under current and projected climatic conditions; parasites that previously could not have established, might now succeed [10].

These cases illustrate transmission pattern shifts attributed primarily to temperature-driven changes in the ecology of the parasite stages that live and develop in the environment or in insect vectors or gastropod intermediate hosts. Such factors do not exist in isolation and shifting patterns in host behaviour and food webs are also critical. For example, reductions in sea ice impact the ecology of walruses and polar bears, affecting their behaviour and diets, and thus parasite diversity and abundance (e.g. *Trichinella* [36]). The majority of macroparasites of barrenground caribou are transmitted during the summer, and temporal and spatial shifts in migration patterns will alter host–parasite interactions in as yet unknown ways.

Examination of northern host-parasite systems provides opportunity for reflection on the ecology of parasitism. The Arctic climate is changing at a rapid rate, permitting real time exploration of climate-linked tipping points and pathogen emergence. The polar environment is highly seasonal and winter can be a great equalizer in the host-parasite battle, reducing or stopping transmission. Slight alterations in summer season length and temperatures can release the parasites from this constraint, serving as a tipping point in which the system shifts into a different state (e.g. from a two year to one year transmission cycle as seen with *U. pallikuukensis*). Predictive models, constructed from empirical data and incorporating climate change scenarios, are useful for exploring these temporal and spatial tipping points. Additionally, the simplicity of the Arctic provides an opportunity to explore parasite flow among hosts. Research demonstrating maintenance of T. gondii on Svalbard, in the absence of definitive hosts, provides insights into alternate transmission routes, such as migratory waterfowl as an ongoing source for fox infection [50]. Adaptations of Arctic parasites could also provide insight into important physiological mechanisms of relevance across taxa (e.g. freeze tolerance in Trichinella).

The resilience of Arctic species in adapting to a changing environment is uncertain and various questions regarding host–parasite interactions remain unresolved (Box 1). Arctic hosts and parasite fauna have evolved to thrive under conditions of prolonged extreme cold, vast spaces, high seasonality and generally limited species density and diversity. It is currently unknown whether endemic fauna have the resilience, including physiological capabilities, behavioural capacity, and immunological and genetic diversity, to adapt to the ongoing and predicted pronounced environmental changes in the Arctic. From a parasite-centric point of view, we might contemplate whether Arctic parasites are at the same, or perhaps greater, risk of

Box 1. Key themes and unanswered questions in Arctic wildlife parasitole	Box 1. Key themes and	d unanswered questi	ions in Arctic wildlif	e parasitology
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Themes and questions	Potential approaches and mechanisms for addressing these subject	
What is the current parasite biodiversity in the Arctic?	Synoptic survey and inventory	
	Passive surveillance and community-based surveillance	
	Archival specimen and DNA-based collections	
	Databases	
How do different types of host-parasite systems	Empirical data collection - field and laboratory experiments.	
vector-borne, direct transmission, gastropod	Epidemiological analyses of existing datasets	
ntermediate hosts, etc.) respond to climate perturbations?	Modelling	
How immunologically well equipped are Arctic species	Experimental investigation	
o respond to new pathogen threats?	Immune function studies	
What are the impacts of increased host and parasite	Targeted surveillance and detailed parasitological investigation	
diversity on endemic Arctic host species? Which patterns	Experimental exposure studies and modelling	
of parasite emergence and disease (epidemic, endemic, parasite-mediated competition etc.) are expected?		
What are the tipping points in the Arctic host-parasite	Empirical and theoretical models	
systems? Are these preventable?		
What is the role of winter in parasitic invasions of	Analyses of winter versus summer transmitted parasites and	
northern ecosystems?	winter versus summer sympatry of invasive and endemic hosts	
	and vectors both migratory and non-migratory	
	Evaluate freeze-tolerance in potential invaders	
How do shifting temporal and spatial patterns of animal	Experimental and field-based studies to determine:	
pehaviour and migration interact with seasonal availability	Basic lifecycles	
of parasites, climate, and photoperiod?	Effects of temperature on parasite temporal and spatial availability	
	• Effects of photoperiod on parasite behavior (e.g. questing	
	behavior of ticks)	
Are there genotypic and/or phenotypic characteristics of	Population genetics	
parasites that permit them to persist at the extremes	Strategic sampling	
of their ranges?		
And what are the impacts of changes in mean climatic	Modelling	
conditions versus changes in climate extremes? How can we best distinguish between		
regional and local phenomena?		
How can we use Arctic host-parasite systems as models	Evaluate if knowledge from Arctic host-parasite systems provide	
for climate change responses elsewhere?	insights into dynamics of taxonomically related species elsewhere	
	(e.g. filarioid nematodes in the Arctic as a model for <i>Onchocerca</i>	
	in the tropics?)	
What are the socio-economic implications of emergence	Sociological studies to evaluate the responses of communities	
of new parasitic diseases in the Arctic?	to real or perceived changes in animal distribution, animal health	
	and environmental changes (e.g. water purity and availability)	

extinction, than their more charismatic hosts, such as polar bear.

Conclusions

Wild and semi-domesticated animals in the Arctic are important for ecosystem integrity, food, tourism, as a focus of cultural activities, and for the subsistence and wage economies. Zoonotic pathogens in wildlife can be transmitted to people through consumption or environmental exposure. Food and water safety remain significant issues in the Arctic, and will probably become even more important in the future, as climate changes exacerbate the potential for transmission of waterborne agents. Implementation of appropriate risk assessments can be useful in protecting human and animal health from foodborne [3] and waterborne parasitic infections, but reliable prevalence and monitoring data are essential for such assessments to be developed. In situations in flux, such assessments must permit continual updating as conditions change and new information becomes available.

Parasitic diseases can influence the health and sustainability of wildlife populations, with downstream effects on ecosystems. Recent work on parasite distribution, abundance, and epidemiology in local populations has greatly advanced our understanding of these systems, but data gaps remain. The logistical challenges to filling these data gaps are many [3]. Limiting factors to achievement include the poorly developed infrastructure, difficulties in gaining access to relevant populations, and the extreme seasonality of the Arctic. Networks such as the Polar Parasitology Network (POPAN, www.PoPan.net), the Beringian Coevolution Project (http://www.msb.unm.edu/mammals/Cook/ CurrentProjects/0051.html), and the CircumArctic Rangifer Monitoring and Assessment Network (CARMA, www.carmanetwork.com) work towards the exchange of knowledge and harmonization of methods on a global scale, as well as at a local level. CARMA has promoted standardized sampling protocols and the active involvement of communities in health surveillance, allowing comparison of data between Rangifer populations on different continents.

Properly maintained archival material, with associated databases, are essential for the investigation of changes in parasite dynamics [51]. Integrated research frameworks, combining baseline data, field and experimental studies, traditional and molecular parasitology, as well as epidemiological and climatological modelling are needed to elucidate the role of climate change, invading species, and ecological perturbations in changing parasite fauna and pathogenicity [3]. Furthermore, increasing the role of local communities, who perhaps have the most to gain, but certainly have the most to give, is essential.

Arctic fauna can provide fascinating insights into wild-life ecology, relevant both locally and globally. Arctic parasites, as well as their hosts, are facing new challenges. The Arctic ecosystem is currently undergoing real and measurable climate changes, and the impacts of these on parasite lifecycles can already be observed, with shifts in transmission patterns and extended vector, host and parasite ranges. The significance of vector-transmitted parasites is increasing [48], and host switching could become an issue of relevance. Importantly, exploring Arctic parasitology can provide new and significant insights into ecology of parasitism elsewhere.

The extreme seasonality of the Arctic environment and the lack of other significant anthropogenic environmental perturbations allow investigation of impacts of climate changes on well-defined transmission windows. Thus, the relative simplicity of this system, coupled with a strong directional climate change signal, provides the opportunity for research that should enhance our understanding of parasite ecology [6]. Furthermore, comparisons between Arctic fauna and relocated satellite populations at the edge of their climatic range (e.g. muskoxen imported to Norway from Greenland during the past century [52]) can provide early warnings for potential threats to Arctic fauna resulting from alterations in the environment, such as climate change.

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