Patterns and processes influencing helminth parasites of Arctic coastal communities during climate change

K.V. Galaktionov[1,2]*

[1]Zoological Institute, Russian Academy of Sciences, St. Petersburg 199034, Russia: [2]Department of Invertebrate Zoology, St. Petersburg State University, St. Petersburg 199034, Russia

Abstract

This review analyses the scarce available data on biodiversity and transmission of helminths in Arctic coastal ecosystems and the potential impact of climate changes on them. The focus is on the helminths of seabirds, dominant parasites in coastal ecosystems. Their fauna in the Arctic is depauperate because of the lack of suitable intermediate hosts and unfavourable conditions for species with free-living larvae. An increasing proportion of crustaceans in the diet of Arctic seabirds would result in a higher infection intensity of cestodes and acantho-cephalans, and may also promote the infection of seabirds with non-specific helminths. In this way, the latter may find favourable conditions for colonization of new hosts. Climate changes may alter the composition of the helminth fauna, their infection levels in hosts and ways of transmission in coastal communities. Immigration of boreal invertebrates and fish into Arctic seas may allow the circulation of helminths using them as intermediate hosts. Changing migratory routes of animals would alter the distribution of their parasites, facilitating, in particular, their trans-Arctic transfer. Prolongation of the seasonal 'transmission window' may increase the parasitic load on host populations. Changes in Arctic marine food webs would have an overriding influence on the helminths' circulation. This process may be influenced by the predicted decreased of salinity in Arctic seas, increased storm activity, coastal erosion, ocean acidification, decline of Arctic ice, etc. Greater parasitological research efforts are needed to assess the influence of factors related to Arctic climate change on the transmission of helminths.

Introduction

Coastal and marine ecosystems are among the most productive ecosystems in the world (Brown *et al.*, 2006). The diverse and abundant fauna in intertidal and upper subtidal zones attracts huge numbers of predators: marine and coastal birds as well as marine and some terrestrial mammals. High concentrations of predators and prey are conducive to a wide occurrence of trophically transmitted helminths with complex life cycles. These parasites

exercise a considerable influence on the population dynamics of their hosts. They are also involved in food webs (and modify them), and in substance and energy flows. Last, but not least, they affect the composition, structure and functioning of coastal communities (e.g. Minchella & Scott, 1991; Galaktionov, 1993; Combes, 1996; Thomas *et al.*, 1998; Mouritsen & Poulin, 2002a, 2010; Dobson *et al.*, 2008; Kuris *et al.*, 2008; Lafferty *et al.*, 2008; Thieltges *et al.*, 2008).

It is therefore unsurprising that interactions between hosts and parasites in coastal communities are attracting increasingly more scientific attention. The emphasis has recently been shifting to the assessment of the possible

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*E-mail: kirill.galaktionov@gmail.com

impacts of climate change on the transmission of parasites. Global climate warming has an equally strong effect on the terrestrial and the marine biota. It may cause an increase in the development rate and productivity of parasites, an intensification of their transmission, range extension and expansions into new hosts (e.g. Marcogliese, 2001; Harvell *et al.*, 2002; Kutz *et al.*, 2005; Dobson *et al.*, 2008; Lafferty, 2009; Mas-Coma *et al.*, 2009; Polley *et al.*, 2010; Rohr *et al.*, 2011).

Trematodes, the dominant helminths in marine coastal ecosystems, have attracted considerable interest because of the expected increase in the water temperature and the prolongation of the warm season ('transmission window') favourable for their transmission (Marcogliese, 2001; Galaktionov *et al.*, 2006; Poulin, 2006; Poulin & Mouritsen, 2006). Trematodes differ from other helminths in having an obligatory stage of parthenogenetic reproduction in the molluscan host (in the case of Aporocotylidae, in the polychaete host) in their complex life cycle (Cribb *et al.*, 2003; Galaktionov & Dobrovolskij, 2003). The production of great numbers of dispersive larvae (cercariae) by the parthenitae (rediae or daughter sporocysts) provides a powerful boost for further passage of the life cycle, culminating in the adult worm in the final host. Since molluscan hosts are ectotherms, the reproduction of parthenitae depends greatly on the ambient temperature, and so does the life activity of free-living cercariae. Therefore, an increase in the water temperature in the coastal waters is likely to influence the transmission of trematodes in the first place.

Almost all studies of helminths circulating in coastal ecosystems have been carried out in boreal seas (<60°N). Coastal areas of the Arctic and the subarctic seas are poorly studied in parasitological respects (Galaktionov, 1996a, 2016; Hoberg *et al.*, 2013). At the same time, the climate change is especially pronounced in these regions. While a general increase in the surface air temperature by the end of the 21st century, as compared with 1986–2005, is forecast by different climatic scenarios to be, on average, 1–3.7°C, in the Arctic it is forecast to be 2.2–8.3°C (Stocker *et al.*, 2013). Besides, other effects associated with climate change would also be especially pronounced in the Arctic, such as the freshening of seawater, a decrease in the area of pack ice in the Arctic Ocean, erosion of seacoasts, permafrost melt, changes in the structure of currents, ocean acidification, etc. (Symon *et al.*, 2005; Stocker *et al.*, 2013). These processes have a profound impact on the biota of high latitudes, which explains a growing interest in their comprehensive study. Attempts to forecast the consequences of the ongoing transformation of Arctic ecosystems are being made (Phoenix & Lee, 2004; Meltofte *et al.*, 2013). Parasites circulating in Arctic coastal ecosystems, once their importance for ecosystem processes has been realized, have also come into focus in such studies (Hoberg *et al.*, 2013).

In this review, I have tried to identify the patterns of biodiversity, distribution and transmission of helminths in the coastal ecosystems of the Arctic seas. The review focuses on the helminths of seabirds, since they are the largest component of the fauna of parasites circulating in these ecosystems. Huge colonies (seabird cliffs) formed by birds on the Arctic coasts promote the transmission of parasites in coastal ecosystems. Trematodes play a

unique role in coastal communities and are comparatively better studied, therefore I give this helminth taxon most attention, especially when considering the effect of Arctic warming.

Biodiversity and distribution of helminths

Low biodiversity is a characteristic feature of the Arctic (Meltofte *et al.*, 2013). Helminths associated with coastal communities are no exception (Markov, 1941; Baer, 1956, 1962; Threlfall, 1968, 1971; Bishop & Threlfall, 1974; Hoberg, 1986; Galaktionov *et al.*, 1993; Galaktionov, 1996a; Kuklin, 2001; Hoberg *et al.*, 2013). The number of helminth species in the Arctic regions is much smaller than that in the nearshore areas of the boreal seas (fig. 1). There are almost no trematodes in the high Arctic (Markov, 1937, 1941; Baer, 1956; Galaktionov *et al.*, 1993; Galaktionov, 1996a; Kuklin, 2001). To give an example, the number of trematode species parasitizing the common eider, a seabird with the richest trematode fauna, decreases from 15 in The Netherlands (Borgsteede *et al.*, 2005) to a single species in Franz Josef Land (FJL) (Galaktionov *et al.*, 1993) (fig. 1b). These dramatic differences are due to the fact that intermediate hosts of most trematodes of the coastal complex are boreal invertebrates, which are absent in the Arctic. This is true, first of all, for molluscs, the obligate first intermediate hosts in the digenean life cycle. Digeneans, with a few exceptions, have a narrow host specificity for these invertebrates (Cribb *et al.*, 2003; Galaktionov & Dobrovolskij, 2003).

The recent meta-analyses of trematode richness in intertidal gastropods did not reveal any significant effect of latitude along European coasts (Poulin & Mouritsen, 2003; Thieltges *et al.*, 2009). These authors offered a reasonable explanation: the large-scale latitude effect is camouflaged by local factors (local abundance of final and intermediate hosts, the exposure level of the coast, etc.). These factors may prevent or, on the contrary, promote the transmission of trematodes at nearby coastal areas. Besides, only data on temperate regions (<60°N) were involved in that meta-analyses. If we take into account data on high latitudes, handle large regions to smooth the effect of the low-scale factors and use the annual surface seawater temperature (SST) rather than latitude as a predictor, we will get a decrease in the species richness of trematodes associated with intertidal gastropods (fig. 2). The use of the annual SST as a predictor is justified by the fact that the climate along the northern coast of Europe is mainly determined by the Gulf Stream and its influence weakens eastwards.

For instance, in the areas of northern Norway (southwest of the Barents Sea: Tromsø, 69°40′58″N, 18°56′34″E) and of the Kola Peninsula (south-east of the Barents Sea: Dalnie Zelentzy, 69°07′05″N, 36°03′30″E) situated at approximately the same latitude, the annual SST is 7.3°C and 4.8°C, correspondingly. This difference underlies a somewhat lower species richness of trematodes in the most common intertidal periwinkles *Littorina (Neritrema)* spp. in the latter area (fig. 2). The effect of decreasing trematode species richness in the boreal periwinkle *Littorina (Littorina) littorea* can be seen only at the northern distribution boundary of this species at the Barents Sea
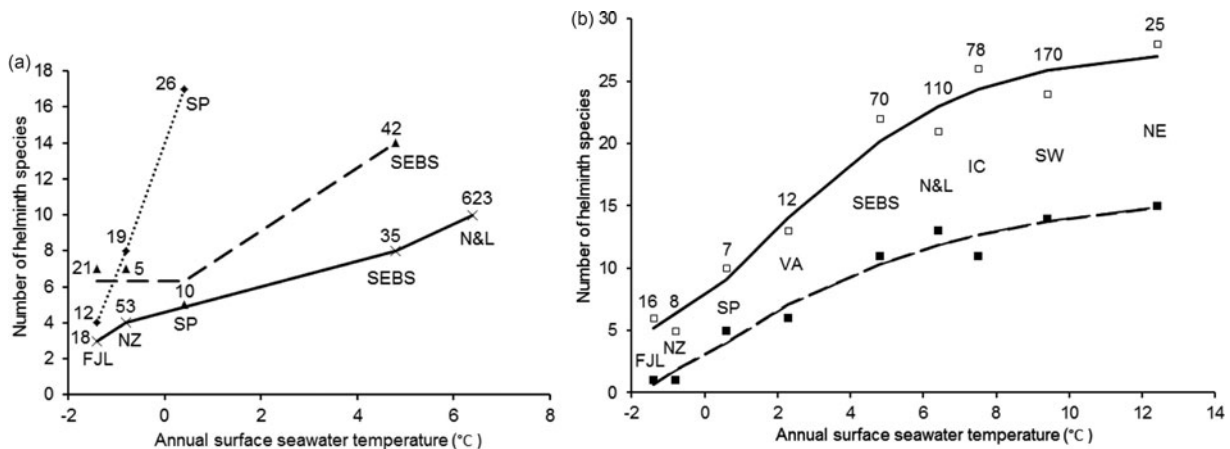
Fig. 1. Dependence of the number of parasite species (N) on the average annual surface seawater temperature (t, °C). A logistic regression model was used to construct the trend line [N = 1/(1 + e^(a + bt)) + c] since the dependence was non-linear (as indicated by a preliminary analysis of residuals of linear regression) and limited 'above' and 'below' by the tolerance temperature range of the host and/or the range of temperatures in which the life cycle of the parasite may be implemented. Numbers in the graph denote the number of birds examined in each of the regions. (Based on data in Markov (1937, 1941), Belopolskaya (1952), Threlfall (1971), Bishop & Threlfall (1974), Persson et al. (1974), Galaktionov et al. (1993), Galaktionov (1996a), Kuklin (2001), Borgsteede et al. (2005), Kuklin & Kuklina (2005), Kuklin et al. (2005), Skírnisson (2015) and our data.) (a) Thick-billed murre (Uria lomvia; ×, —); black-legged kittiwake (Rissa tridactyla; triangles, – –); glaucous gull (Larus hyperboreus; diamonds, .. …..); (b) common eider (Somateria mollissima): open squares (—), all helminth parasites; closed squares (– –), trematodes. FJL, Franz Josef Land; IC, Iceland; NE, The Netherlands; N&L, Newfoundland and Labrador; NZ, Novaya Zemlya; SEBS, south-east of the Barents Sea; SP, Spitsbergen; SW, Sweden; VA, Vaygach Island. Average annual surface seawater temperature (SST-AA) values: here and in fig. 2 SST-AA values were taken from the following sources. For different regions of the Barents Sea (FJL, NZ, SEBS, SP, south-west of the Barents Sea (SWBS), VA) values were taken from Tereschenko et al. (1985), Averintsev (1989), Loeng et al. (1992), Węsławski & Stempiewicz (1995), Adrov & Denisenko (1996) and Denisenko (2013), for the White Sea (WS) they were taken from Babkov (1998) and for other regions, from the website World Seawater Temperatures (https://www.seatemperature.org/)

coast of the Kola Peninsula, where these molluscs are not infected with trematodes (Chubrik, 1966; Podlipaev, 1979; our data). This is probably due to the low density of L. littorea, since trematodes recorded in this snail in northern Norway (Cryptocotyle lingua, Podocotyle atomon, Himasthla sp., Microphallus pygmaeus and Microphallus similis) circulate in the nearshore areas of the Kola Peninsula using periwinkles Littorina saxatilis, L. obtusata and L. compressa (Chubrik, 1966; Podlipaev, 1979; Galaktionov & Rusanov, 1983; Galaktionov & Bustnes, 1999) as first intermediate hosts.

The absence of suitable intermediate hosts, or their low density, are not the only reasons preventing the dispersion of trematodes into the Arctic. Certain features of their life cycles also play an important role. A rich fauna of trematodes associated with intertidal molluscan hosts has been described from the coast of Great Britain and the Atlantic coast of France (fig. 2). Intermediate and final hosts of most of these trematodes also occur in the nearshore areas of Iceland and Norway (south-west of the Barents Sea) but there the trematode fauna associated with these molluscs is much poorer (fig. 2). The reason is that the life cycle of these trematodes includes miracidia and/or cercariae, that is, stages active in the environment. They seem to be very vulnerable to the extreme environmental conditions of the Arctic coasts, making further distribution of boreal trematode species northwards impossible (Galaktionov & Bustnes, 1999).

Few coastal trematodes (less than 20–30%) have free-swimming miracidia. In most of them, the miracidium hatches only after the ingestion of the egg by the molluscan host (Galaktionov, 2016). However, most species of coastal trematodes (up to 80–90% in boreal waters) have free-living cercariae (Galaktionov, 2016). This difference is due to the fact that the loss of the free-living miracidium does not hamper transmission much: the dispersive potential of these microscopic (up to 200 μm) larvae is low. In contrast, cercariae, first, have a much broader dispersion than miracidia because of their own activity, and, second, infect the second intermediate hosts (invertebrates or fish). These hosts ensure the spatial dispersion of the parasites and the transmission of infection to the final host via food web links. Therefore, the loss of free-living cercariae has an adverse effect on transmission. These considerations explain the success of trematode species with three-host life cycles (Cribb et al., 2003; Galaktionov & Dobrovolskij, 2003).

On the other hand, two-host life cycles – especially the so-called autonomous life cycles lacking larvae active in the environment – are effective for transmission in ecosystems with extreme environmental conditions, including those of the Arctic intertidal zone. The most common trematodes with two-host life cycles in the nearshore areas of northern Palaearctic seas are microphallids of the 'pygmaeus' group (MPG). Their first intermediate hosts, periwinkles Littorina spp., become infected by ingesting eggs containing miracidia, and metacercariae develop inside the daughter sporocysts parasitizing the molluscan host. The MPG dominate among trematodes associated with intertidal molluscan hosts Littorina (Neritrema) spp.
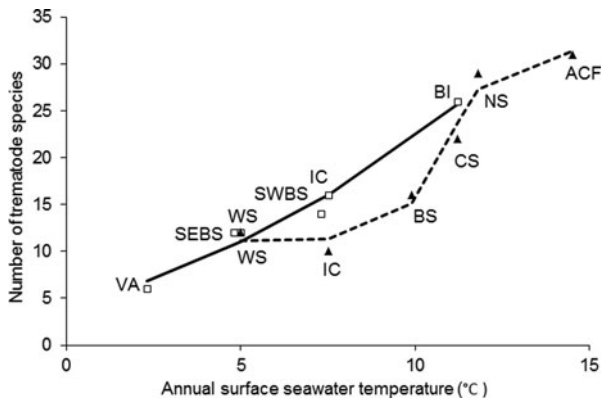
Fig. 2. Dependence of the number of trematode species (N) associated with intertidal molluscs *Littorina* spp. (open squares, ——) and *Hydrobia* spp. (triangles, – –) in different parts of the European seacoast on the average annual surface seawater temperature (SST-AA). A logistic regression model was used to construct the trend line ($N = 1/(1 + e^{(a + bt)}) + c$) (see legend to fig. 1). The number of molluscs examined in each of the regions was more than 1000. (Based on data in Chubrik (1966), James (1968a, b, 1969), Combescot-Lang (1976), Podlipaev (1979), Lauckner (1980), Deblock (1980), Irwin (1983), Matthews *et al.* (1985), Galaktionov & Bustnes (1999); Galaktionov & Skírnisson (2000), Skírnisson & Galaktionov (2002, 2014), Skírnisson *et al.* (2004), Thieltges *et al.* (2009) and our data.) ACF, Atlantic coast of France; BI, British Isles; CS, Celtic Sea; BS, Baltic Sea; NS, North Sea; IC, Iceland; SEBS, south-east of the Barents Sea; SWBS, south-west of the Barents Sea; VA, Vaygach Island; WS, White Sea.

regarding the frequency of occurrence everywhere along the southern coast of the Barents Sea (Galaktionov & Bustnes, 1999) (fig. 3). There is a clear trend towards increasing frequency of occurrence of MPG in the areas with a more pronounced Arctic climate (eastwards) (fig. 3b). The prevalence of these trematodes first grows, reaching a maximum at the longitudes 30–40°E (White Sea, the southern coast of the Barents Sea), and then decreases abruptly, sinking to a minimum at the Arctic coast of Vaygach and Novaya Zemlya (55–60°E) (fig. 3c).

The western coast of these islands coincides with the north-eastern boundary of the distribution of *L. saxatilis*. This species advances further into the Arctic than any other periwinkle. It seems that even MPG cannot do well under the hostile conditions of the Arctic nearshore waters. Optimal conditions for their transmission are associated with subarctic regions such as the White Sea and the Barents Sea coast of the Kola Peninsula. Further westwards (Varanger-fjord and Tromsø) the prevalence of MPG decreases, while the frequency of occurrence and the prevalence of trematodes with three-host life cycles, including free-living larval stage(s), increase considerably (fig. 3d). This trend strengthens further into boreal waters. In south-west Iceland, trematodes with two-host life cycles and those with three-host cycles have similar values of these parameters (Skírnísson & Galaktionov, 2002). On the coast of the British Isles and the Atlantic coast of France, trematodes with three-host life cycles and free-living cercariae reign supreme, while MPG are scarce (James, 1968a, b, 1969; Combescot-Lang, 1976; Irwin, 1983; Saville *et al.*, 1997; Galaktionov *et al.*, 2004).
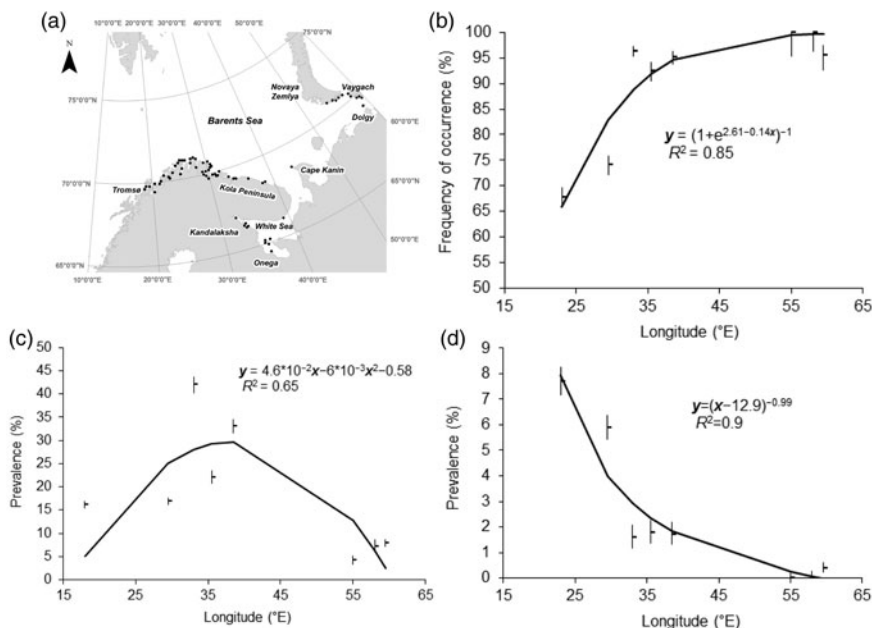

Fig. 3. Distribution of intramolluscan stages of trematodes parasitizing seabirds in periwinkles *Littorina (Neritrema)* spp. along the southern coast of the Barents Sea (based on data in Galaktionov & Bustnes, 1999). Error bars are confidence intervals. The number of periwinkles examined in each of the regions was in the range of 1500–10,000. (a) The distribution of sampling stations; (b) frequency of occurrence of trematodes with two-host life cycles (predominantly MPG) as a function of longitude; (c) prevalence of trematodes with two-host life cycles as a function of longitude; (d) prevalence of trematodes with three-host life cycles as a function of longitude.

Cestodes (Tetrabothriidae, Dilepedidae, Aploparaksidae, Hymenolepididae) and acanthocephalans (Polymorphidae, Filicolidae) that parasitize seabirds have no free-living larvae. This eliminates an important obstacle on their way into the Arctic. Intermediate hosts of these parasites are crustaceans, which are abundant in the nearshore areas of the Arctic seas. For these reasons, the fauna of cestodes and acanthocephalans in the Arctic is less depauperate than that of trematodes (Markov, 1941; Baer, 1956, 1962; Threlfall, 1968, 1971; Hoberg, 1986; Galaktionov, 1996a; Kuklin, 2001; Hoberg et al., 2013). Cestodes (e.g. Lateriporus spp., Alcataenia spp., Microsomacanthus spp., Tetrabothrius spp.) and some acanthocephalans (e.g. Polymorphus phippsi and Corynosoma strumosum) circulate successfully both in the high Arctic and in the coastal ecosystems of lower latitudes (Threlfall, 1968, 1971; Leonov & Belogurov, 1970; Leonov et al., 1970; Bishop & Threlfall, 1974; Leonov, 1979; Bakke, 1985; Galkin et al., 1994; Kuklin & Kuklina, 2005, 2013; Regel & Atrashkevich, 2008). At the same time, some species of cestodes and acanthocephalans do disappear, similarly to trematodes, in the higher latitudes because of the absence, or a low density, of intermediate hosts.

One such species is the acanthocephalan Profilicollis botulus, a common parasite of waterfowl in North Atlantic seas. Its intermediate hosts, decapods (Petrochenko, 1958; McDonald, 1988), are mainly represented in boreal waters by the green crab (Carcinus maenas) (Thompson, 1985). In the south-eastern part of the Barents Sea, where the green crab does not occur, the cystacanths of P. botulus develop in crabs Hyas araneus and hermit crabs Pagurus pubescens (Uspenskaya, 1963). In the north-west of the Barents Sea and in the nearshore areas of the Arctic archipelagos Novaya Zemlya and FJL, these decapods are rare and the transmission of P. botulus cannot be successful (Galaktionov et al., 1993). Notably, the acanthocephalan P. phippsi, which is common in these areas, uses amphipods as intermediate hosts, which are abundant in the nearshore areas of the Arctic archipelagos.

The circulation ways of most nematodes parasitizing seabirds in the Arctic and the Subarctic (representatives of Capillariidae, Streptocaridae, Acauriidae, Anisakidae and some other families) are unknown. Anisakid nematodes Anisakis simplex, Pseudoterranova decipiens and Contracaecum osculatum, which are very common in marine ecosystems, use various invertebrates (mainly crustaceans) and fish as intermediate hosts (Nagasawa, 1990; Andersen et al., 1995; Køie & Fagerholm, 1995). These nematodes can reach maturity only in marine mammals, while fish-eating birds, where their larvae are often found, are the dead end of their development. Curiously, anisakid nematodes (single individuals) were only recorded at FJL from the thick-billed murres (Uria lomvia) (our data) although there are many marine mammals in the area. This might be due to the small proportion of fish in the diet of birds at FJL (see below).

Spirurid nematodes Paracuaria adunca, P. tridentata, Cosmocephalus obvelatus and Streptocara crassicauda, which are common in fish-eating seabirds, use crustaceans as intermediate hosts (mysids, amphipods) and fish as paratenic hosts (Anderson & Wong, 1982; Wong & Anderson, 1982; Marcogliese, 1992; Anderson, 2000). Similarly to anisakids, these nematodes have no larvae in the environment (Anderson, 2000). This promotes their circulation

in the coastal ecosystems of the Arctic seas. Spirurid nematodes have been recorded from birds at Svalbard and FJL (Kuklin et al., 2005; Kuklin & Kuklina, 2013; our data).

Birds in the high Arctic do not harbour helminths whose life cycles are associated with freshwater or terrestrial ecosystems. The only known exception is that of strongylid nematodes Amidostomum sp. found in the common eider at FJL (our data). Their larvae either penetrate the final host actively via the skin or are swallowed with food or water (McDonald, 1969; Baruš et al., 1978; Anderson, 2000; Borgsteede et al., 2006). It is unclear where the common eider becomes infected – on land, where females spend a long time during the nesting period, or also in the sea (Borgsteede et al., 2006). Amidostomum sp. seems to spend the cold season in the host and implements the part of their life cycle in the environment during the short Arctic summer. It is unknown whether its eggs and larvae can survive the long winter freezing, although this may well be so, since freezing tolerance has been reported for soil nematodes of the polar regions (Treonis & Wall, 2005; McGill et al. 2015)

'Borealization' – colonization of high latitudes by boreal species – is one of the consequences of Arctic warming (Payer et al., 2013). Among the boreal species advancing into the Arctic are marine invertebrates and fish (e.g. Berge et al., 2005, 2009; Węsławski et al., 2010, 2011; Denisenko, 2013; Josefson et al., 2013; Kędra et al., 2015). Some of them are the intermediate hosts of helminths circulating in the nearshore areas of boreal seas. The presence of suitable hosts and the climate warming in the Arctic might allow these parasites to carry out their life cycles in high latitudes. In particular, one may expect trematode species with three-host life cycles and the stage of free-living cercaria to advance into Arctic regions. This hypothesis is supported by observations in the nearshore areas of Svalbard. The south-western coast of western Spitsbergen, the largest island of the archipelago, is washed by the warm West and South Spitsbergen Currents (branches of the North Atlantic Current, which is an extension of the Gulf Stream). Owing to these warm currents, some boreal molluscs such as L. littorea, L. saxatilis, Cryptonatica clausa and Onoba aculeus (Golikov & Kusakin, 1978; Koszteyn et al., 1991) occur there. This, in turn, makes possible the circulation of several trematode species with three-host life cycles associated with them (Kuklin et al., 2005; Kuklin & Kuklina, 2013).

The ongoing climate changes also affect the final hosts of parasites. Many birds have already extended their distribution northwards, and this process is likely to intensify (Newton, 2003; Rehfisch & Crick, 2003; Valiela & Bowen, 2003; Sparks et al., 2005; Ganter et al., 2013). Some of the helminths parasitizing these birds may find favourable conditions for the implementation of their life cycles in the Arctic ecosystems transformed by the warming. This would result in the northwards expansion of these parasites.

Helminth abundance and host colonization

Crustaceans are abundant in Arctic nearshore waters, while the abundance of fish is relatively low. For these

reasons, crustaceans, especially amphipods, are an important component of the seabird diet (Belopolsky & Shuntov, 1980; Lydersen *et al.*, 1989; Mehlum & Gabrielsen, 1993; Węsławski *et al.*, 1994). This means that seabirds in the Arctic are quite heavily infected with cestodes and acanthocephalans, which use crustaceans as intermediate hosts (Baer, 1956, 1962; Threlfall, 1968, 1971; Leonov & Belogurov, 1970; Leonov *et al.*, 1970; Bishop & Threlfall, 1974; Galaktionov *et al.*, 1993; Galaktionov, 1996a, b; Kuklin, 2001; Kuklin & Kuklina, 2005; Kuklin *et al.*, 2005). For instance, at FJL the infection intensity of the common eider (*Somateria mollissima*) with cestodes *Microsomacanthus* spp. reaches 200,000 individuals, and that with the acanthocephalan *P. phippsi* reaches 1000 individuals (Galaktionov, 1996a). In the south of the Barents Sea the maximum values of this parameter are 19,500 individuals for *Microsomacanthus* spp. and 247 individuals for *P. phippsi*, while at the White Sea these values are 55,000 individuals and 57 individuals, respectively (Belopolskaya, 1952; Kulachkova, 1979). This is unsurprising, since amphipods are the second largest component of the diet of the common eider at FJL after the molluscs *Margarites* spp. (Węsławski *et al.*, 1994). Further south, the common eider feeds mostly on blue mussels and some other bivalve and gastropod species (Bianki *et al.*, 1979; Krasnov *et al.*, 2009).

A high infection intensity of seabirds in the Arctic with cestodes and acanthocephalans is bound to influence their population dynamics. All these helminths are pathogenic for their hosts and may cause death, especially in chicks, if the infection is intensive (Clark *et al.*, 1958; Garden *et al.*, 1964; Kulachkova, 1979; Itamies *et al.*, 1980). The negative impact of helminths on seabirds may be not so evident but is nevertheless important (Galaktionov, 1996b; Thieltges *et al.*, 2006). Breeding success of the common eider nesting in the north of Norway was found to decrease as a consequence of infection with intestinal parasites (Warelius, 1993). Antiparasite treatment of female eiders in low body condition, which had lost or abandoned their nests, considerably increased their chances of next-year reproduction compared with untreated individuals (Hanssen *et al.*, 2003). Bustnes *et al.* (2006) showed that in glaucous gulls nesting on Bear Island (Norwegian Arctic) helminths may be an important factor in triggering negative effects of organochlorine pollutants on reproduction. In addition, the negative effect of parasitism may also be aggravated by the extreme environmental conditions in the Arctic.

An increasing proportion of crustaceans in the diet of birds in the Arctic promotes the colonization of non-specific final hosts by helminths. Non-specific parasitism – the occurrence of parasites in unusual host species – is characteristic of cestodes and acanthocephalans parasitizing Arctic birds. For instance, at Svalbard the cestodes *Microsomacanthus diorchis* and *M. microsoma*, which typically parasitize anatids, were recorded from black-legged kittiwakes and glaucous gulls. These birds were also found to harbour dilepidid cestodes *Arctotaenia tetrabothrioides*, earlier recorded only in shorebirds (Kuklin *et al.*, 2005). All these cestodes were mature, and their intensity of infection was considerable, especially in glaucous gulls (*M. diorchis*, up to 254 individuals; *A. tetrabothrioides*, up to 154 individuals).

The acanthocephalan *P. phippsi* is a vivid example of non-specific parasitism (Galaktionov & Atrashkevich, 2015). Its final host in the Arctic is the common eider, but it has also been recorded from some other birds such as gulls, guillemots and the purple sandpiper (*Calidris maritima*). These birds mostly serve as eliminative hosts for *P. phippsi*. However, some individuals of this acanthocephalan can reach maturity in the black-legged kittiwake (*Rissa tridactyla*), the Arctic turn (*Sterna paradisaea*), the little auk (*Alle alle*) and, probably, in Sabine's gull (*Xema sabini*). Calculations for one of the FJL areas showed that infection flows through these hosts were very low (Galaktionov & Atrashkevich, 2015) (fig. 4). Nevertheless, it is a case of a parasite colonizing new hosts, phylogenetically unrelated to the main one. The extreme conditions of the Arctic seem to promote this process. Arctic birds expend more energy on the maintenance of physiological processes as compared to birds in southern areas, including greater energy expenditure on the maintenance of the optimal body temperature. This may reduce expenditure on the maintenance of a high-level immune status. This, in turn, promotes the survival and development of parasites in non-specific hosts.

This state of things may be compared with that in coastal refugia of the northern Holarctic during the Quaternary glacials. As ice advanced along the Atlantic and the Pacific coast of the mainland and islands, marine refugia were formed. Seabirds and marine mammals that accumulated in these refugia fed on the same available foods. Hoberg (1992, 1995) and Hoberg & Adams (1992, 2000) suggested that such a situation opened new vistas for colonization of new hosts and thus accelerated speciation via host switching (the Arctic refugium hypothesis). In a way, the present-day conditions of parasites' transmission in the high Arctic are comparable with those in the glacial refugia. The instances of non-specific parasitism can be considered as a model demonstrating different stages of lateral incorporation (*sensu* Parker *et al.*, 2015) of new hosts, which may result in speciation of helminths.

The cestode *Microsomacanthus ductilis* (Linton, 1927) *sensu* Galkin *et al.*, 1999 deserves mention in this respect. It has been recorded in the common eider at FJL and in some seaducks at Chukotka (Galkin *et al.*, 1999; Regel, 2005). This species is remarkably close to *M. ductilis* (Linton, 1927), a typical parasite of gulls, which might indicate that it formed by host switching under Arctic conditions.

The rising temperature of waters over the Arctic shelves (due to increasing area and duration of open water) is likely to result in an increase in the abundance and biomass of boreal species, including zooplankton. Pelagic-feeding animals (some fish, marine mammals and seabirds) may consequently increase in abundance (Kędra *et al.*, 2015). This may promote the intensification of transmission of helminths and their increasing load on the host populations. However, climate warming is also likely to bring about considerable changes in the Arctic marine food webs (Węsławski *et al.*, 2011; Kędra *et al.*, 2015). This would have a negative impact, first of all, on ice-depending organisms, such as some crustaceans and some fishes. Increased pelagic grazing and recycling in the water column may lead to a decrease in the biomass
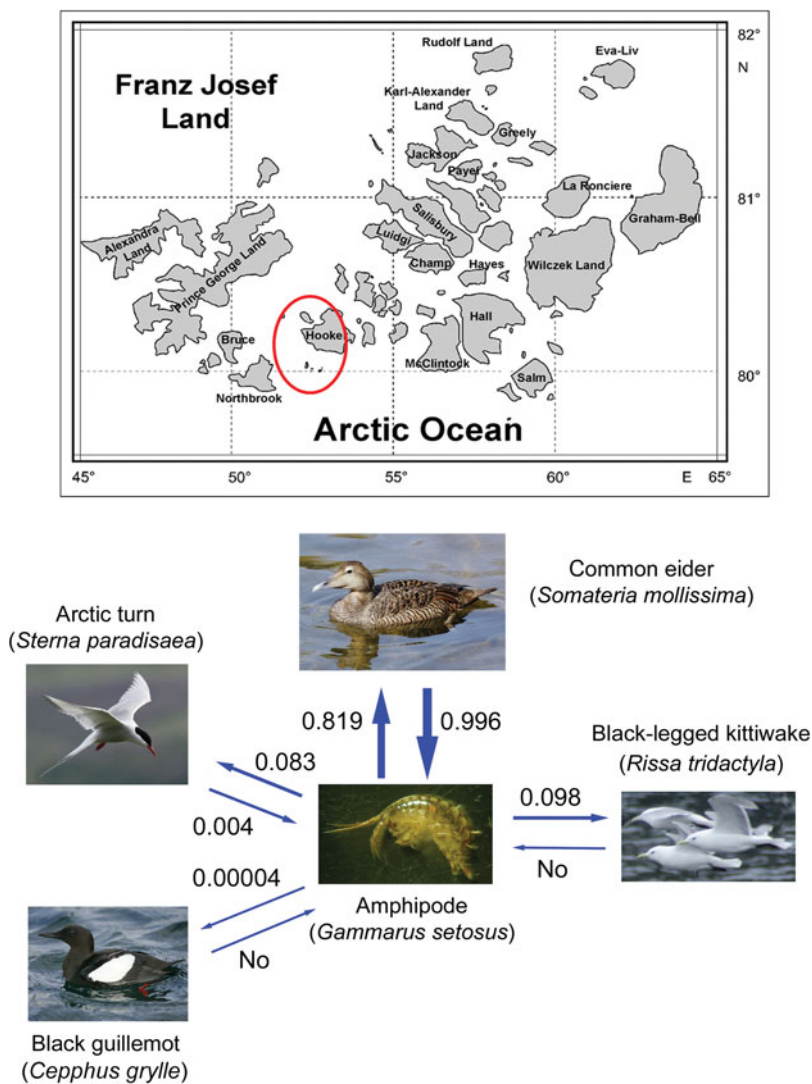
Fig. 4. Flowchart summarizing circulation and transmission dynamics of the acanthocephalan *Polymorphus phippsi* at Franz Josef Land (modified from Galaktionov & Atrashkevich, 2015). The study area (vicinity of the islands Hooker, May and Etteridge) is marked with a red oval; all numbers are proportions.

of benthic species, including intermediate hosts of helminths. The change in the species composition of zooplankton (which is already being observed), the penetration of boreal fish species into the Arctic waters and their growing abundance may shift (are, in fact, shifting – see Kidawa *et al.*, 2015) priorities in the food choice by seabirds. The consequences for the transmission of helminths are difficult to predict. They would depend on the life-cycle features of the given parasite species and the impact of these changes on the hosts.

Transarctic transfer of helminths: retrospectives and perspectives

The modern parasitic fauna of marine mammals and birds of the Arctic areas of the Atlantic and the Pacific formed in the course of the Pleistocene glacial cycles, numbering *c*. 20 events (Hoberg, 1992, 1995; Hoberg & Adams, 1992, 2000; Waltari *et al.*, 2007; Hoberg & Brooks, 2008). The exchange between the faunas of the North Atlantic (NA) and North Pacific (NP) was interrupted during glacials/stadials, but was resumed to some extent during warm interstadials/interglacials. The dispersive potential of heteroxenous helminths is usually thought to be associated with the activity of the most vagile host in their life cycle. In this way, the modern composition of the cestode fauna of marine mammals and birds of NA and NP was determined by transarctic migrations of these hosts. These migrations became possible during some interstadials/interglacials of the Pleistocene (Hoberg, 1992, 1995; Hoberg & Adams, 1992, 2000). Two other factors contributed to this process: the lack of narrow specificity of cestodes to their intermediate hosts,
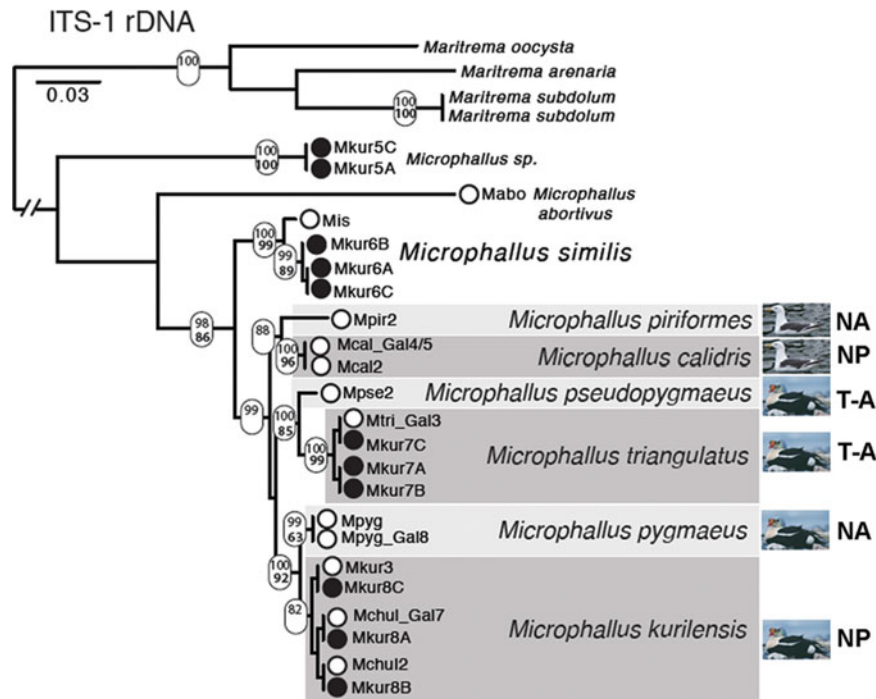
Fig. 5. Bayesian inference phylogram of microphallids of the '*pygmaeus*' group (MPG) derived from internal transcribed spacer 1 (ITS1) rRNA gene sequences with posterior probability and bootstrap percentage values above and below, respectively, within ellipses (modified from Galaktionov *et al.*, 2012). Black dots indicate adult specimens sequenced, whereas white dots indicate sporocysts or metacercariae stages sequenced. The main final hosts for each MPG species are indicated by the sign of the corresponding bird (gull or eider). Range of MPG species is indicated by letters (NA, North Atlantic; NP, North Pacific; T-A, transarctic).

crustaceans and fish (if they serve as second intermediate or paratenic hosts) and the broad transarctic distribution of many of these host species.

Although vertebrate hosts are extremely important for the geographic expansion of helminths, their vagility is not the only factor deciding the character of the expansion. In trematodes, with their narrow specificity to the first intermediate (molluscan) host, it is the range of the least vagile host that limits distribution (Brooks *et al.*, 2006; Miura *et al.*, 2006; Galaktionov *et al.*, 2012). For instance, there are MPG species (*Microphallus calidris* and *M. kurilensis*) whose distribution area is limited to NP as well as MPG species (*M. pygmaeus* and *M. piriformes*) with a NA distribution (fig. 5). The most vagile final hosts in their life cycle, marine and coastal birds, do not make transarctic migrations nowadays. Birds from the Pacific populations fly as far eastwards as the Taimyr Peninsula, where they may encounter birds from the Atlantic populations (Johnson & Herter, 1990; Dau *et al.*, 2000; Webster *et al.*, 2002; Petersen *et al.*, 2006; Alerstam *et al.*, 2007; Bustnes *et al.*, 2010). However, at the coast of the Siberian seas, including the Taimyr nearshore waters, periwinkles, the first intermediate hosts of MPG, do not occur at present (Reid, 1996). They are also absent in the Beaufort Sea and at the coast of the Canadian Arctic Archipelago (Reid, 1996). This prevents the transmission of the MPG species in question in these areas and, correspondingly, limits the possibilities of genetic exchange between the Atlantic and the Pacific populations of these

species (Galaktionov *et al.*, 2012). At the same time, one MPG species, *Microphallus pseudopygmaeus*, uses numerous species of gastropods as the first intermediate hosts, including the subtidal *Margarites helicinus*, *M. groenlandicus umbilicalis* and *Cryptonatica clausa*, widely distributed in the nearshore areas of Arctic seas. Unsurprisingly, *M. pseudopygmaeus* has a transarctic distribution. The reasons why the same distribution formed in *Microphallus triangulatus* are as yet unclear.

Besides the vagility of the host and the availability of suitable first intermediate hosts, an important factor contributing to successful colonization of new geographic areas by trematodes are the life-cycle characteristics. One of these is the lifespan of parasites in the most vagile host. For example, the trematode *Tristriata anatis* (Notocotylidae), which has a two-host life cycle with cercariae encysting in the open, circulates in the same range of hosts (molluscan hosts *Littorina* spp. – waterfowl birds) and in the same geographic regions (nearshore waters of the northern Palaearctic seas) as MPG. The formation of *T. anatis* and MPG was accompanied by the same historical events. However, in contrast to MPG, representatives of *T. anatis* in NA and in NP did not diversify further than geographic races, identified by sequence analysis of the mitochondrial gene CO1 (Gonchar & Galaktionov, 2017).

This difference appears to be associated with a different lifespan of these parasites. Adult MPG never live for more than 7–10 days in the final host (Galaktionov, 1993), while

adult notocotylids may survive for months (Filimonova, 1985). A greater longevity of *T. anatis* adults seems to have increased the probability of their transarctic transfer by migratory birds. In this way, the eggs of these parasites were more likely to get into the areas of the NA and NP where periwinkles occurred. This could happen repeatedly during warm Quaternary interglacials/interstadials (e.g. during the most recent interglacial, the Eemian (from 130 ky BP to about 107 ky BP), when the climate was warmer than at present), ensuring a rather intensive gene flow between the Atlantic and the Pacific populations of *T. anatis*. The gene flow between them ceased during the last Ice Age and never resumed because of the modern distribution of periwinkles (see above) and the migratory pathways of birds in the northern Palaearctic.

The above considerations indicate that the interpenetration of the Pacific and the Atlantic parasitic faunas may be one of the consequences of Arctic warming. The ongoing borealization of the Arctic and the changes in the migratory pathways of the intermediate and the final hosts of helminths contribute further to this process. There is also an example of a helminth of Pacific birds penetrating into the Atlantic. The cestode *Alcataenia longicervica*, previously considered as endemic to the Pacific Ocean (Hoberg, 1986), has recently been found in Atlantic populations of murres (*Uria aalge* and *U. lomvia*) (Muzaffar *et al.*, 2005; Muzaffar, 2009). The intermediate hosts of this cestode are planktonic euphausiids *Thysanoessa* spp. These crustaceans are probably responsible for the penetration of *A. longicervica* into Atlantic populations of murres. Pacific euphausiids, abundant in the Bering Sea, the Chukchi Sea and the Beaufort Sea, made it into the nearshore waters of Siberia and Labrador as a result of the changing structure of currents due to Arctic warming. Some of them were infected with the larvae of *A. longicervica*, which, in this way, arrived at the border of the distribution area of the Atlantic populations of murres (Muzaffar, 2009).

Temperature and transmission of helminths

Parasite transmission in ecosystems is controlled by environmental temperature. It has a huge influence on the development of parasites in intermediate hosts (mostly ectothermic animals), the emergence of larvae into the environment, their infectivity and the process of host infection (Marcogliese, 2001; Mouritsen & Poulin, 2002b; Pietrock & Marcogliese, 2003; Poulin, 2006; Poulin & Mouritsen, 2006; Thieltges & Rick, 2006; Studer *et al.*, 2010; Morley & Lewis, 2013, 2014, 2015). One might assume that a lower transmission rate in cold waters results in lower infection levels of marine organisms. However, this idea was not supported by recent studies of marine bivalve infection with trematode metacercariae across a broad latitude (and temperature) range. Studer *et al.* (2013b) found no significant differences in the infection rates of cockles *Austrovenus stutchburyi* with metacercariae of *Curuteria* spp. and *Acanthoparyphium* spp. along the coast of New Zealand (12° latitude gradient, *c.* 7°C annual temperature range (12–18°C)). Similar data were obtained by Galaktionov *et al.* (2015), who analysed the infection of blue mussels *Mytilus edulis* with metacercariae of *Himasthla* spp., *Renicola* spp. and *Gymnophallus bursicola*

on the coasts of northern Palaearctic seas from Ireland in the south-west to the Barents Sea in the north-east (latitude and longitude gradients were 14° and 81°, respectively; 14°C gradient of maximal SST (8–22°C)). The influence of the temperature is often camouflaged by local factors, such as a local abundance of final hosts, the density of intermediate hosts, sheltered or exposed shore, etc. (Studer *et al.*, 2013a, b; Wilson *et al.*, 2013; Galaktionov *et al.*, 2015) but, as it turns out, not only by them.

According to recent meta-analyses, the average daily cercarial output (the number of larvae shed by an infected marine mollusc, on average, during 24 h) does not differ significantly in low (≤35°N) and middle (36–60°N) latitudes (Thieltges *et al.*, 2008; Studer & Poulin, 2014). Moreover, it does not differ considerably from the cercarial output recorded by Prokofiev *et al.* (2016) in the same or closely related trematode species at the White Sea (66°N). This is due to the high acclimation potential of trematodes, underlying a broad variation of the optimal temperature range for the transmission of their larvae at different latitudes (Morley & Lewis, 2013, 2014, 2015).

Cercarial development, emergence and survival, as well as the survival of miracidia, are not much influenced by temperature over optimum temperature ranges (Morley, 2011, 2012; Morley & Lewis, 2013, 2015). For instance, average daily cercarial output of *Renicola* spp. from the molluscan hosts *L. littorea* and *Nucella lapillus* is similar at the Barents Sea (69°N) and the White Sea (66°N) (fig. 6), and does not differ significantly from that of *R. roscovita* from *L. littorea* in the Wadden Sea (54°N) (Prokofiev *et al.*, 2016). However, in the Wadden Sea, cercarial emergence stops altogether when the water cools down to 10°C (Thieltges & Rick, 2006). In the White Sea, cercarial emergence of *Renicola* spp. remains stable at 10°C, but the average daily cercarial output decreases *c.* threefold as compared with that at the optimal temperature (15–22°C). At the Barents Sea, 10°C falls within the temperature range optimal for cercarial emergence (Prokofiev *et al.*, 2016).

Besides the shift of the temperature optimum of cercarial emergence, there is at least one more temperature-associated phenomenon contributing to the levelling-out of the differences in the average daily cercarial output at different latitudes (Prokofiev *et al.*, 2016). In the nearshore areas of temperate and even subarctic seas, the differences between the minimum and the maximum daily values of temperature and light intensity are quite large, as compared with Arctic seas. During our study of the rhythms of cercarial emergence at the intertidal of the White Sea and the Barents Sea, the amplitude of daily temperature at the White Sea was 10–15°C and that of light intensity was tens to hundreds thousands lux, while at the Barents Sea the corresponding values were 3–4°C and 200 lux (Prokofiev *et al.*, 2016). A rapid increase in the temperature and light intensity stimulated a mass emergence of cercariae of the White Sea species. As a result, almost all the accumulated mature larvae left the molluscan host over a relatively short period, after which the emergence stopped for some time ('precipitous emergence') (fig. 7a). At the Barents Sea, considerably fewer cercariae emerged in a unit of time but the emergence lasted over a longer period ('prolonged emergence') (fig. 7b). In this way, trematodes at the Barents Sea can release considerable numbers
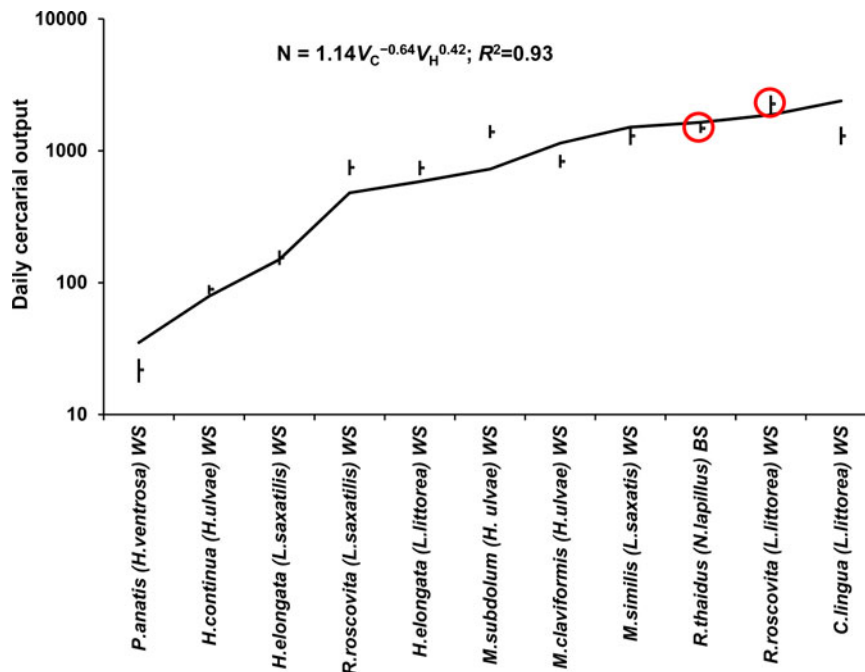
Fig. 6. Daily cercarial output (DCO) (number cercariae/snail per day; *N*) of trematode species parasitizing intertidal snails in the White Sea and the Barents Sea (molluscan species are indicated in parentheses) as a function of cercarial size (cercarial volume, mm³; V_C) and snail host size (shell volume, mm³; V_S). The set of expected (line) and observed values (dots with bars; bars mark 95% confidence intervals) of DCO is arranged in the order of ascending expected DCO value (based on data in Prokofiev *et al.*, 2016). The trematode species mentioned in the text are indicated by red ovals. Trematode species: *Paramonostomum anatis*, *Himasthla continua*, *H. elongata*, *Renicola roscovita*, *R. thaidus*, *Maritrema subdolum*, *Microphallus claviformis*, *M. similis* and *Cryptocotyle lingua*. Molluscan host species: *Littorina littorea*, *L. saxatilis*, *Hydrobia ulvae*, *H. ventrosa* and *Nucella lapillus*. BS, Barents Sea; WS, White Sea.

of cercariae during the day – almost as many as in boreal seas (fig. 6). This adaptation is one of the keys to the success of trematode transmission in the intertidal ecosystems of cold-water seas.

Acclimation potential of parasites, although considerable, is not unlimited. In the nearshore areas of Arctic and subarctic seas, the development and transmission of parasites are possible only during the warm season, the 'transmission window'. At that time, all categories of host necessary for the implementation of the parasites' life cycle are present, while the water is warm enough for the free-living stages to find and infect intermediate hosts. For trematodes at the White Sea, a temperature of 3–5°C blocks cercarial emergence from the infected molluscan hosts (fig. 8). If this temperature persists, the formation of embryos in the parthenitae stops temporarily, and their groups come into the state of developmental arrest (Galaktionov *et al.*, 2006). The same applies to the larvae contained in eggs in the environment. In experiments where the White Sea molluscan hosts *Hydrobia ulvae* were infected with the eggs of trematodes *Bunocotyle progenetica*, the eggs ingested by mudsnails passed through their gut in intact condition at 4°C: miracidia did not hatch and the molluscan host remained uninfected (Galaktionov *et al.*, 2006).

The effect of temperature on cercarial emergence is certainly not the only impact of this factor on the life activity and transmission of marine trematodes. Locomotor activity of the larvae, their infectivity and lifespan, as well as reorganization in the group of parthenitae (sporocysts and rediae) in the molluscan host, also depend on temperature (Galaktionov *et al.*, 2006; Thieltges & Rick, 2006; Studer *et al.*, 2010; Studer & Poulin, 2014). Besides, cercariae show high interspecific and intraspecific variations in their response to temperature, which should also be taken into account (Koprivnikar & Poulin, 2009; Koprivnikar *et al.*, 2010; Morely, 2011; Studer & Poulin, 2014). All these impacts are superimposed on local factors of the habitat, which may favour or prevent the transmission of a given trematode species. The totality of these factors makes a general assessment of the consequences of the climate warming on trematode transmission difficult. One can only say that these impacts are likely to be species-specific in different localities.

We may, however, conclude that, contrary to some earlier suggestions (Marcogliese, 2001; Galaktionov *et al.*, 2006; Poulin, 2006), global warming is unlikely to result in an unambiguous intensification of trematode transmission in marine coastal ecosystems. According to recent models, the climate warming in the Arctic would be gradual, with the average annual air temperature increasing by 2.2–8.3°C by 2100 (Stocker *et al.*, 2013). Taking into account the temperature acclimation potential of trematodes (see above), a gradual increase in the summer temperature is unlikely to intensify their transmission much (Morley & Lewis, 2013; de Montaudouin *et al.*, 2016a, b; Prokofiev
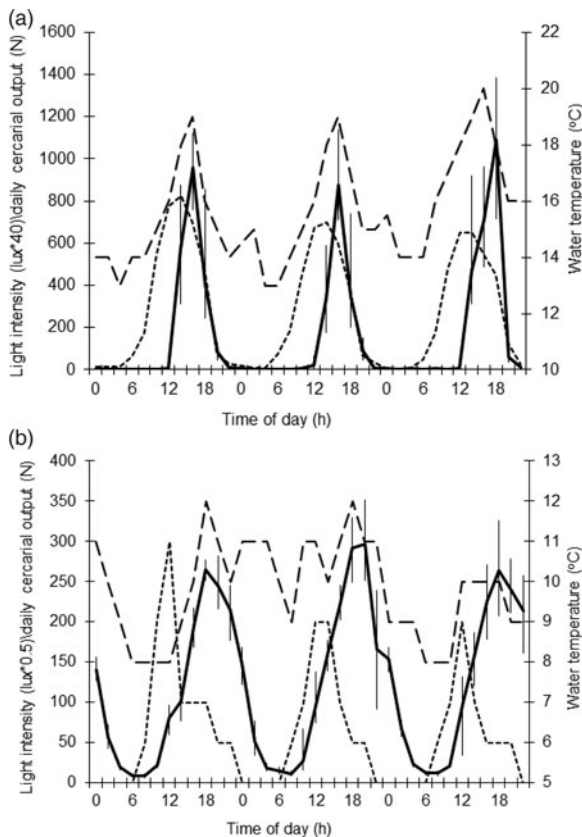
Fig. 7. Daily emergency rhythm of cercariae of (a) *Renicola roscovita* from the White Sea periwinkle *Littorina littorea* (the water temperature during observations was 15.5 ± 0.5°C (13–20°C)) and (b) *Renicola thaidus* from the Barents Sea dog whelk *Nucella lapillus* (the water temperature during observations was 9.7 ± 0.4°C (8–12°C)) (data obtained from *in situ* experiments described in Prokofiev *et al.*, 2016). ——, Average number of emerged cercariae per snail (confidence intervals are indicated); - - -, light intensity, lux; …..., average water temperature, °C.
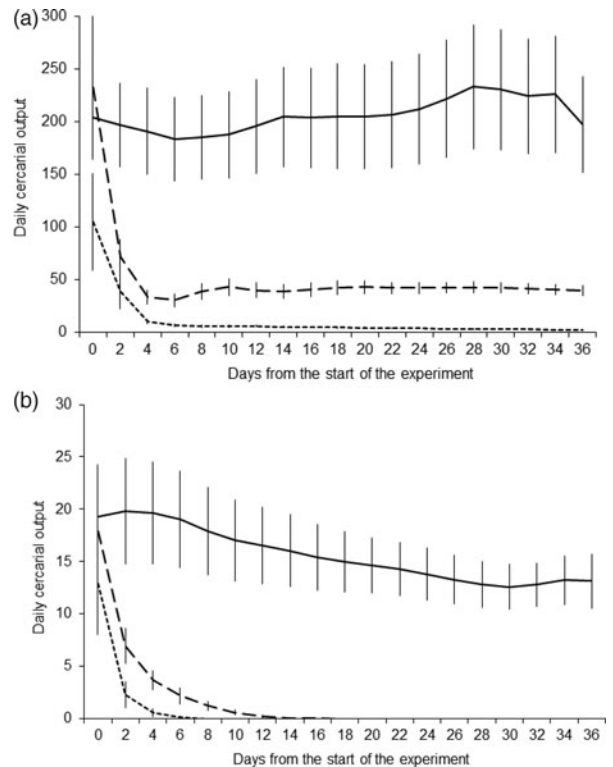

Fig. 8. The general trend in long-term emergence dynamics of 'psychrophilic' cercariae of *Cryptocotyle concava* (a) and 'thermophilic' cercariae of *Himasthla continua* (b) from the White Sea mudsnail *Hydrobia ulvae*, extracted by singular spectral analysis (for description of the method see Prokofiev *et al.*, 2016). Based on the original data obtained from a 37-day-long laboratory experiment under different constant temperatures: ——, 10°C; - - -, 5°C; …..., 3°C. The confidence intervals are indicated.

et al., 2016). This also appears to be the case for other parasitic worms, even though their temperature adaptations in the nearshore areas of the polar seas are as yet unstudied.

In some years, climate warming may also be accompanied by a sudden and abrupt rise of the summer temperature, which may be more or less prolonged. In such a case, acclimation is impossible, and the consequences may be catastrophic on a local scale. For instance, an abnormally high water temperature (26°C) in May 1990 at the Wadden Sea coast stimulated cercarial production by infected snails *H. ulvae*, and this resulted in an intensive infection of the second intermediate hosts, amphipods *Corophium volutator*, with metacercariae, and their mass mortality due to hyperinfection (Jensen & Mouritsen, 1992; Mouritsen & Jensen, 1997). However, extreme temperatures have a different impact on different host–helminth associations and this impact is not necessarily as catastrophic as that. In experiments with intertidal molluscs (*Littorina* spp., *Hydrobia* spp., *Cerithidea californica*, *Zeacumantus subcarinatus*), the mortality rate of individuals infected with trematode parthenitae under the impact of extreme temperatures did not differ significantly from that of non-infected molluscs, and sometimes was even lower (Riel, 1975; Galaktionov, 1990, 1993; Berger *et al.*, 2001; Bates *et al.*, 2011). Therefore, the effect of extreme impacts is also specific, depending on the helminth species and the host–parasite association.

It should be emphasized that the greatest warming in the Arctic is forecasted for autumn and winter (Kattsov & Källén, 2005; Overland *et al.*, 2011; Dahl-Jensen *et al.*, 2012). This means that the warm season – in other words, the seasonal 'transmission window' – would be prolonged. For trematodes, this would mean the prolongation of the season favourable for the functioning of parthenitae in molluscan hosts, the normal functioning of miracidia and cercariae in the environment, and the infection of hosts (Galaktionov *et al.*, 2006; Hakalahti *et al.*, 2006; Morley & Lewis, 2013; de Montaudouin *et al.*, 2016b; Prokofiev *et al.*, 2016). It may trigger a cascade effect, enhancing transmission of the parasites along the entire chain of the hosts (Galaktionov *et al.*, 2006; Poulin, 2006; Thieltges *et al.*, 2008; Hoberg *et al.*, 2013; Prokofiev *et al.*, 2016).

A model suggested in a recent study (de Montaudouin *et al.*, 2016b) simulated the effect of water temperature increase on the infection of cockles by larvae of the trematode *Himasthla quissetensis* in Arcachon Bay (the south-western Atlantic coast of France). The authors came to the conclusion that an increase in the temperature by +0.5 to +6°C would not result in any considerable increase in cercarial emergence and an increased prevalence in cockles (de Montaudouin *et al.*, 2016b). The explanation was that the temperature in the warmest season would be above the optimal for cercarial emergence. Emergence would be suppressed and not even prolongation of the 'transmission window' would compensate for this effect.

However, de Montaudouin *et al.* (2016b) conducted their study in an area where the summer water temperatures are, even now, close to those inhibiting cercarial emergence (>22°C). Under these conditions, even a small increase prolongs the season when the water warms up above the optimal temperature for cercarial emergence. This is an unlikely scenario for subarctic and Arctic seas, with their low temperatures of the coastal waters. Besides, the model suggested by de Montaudouin *et al.* (2016b) implies the same temperature increase in all the seasons. However, if the increase, as predicted, would be smaller in summer and greater in autumn, the suppression of cercarial emergence, if any, would be inconsiderable. It is highly unlikely that it would override the effect of prolongation of the emergence in autumn/winter.

Other effects of climate change

As noted in the Introduction, global climate changes are accompanied not only by an increasing temperature but also by some other environmental changes possibly influencing the transmission of helminths in Arctic coastal ecosystems. Their effect is difficult to assess because these changes, especially in high-latitude seas, are poorly studied. The scarce available evidence has been obtained almost exclusively from trematodes.

Climate warming is expected to increase the freshwater flux into the Arctic Ocean. This is associated with the increasing main sources of freshwater entering the Arctic Ocean: river discharge, rainfall and meltwater from land ice (Loeng *et al.*, 2005; Doney *et al.*, 2012; Symon, 2012). A possible effect of these events will be a change in the structure of currents (Loeng *et al.*, 2005), which, in turn, would first of all affect plankton and organisms trophically connected with it. The effect of these events on the transmission of parasites is difficult to predict. It is likely to be determined largely by changes in the food webs of Arctic seas. The penetration of the Pacific metacestode *A. longicervica* into the Atlantic together with planktonic crustaceans illustrates a possible scenario (see above).

Freshening of coastal waters would be another consequence. By 2050, the salinity of the Arctic Ocean is expected to decrease by 0.3–0.5 practical salinity units (psu) and by 2100, by 0.5–1.0 psu (Loeng *et al.*, 2005). Such a slight decrease of salinity is unlikely to have a noticeable effect on the transmission of helminths on the coasts of northern seas. Their intermediate hosts, invertebrates and fish (especially intertidal species), constantly experience considerable freshening during spring melting

of land snow and ice, and during rain at low tides. Being adapted to these conditions, they have a high salinity tolerance (Berger, 1986; Berger & Kharazova, 1997). This is also true of the helminths parasitizing these animals. Prokofiev *et al.* (2016) did not find any significant differences in the daily cercarial output (DCO) from infected snails for the same, or closely related, trematode species at the White Sea (salinity ∼26 psu) and the Barents Sea (salinity ∼35 psu). No significant effect of decreased salinity on cercarial emergence in the range of 6–10 psu was recorded for some other marine trematodes (Rees, 1948; Sindermann, 1960; Sindermann & Farrin, 1962; Prokofiev, 1999, 2001, 2006; Mouritsen, 2002; Lei & Poulin, 2011; Studer & Poulin, 2012). If salinity drops considerably, DCO decreases. Salinity may have quite different effects on cercarial emergence in different species, as shown for two opecoelid trematodes, whose parthenitae develop in molluscs *Gibbula adansonii* in Mediterranean lagoons. In a salinity gradient of 45–25 psu the output of cercariae of *Macvicaria obovata* did not change significantly, while that of *Cainocreadium labracis* decreased considerably with decreasing salinity (Born-Torrijos *et al.*, 2014).

The lifespan and infectivity of cercariae are unaffected by salinity changes over a broad range (Stunkard & Shaw, 1931; Rees, 1948; James, 1971; Prokofiev, 1999, 2006; Mouritsen, 2002; Studer & Poulin, 2012). Local adaptations seem to play an important role in determining the resistance to decreased salinity, as they do in respect of temperature (see above). In the experiments of Prokofiev (1999, 2001, 2006), a significant decrease in the lifespan of cercariae shed by infected intertidal molluscs at the Barents Sea (salinity ∼35 psu) was observed starting from 16 psu, while the corresponding threshold for cercariae shed by molluscs at the White Sea (salinity ∼26 psu) was 8 psu. The infectivity of cercariae of *Himasthla elongata* shed by the periwinkle *L. littorea* at the White Sea did not change in the range of 32–16 psu but decreased significantly starting from 8 psu, that is, showing the same kind of dependence on salinity as the lifespan (Nikolaev, pers. obs.).

Decreasing salinity also influences the survival of marine organisms infected with helminths. This phenomenon has been studied in detail for intertidal molluscs of the White Sea and Barents Sea infected with parthenitae and larvae of trematodes (Berger, 1986; Sergievsky *et al.*, 1986; Galaktionov, 1990, 1993; Berger *et al.*, 2001; Galaktionov *et al.*, 2002). However, in this case, too, a significant negative effect is observed only when the decrease in salinity is considerable. Mass mortality of the periwinkles *L. saxatilis* and *L. obtusata* was observed at the Barents Sea coast in some years when there was a strong freshening of the intertidal resulting from a rapid spring melting of land snow and ice; the prevalence of trematode parthenitae in the dead periwinkles reached 70% (Galaktionov, 1990).

These data indicate that the transmission of helminths in the nearshore areas of Arctic seas may be negatively affected by the seasonal prolonged and strong freshening of coastal waters during rapid melting of land snow and ice, which is forecast (Symon, 2012), and the expanding of zones with a low salinity due to an increased river discharge. This has been supported by our observations in river estuaries at the White Sea: snails *Littorina* spp.

occur there under conditions of low salinity but are almost uninfected with parthenitae and larvae of trematodes.

Climate-induced effects on species and ecosystems associated with a decrease in sea-ice extent and duration are already being observed in the marine Arctic (Loeng *et al.*, 2005). In areas of reduced sea-ice cover, primary production is very likely to increase, which in turn is likely to increase zooplankton and possibly fish production (Loeng *et al.*, 2005; Stocker *et al.*, 2013). At the same time, this would negatively affect ice-depending organisms, such as criopelagic plankton and fishes, seabirds (e.g. ivory gull (*Pagophila eburnea*) and little auk), ice-dependent seals (e.g. ringed seal (*Pusa hispida*), ribbon seal (*Histriophoca fasciata*) and bearded seal (*Erignathus barbatus*)), polar bears (*Ursus maritimus*), etc. Undoubtedly, these events would influence (possibly, are already influencing) the transmission of helminths in Arctic coastal ecosystems. Unfortunately, the lack of monitoring parasitological research in the marine Arctic makes a meaningful discussion impossible. Only one thing seems certain: the effect of the ongoing changes on the transmission of helminths will be species-specific and will depend on the life-cycle features of a given parasite species and the range of hosts involved therein.

Climate change is also expected to be manifested in an increase in storm activity in some regions (e.g. the Labrador, Nordic, Bering and Beaufort Seas) (Loeng *et al.*, 2005; Symon, 2012). This may have adverse consequences for the transmission of helminths since their free-swimming larvae, such as trematode cercariae and miracidia, are sensitive to increased water turbulence (James, 1968b; Galaktionov, 1993; Galaktionov & Bustnes, 1999). The ongoing rise of the world ocean level due to melting of glaciers and ice sheets, which is predicted to be 0.9–1.6 m above the 1990 level by 2100 (Symon, 2012), is also sure to affect the transmission of helminths in coastal waters. The erosion of the seacoast would destroy the habitat of intertidal organisms, which serve as intermediate hosts of many, if not all, helminths circulating in the coastal ecosystems, with all the expected consequences for their transmission.

Another threat for the transmission of helminths may be a growing ocean acidification, which is already considerably affecting marine ecosystems (e.g. Doney *et al.*, 2009, 2012; Feely *et al.*, 2009; Kroeker *et al.*, 2010). It is caused by rising concentrations of atmospheric carbon dioxide (CO_2), which drive changes in seawater carbonate chemistry and reduce the pH (Gattuso & Buddemeier, 2000). The largest pH changes are predicted to occur in Arctic surface waters, where the hydrogen ion concentration would increase by up to 185% by the end of the 21st century ($\Delta pH = -0.45$ to -0.5) (Feely *et al.*, 2009; Steinacher *et al.*, 2009; Stocker *et al.*, 2013). Studies of the effect of decreasing pH on free-living larvae of helminths and on stages of their life cycles parasitizing marine invertebrates and fish are just beginning. So far, such studies have only been made on trematodes. They show that a low pH ($\Delta pH = -0.5$ to -0.7) decreases the survival of cercariae and metacercariae encysting in the open, although this effect is species-specific (MacLeod & Poulin, 2015). Harland *et al.* (2015) demonstrated that a lower survival of *Maritrema novaezealandense* cercariae under acidified conditions did not prevent them from infecting amphipods

successfully. At the same time, the infection success was higher at the lowest acidity tested (pH = 7.4). This seems to be associated with the negative impact of the acidification on the resistance of amphipods to parasitic infection (Harland *et al.*, 2015). The study of Harland *et al.* (2015) indicates that an experimentally revealed effect of a factor (in this case, acidification) on a certain life-cycle stage of a helminth cannot be automatically extrapolated to its transmission under natural conditions, where it is affected by various interacting factors.

If we assume that the defence mechanisms of marine animals against parasitic infection generally weaken under conditions of reduced pH, it follows that ocean acidification may result in an increased parasitic load on their populations. However, it would be premature to derive this conclusion from a study of a single host–parasite association. It should be borne in mind that pH is likely to decrease gradually, over a number of years, rather than all at once. Therefore, considering ocean acidification, we should take into account the capacity of marine organisms, including helminths, to acclimation and genetic adaptation (Kelly & Hofmann, 2013), as we did when we discussed the effect of temperature (see previous section).

Assessing the effect of various stressors on helminth transmission, it should be emphasized that, in contrast to experimental conditions, in nature we deal with a synergic effect of various heterogeneous factors. The impact of a factor may be levelled or, on the contrary, intensified during interaction with another factor or factors. For instance, a lower and a higher salinity affected the emergence of *Maritrema subdolum* cercariae differently at different temperatures (Mouritsen, 2002), while the lifespan of *M. novaezealandense* cercariae was determined by interactions of several factors, of which the interactive negative effect of temperature and UV radiation was the most important (Studer & Poulin, 2013). Besides, as shown in the experiments described above, where amphipods were infected with *M. novaezealandense* cercariae under acidified conditions, a factor may have an ambiguous effect on helminth transmission (Harland *et al.*, 2015). In that study, the effect was, on the one hand, negative (a shortened lifespan of transmissive larvae) and, on the other hand, positive (increased susceptibility of amphipod hosts to infection). Increased UV radiation has a similar net effect on the transmission of *M. novaezealandense* cercariae (Studer *et al.*, 2012). Therefore, when discussing the effect of climate changes on the circulation of helminths, we should take into account both a possible interaction of different factors and, sometimes, their possible antagonistic influence on various aspects of transmission and on interaction between parasites and hosts.

Conclusions and future research

In summary, the depauperation of the helminth fauna in the nearshore waters of Arctic seas is associated with the lack of suitable intermediate hosts (boreal invertebrates and fish) and with unfavourable conditions for the normal functioning of their free-living larvae. Species without these stages have an advantage under these conditions. Cestodes and acanthocephalans

Table 1. Stressors related to climate change and their possible impact on helminth (mostly trematode) transmission in Arctic coastal ecosystems.

Proposed climate-change effects	Possible impact on helminth transmission
Moderate gradual summer warming by 2100	Negligible effect (or absence thereof) on transmission of native species, their expansion into high Arctic; expansion into Arctic helminth species (especially trematodes) with free-living larva/larvae in their life cycle
Abnormally high summer temperature in some years	Temporarily intensified transmission of helminths, high probability of mass mortality of infected intermediate hosts: ectothermic invertebrates and fish juveniles
Prolongation of warm season	Enhanced transmission (cascade effect) due to prolongation of transmission window
Expansion of boreal marine invertebrates and fish into Arctic seas ('borealization')	Expansion of boreal helminth species in the wake of their hosts
Changes in planktonic and benthic trophic webs due to Arctic warming, increased melting of glaciers, change in surface water salinity, increased UV radiation, etc.	Species-specific effect, favourable for transmission of some species and unfavourable for the transmission of others; formation of conditions for transmission of species previously absent in high latitudes
Changes of migratory routes of marine animals and possibility of transarctic migration	Transarctic transfer of helminths, exchange between the North Atlantic and the North Pacific helminth fauna
Change of the structure of currents in the Arctic Ocean	Consequences are difficult to predict, being determined by changes of migration routes of hosts (plankton and animals trophically associated with it) and changes in trophic webs
Gradual decrease of salinity according to climatic models (by 0.5–1.0 psu by 2100)	Weak effect or absence thereof
Freshening of coastal areas due to increased precipitation, active melting of snow and land ice, increased river runoff, etc.	Depressed transmission due to decreased efficiency of free-living larvae and parasitic stages in osmoconformers; local mortality of infected sedentary and slow-moving invertebrate hosts
Shortening of the ice cover period in coastal waters of the Arctic seas	Possible enhancement of transmission due to prolongation of transmission window
Reductions in Arctic sea-ice extent	Favourable conditions may be created for helminth transmission in high Arctic, but negative effect on species associated with ice-depending animals (both final and intermediate hosts) may also be expected
Increased force and frequency of storms and related coastal erosion	Negative effect on transmission of species associated with intertidal animals
Increase of sea level	The same as above
Acidification of Arctic Ocean	Lack of effect or weak effect if the increase is inconsiderable; if the increase is greater, species-specific net effect on various aspects of life activity of helminths and their interactions with hosts may be expected
Increasing levels of UV radiation	The same as above; a negative effect is also possible as a consequence of decreased productivity of Arctic marine ecosystems at the base of food chain (because of the negative effect of increased UV radiation on primary producers, the phytoplankton)

dominate in the helminth fauna of seabirds in the Arctic because of the greater proportion of the intermediate hosts, crustaceans, in their diet. A high intensity of infection of birds with cestodes and acanthocephalans in the Arctic indicates that these helminths, which are highly pathogenic, especially acanthocephalans, may considerably influence the host populations, aggravating the impact of harsh environmental conditions. Feeding characteristics and, possibly, a weakened immune system of birds in the Arctic promote their infection with non-specific helminths (the effect of non-specific parasitism). In this way, the helminths colonize new hosts more easily. In the long term, this may result in the formation of genetically different intraspecific races and speciation, according to the host-switching scenario.

Climate changes are likely to cause several considerable alterations in the composition of the helminth fauna, the levels of infection of the hosts and transmission pathways in Arctic coastal communities (table 1). 'Borealization' of the Arctic will promote colonization of high latitudes by helminth species with free-living larvae in their life cycles, whose intermediate hosts are boreal invertebrates and fish. We might also expect some degree of interpenetration of NA and NP helminth faunas of migratory animals. The effect of increased ambient temperature is unequivocal and calls for in-depth studies. At present, some intensification of helminth transmission as a result of the prolongation of the seasonal 'transmission window' may be expected. This may entail an increase in the parasitic load on the host populations.

The effect of other factors related to climate change – decreased salinity, pH, coastal erosion, reduced sea-ice cover, enhanced hydrodynamics, etc. – on the transmission of helminths is much more difficult to predict. If, as

assumed by climatic models, these processes are going to intensify gradually, their effect may be levelled due to ac-climation/adaptation of helminths and their hosts. At the same time, a local negative effect may be considerable if the impact of a factor or several factors is especially strong at a given site. An example of this is a strong freshening due to intensified freshwater runoff of a coastal area or its erosion. The predicted changes in Arctic marine food webs, some of which are occurring before our very eyes, are likely to have an especially large impact on the circulation of helminths in the Arctic. The consequences of these changes are unclear. They may well prove favourable for the transmission of some helminths and suppressive for the transmission of some others.

It remains for me to acknowledge that at this stage we do not have enough information for an unbiased assessment of climate change on the transmission of helminths in Arctic coastal communities. The few studies available are patently insufficient. To fill the gaps in our knowledge, systematic parasitological research in the Arctic is necessary. Its priority directions should be:

- monitoring of the ongoing changes in the trophic webs of the Arctic seas and assessment of their effect on the transmission of helminths (at least, the dominant/most abundant and pathogenic species);
- monitoring of the effect of climate changes on the dynamics of infection of host populations by helminths, and the expansion/advancement of new helminth species possibly associated with 'borealization' and transarctic transfer (conducted at reference sites of the sea coast);
- experimental research into the optimal and tolerance ranges of the life-cycle stages of helminths developing in Arctic ectothermic marine animals and their free-living transmissive larvae (in relation to stressors associated with climate changes);
- study of genetic and phenotypic plasticity of populations of helminths and their associations with hosts in respect of stress factors, and the assessment of their capacity to adapt to changing environmental conditions.

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