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Transmission of Parasites in the Coastal Waters of the Arctic Seas and Possible Effect of Climate Change

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Abstract—The review deals with the biodiversity, life cycles, distribution and temperature adaptations of parasites circulating in the coastal waters of northern polar seas. Special attention is given to helminths of marine birds, which are the most common parasites in the coastal waters. Among them, the focus is on trematodes. Factors responsible for the impoverished species composition of parasites in the Arctic are analyzed. It is shown that species without free-living larvae in the life cycle have an advantage in this environment. The abundance of cestodes and acanthocephalans in Arctic seabirds is linked with the high proportion of crustaceans in their diet. The phenomenon of nonspecific parasitism (occurrence of parasites in atypical host species) is analyzed from an evolutionary viewpoint. Characteristic features in the spatial distribution of infection of marine coastal invertebrates with parasite larvae are considered, and factors that determine it are specified. The prevalence of infection in intermediate hosts is closely connected with the abundance of final hosts, which makes it possible to estimate the abundance of final hosts in a given region and reveal trends in its changes. Trematodes have a high potential for temperature acclimation. This facilitates their transmission in the northern seas but, on the other hand, makes it unlikely that the transmission process would be intensified upon an increase in summer temperatures resulting from climate warming. However, intensification of transmission may well occur due to the prolongation of the warm season ("transmission window"), which has been predicted and is already observed. It is suggested that warming in the Arctic promotes both the entry of certain "southern" species into the Arctic and the trans-Arctic interpenetration of the North Atlantic and North Pacific parasitic faunas. A case is made for the necessity to broaden the scope of parasitological research in the Arctic and Subarctic, including parasitological monitoring at the reference sites of the sea coast.

Keywords: parasites, birds, trematodes, temperature adaptations, climate change, the Arctic

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INTRODUCTION

It is now an accepted fact that parasites as the essential components of ecosystems (Beklemishev, 1970) accounting for a considerable proportion of total biodiversity (Poulin, 2014) play an important role in the processes occurring in the biosphere. The recognition of this fact has stimulated research in ecological and evolutionary parasitology, with the development of molecular genetic methods providing new possibilities for analyzing the taxonomic diversity, life cycles, and circulation of parasites. Transformations occurring in ecosystems due to current climate change and increasing anthropogenic impact also contributed to intensification of parasitological research. Studies have been performed to analyze possible effects of such events on the biodiversity of parasites, their

expansion to new geographic regions, infection of new hosts, and the nature of their influence on the populations and communities of free-living organisms (Lafferty, 1997, 2009; Marcogliese, 2001; Harvell et al., 2002; Lafferty and Holt, 2003; Kutz et al., 2005; Brooks and Hoberg, 2007; Morley and Lewis, 2008; Mas-Coma et al., 2008; Studer et al., 2010; Doi and Yurlova, 2011; Rohr et al., 2011; Goedknegt et al., 2015; etc.).

It should be noted, however, that almost all such publications deal with parasites whose transmission takes place at low and temperate latitudes. The Arctic and Subarctic have not been sufficiently studied in this respect, despite that it is in these regions that climate oscillations manifest themselves most distinctly (permafrost thawing, reduction in the Arctic ice pack area,

Table 1. Numbers of helminth species parasitizing seabirds in different geographic regions

Bird species	The Netherlands	Sweden	Iceland	Southwestern Barents Sea	White Sea	Newfoundland and Labrador	Southeastern Barents Sea	Spitsbergen	Novaya Zemlya	Frantz Josef Land
Common eider (*Somateria mollissima*)	28	24	26	25	22	21	11	7	–	6
Black-legged kittiwake (*Rissa tridactyla*)	–	–	–	14	–	–	–	5	7	7
Glaucous gull (*Larus hyperboreus*)	–	–	–	–	–	–	–	17	8	4

Based on the data by Markov (1941), Belopol'skaya (1952), Bishop and Threlfall (1974), Persson et al. (1974), Kulachkova (1979), Galaktionov (1996), Kuklin et al. (2005), Borgsteede et al. (2005), Skírnisson (2015), and original materials.

changes in the structure of ocean currents, etc.) (*Arctic Climate...,* 2005; *Arctic Biodiversity...*, 2013). Studies on parasites circulating at high latitudes are relatively few. Most of them are of a faunistic character and concern terrestrial and freshwater ecosystems (Hoberg et al., 2013). Marine and, in particular, coastal ecosystems have received much less attention. Meanwhile, many parasitic worms undergo their life cycle in the coastal zone, where they find their intermediate hosts among littoral and upper sublittoral invertebrates and fishes that inhabit this zone permanently or seasonally. The same fishes serve as their final hosts, along with marine mammals and birds. The latter play a special role in the transmission of parasitic worms due to their high abundance and close trophic relationships with coastal marine organisms. Not surprisingly, it is coastal marine birds that serve as final hosts for the majority of helminths whose life cycle is connected with coastal ecosystems (Hoberg, 2005).

This fully applies to the Arctic sea coasts, the more so that birds are highly abundant there. Chernov (1999) justly noted that, for a zoologist, the Arctic is associated primarily with birds. They form vast coastal colonies comprising thousands of individuals and feed mainly on marine invertebrates and fish, thereby contributing to the progression of helminth life cycles involving intermediate hosts. On the other hand, the severe climatic conditions of the Arctic and Subarctic cannot but impose limitations on parasite transmission and impart certain specific features to this process. This review is an attempt to summarize the relevant data accumulated to date and, on this basis, to analyze the parasitological situation in the coastal zone of the northern Palearctic seas and estimate the possible effect of climate warming on this situation. Special attention is given to helminths of marine birds and, among them, to trematodes, for which ample data are available on the biology of life cycles in high-latitude coastal waters.

SPECIES DIVERSITY AND LIFE CYCLES

The general trend toward the impoverishment of fauna at high latitudes applies well to parasites (Markov, 1941; Baer, 1956, 1962; Galaktionov, 1996; Kuklin, 2001; Threlfall, 1968, 1971; Hoberg, 1986; Hoberg et al., 2013). The number of helminth species found in arctic regions is markedly lower than at the boreal sea coasts (Table 1). This is especially obvious in the case of trematodes, which almost completely disappear in the high Arctic (Markov, 1937, 1941; Baer, 1956; Galaktionov et al., 1994; Galaktionov, 1996; Kuklin, 2001). The explanation is that the majority of coastal trematodes have intermediate hosts in boreal invertebrate species, which do not spread to arctic regions. In the first place, this concerns mollusks: they serve as the first intermediate hosts of trematodes (obligatory in their life cycle), and these parasites, with rare exceptions, show high specificity for particular mollusk species. An illustrative example is the situation on the Svalbard (Spitsbergen) archipelago in the Arctic Ocean, where the warm Spitsbergen Current (a part of Gulf Stream) runs along the southwestern coast of the West Spitsbergen Island, the largest in the archipelago. Hence, there occur boreal Atlantic and boreal–low Arctic mollusks such as *Littorina littorea, L. saxatilis, Cryptonatica clausa, Onoba aculeus,* etc. (Golikov and Kusakin, 1974; Koszteyn et al., 1991), which provides conditions for the circulation of several trematode species (Kuklin et al., 2005; Kuklin and Kuklina, 2013).

However, the absence of appropriate intermediate hosts is not the only factor interfering with the expansion of trematodes to arctic regions. Specific features of their life cycles also play an important role. A rich fauna of trematodes that use littoral mollusks as the first intermediate hosts has been described in the coastal waters of Great Britain and at the Atlantic coast of France (Table 2). The second intermediate and final hosts for most of these parasites also inhabit the coastal waters of Iceland and Norway, but the

Table 2. Numbers of species of trematode parthenites and larvae developing in marine littoral mollusks at different latitudes

Mollusk species	British Isles and Atlantic coast of France	Iceland	White Sea	Southwestern Barents Sea	Southeastern Barents Sea	Sakhalin and Kuril Islands	Northern Sea of Okhotsk	Bering Sea
Littorina spp. (Atlantic species)	26	16	14	14	6	–	–	–
Littorina spp. (Pacific species)	–	–	–	–	–	14	11	2
Hydrobia spp.	31	10	16	–	–	–	–	–

Based on the data by James (1968, 1969), Combescot-Lang (1976), Tsimbalyuk et al. (1978), Lauckner (1980), Deblock (1980), Irwin (1983), Newell (1986), Galaktionov and Bustnes (1999), Galaktionov and Skírnisson (2000), Skírnisson and Galaktionov (2002, 2014), Galaktionov et al. (2010), and original materials.

trematode fauna associated with them in these regions is significantly poorer (Table 2). The northward spread of boreal trematode species is impeded because their life cycle includes one or two free-swimming larval stages, the miracidium and cercaria.

The miracidium is a small ciliated larva (rarely larger than 150 µm) with a life span of only a few hours that hatches from the egg and seeks out to find and penetrate the first intermediate host (a mollusk). It is difficult to implement such a program in coastal waters, especially in the littoral zone with its complex and variable hydrodynamic regime. Hence, it is not surprising that the majority of trematodes that use littoral mollusks as intermediate hosts have no free-swimming miracidium stage in their life cycle. The miracidium of these species hatch from the egg in the mollusk's gut, after the egg has been ingested with food. The eggs in the water remain infective for a long period of time, which increases the probability of their ingestion.

The proportion of species with free-swimming miracidia among such trematodes is small and shows a tendency to decrease at higher latitudes, although this tendency lacks statistical significance ($P > 0.05$, χ^2 test) (Fig. 1a). For example, *Parorchis acanthus* has the free-swimming miracidium stage in its life cycle and uses the mollusk *Nucella lapillus* as the first intermediate host. Being widespread in the coastal waters of boreal seas, this trematode has been recorded in western Iceland (Galaktionov and Skírnisson, 2000; Skírnisson and Galaktionov, 2002) but is absent in northern Norway. On the other hand, *Renicola thaidus* is also associated with *N. lapillus,* but its miracidia do not hatch from the eggs in the external environment, and this parasite is found even at the northeastern boundary of *N. lapillus* range in eastern Murman (our data).

The cercaria is the second transmissive larval stage in the trematode life cycle. Compared to the miracidium, this is a more advanced organism capable of fairly complex orientation reactions that allow it to find and infect the second intermediate host, an invertebrate or a fish (Combes et al., 1994; Prokofiev and Galaktionov, 2009). The absence of free-living cercaria in the life cycle is observed far more rarely than the absence of free-swimming miracidium, because this leads to the impairment of parasite transmission and life cycle as a whole. The absence of free-swimming miracidium hardly has an effect on the life cycle, because its capacity for dispersal in space is negligible. In contrast, the absence of free-living cercaria makes it impossible to use the second intermediate host, with consequent reduction in the spectrum of potential final hosts and in the range of trematode dispersal, which depends both on the movement of the cercaria itself and the activity of the second intermediate host (Galaktionov, 1993). This is why three-host life cycle including the free-living cercaria stage are the most widespread among trematodes (Galaktionov and Dobrovol'skii, 1986, 1998), and it is the three-host cycles without free-swimming miracidium but with active cercaria that dominate in the coastal zone of boreal seas (James, 1968, 1969; Combescot-Lang, 1976; Irwin, 1983; Newell, 1986; Skírnisson and Galaktionov, 2002).

The proportion of littoral trematode species with free-living cercariae does not differ significantly between boreal and arctic regions, showing only a tendency to decrease at higher latitudes ($P > 0.05$, χ^2 test), as in the case of species with free-swimming miracidium (Fig. 1b). A radically different picture is observed when considering the occurrence frequencies of species with different life cycle types and the prevalence (the proportion of infected individuals in a sample) of the first intermediate hosts by these species. These parameters in species with a three-host life cycle show a distinct trend to decrease in regions with arctic climate (Galaktionov and Bustnes, 1999) (Fig. 2). Dominance in these regions is gained by species with a two-host life cycle, which are largely autonomous from the environment due to the absence of free-living stages (the miracidium and cercaria). The advantages of such
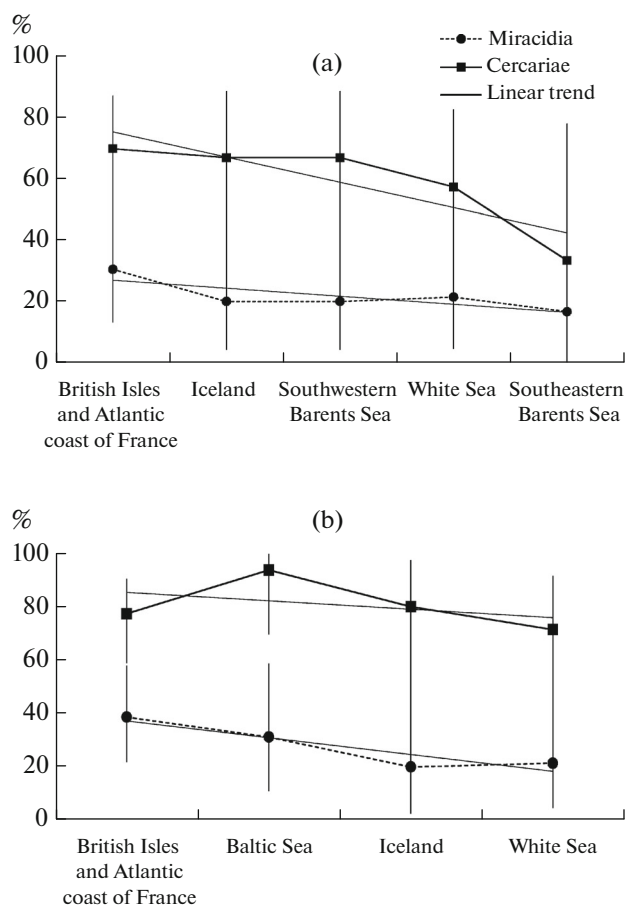
Fig. 1. Proportions (%) of trematode species with free-swimming miracidia and cercariae that use littoral mollusks (a) *Littorina* spp. and (b) *Hydrobia* spp. in coastal waters of North Atlantic seas (95% confidence intervals for each point and linear trends are shown).

landicus umbilicalis, which serve as the first intermediate hosts for *M. pseudopygmaeus* in the region of Franz Josef Land (Galaktionov et al., 1994).

It should be noted that trematode species with a three-host life cycle that use sublittoral mollusks as the first intermediate hosts have expanded farther to the Arctic than species associated with littoral organisms. Apparently, more stable ambient conditions in the sublittoral zone make it easier for cercariae to find their second intermediate hosts. Thus, sublittoral gastropods and bivalves in the Pechora Sea have been found to contain parthenitae and larvae of *Gymnophallus* spp., *Podocotyle reflexa*, *Cercaria nordica I* (*Renicola* sp.), and some other trematode species with the free-living cercaria stage in the life cycle (Galaktionov and Marasaev, 1986, 1990; our unpublished data).

The helminth fauna of seabirds also includes cestodes (Tetrabothriidae, Dilepedidae, Aploparaksidae, Hymenolepididae) and acanthocephalans (Polymophidae, Filicolidae), which have no free-living larvae and infect intermediate hosts (crustaceans) when the latter ingest their eggs. All these parasites spread in the environment only by eggs containing a larva. The infective agent is transmitted from the first intermediate host to the next (second intermediate, paratenic (tranport), or final) only via the food web, i.e., when a predator ingests a host infected by parasitic larvae. Thus, unlike in trematodes, there is no free-living larval stage, which presents an important barrier to parasite expansion to the Arctic. Moreover, crustaceans used by cestodes and acanthocephalans as intermediate hosts are widespread in the polar seas, and the fauna of these helminths is less impoverished in the Arctic, compared to the trematode fauna (Markov, 1941; Baer, 1956, 1962; Galaktionov, 1996; Kuklin, 2001; Threlfall, 1968, 1971; Hoberg, 1986; Hoberg et al., 2013).

Some cestodes (*Lateriporus* spp., *Alcataeinia* spp., *Microsomacanthus* spp., *Tetrabothrius* spp., etc.) and acanthocephalans (*Polymorphus phippsi*, *Corynosoma strumosum,* etc.) successfully circulate in the Arctic as well as in coastal ecosystems at lower latitudes (Threlfall, 1968, 1971; Leonov and Belogurov, 1970; Leonov et al., 1970; Leonov, 1979; Bakke, 1985; Galkin et al., 1994; Kuklin and Kuklina, 2005, 2013; Regel' and Atrashkevich, 2008). On the other hand, the absence or insufficient population density of intermediate hosts result in the disappearance of certain species, as in the case of trematodes. In particular, this concerns the acanthocephalan *Profilicillis botulus,* a widespread parasite of waterfowl in the North Atlantic seas that uses decapods as intermediate host (Petrochenko, 1958). At the eastern Murman coast, the larvae (cystacanths) of this species have been found in crabs *Hyas araneus* and *Pagurus pubescens* (Uspenskaya, 1963). These crustaceans are rare in the northeastern Barents Sea and at the coasts of Novaya Zemlya and Franz
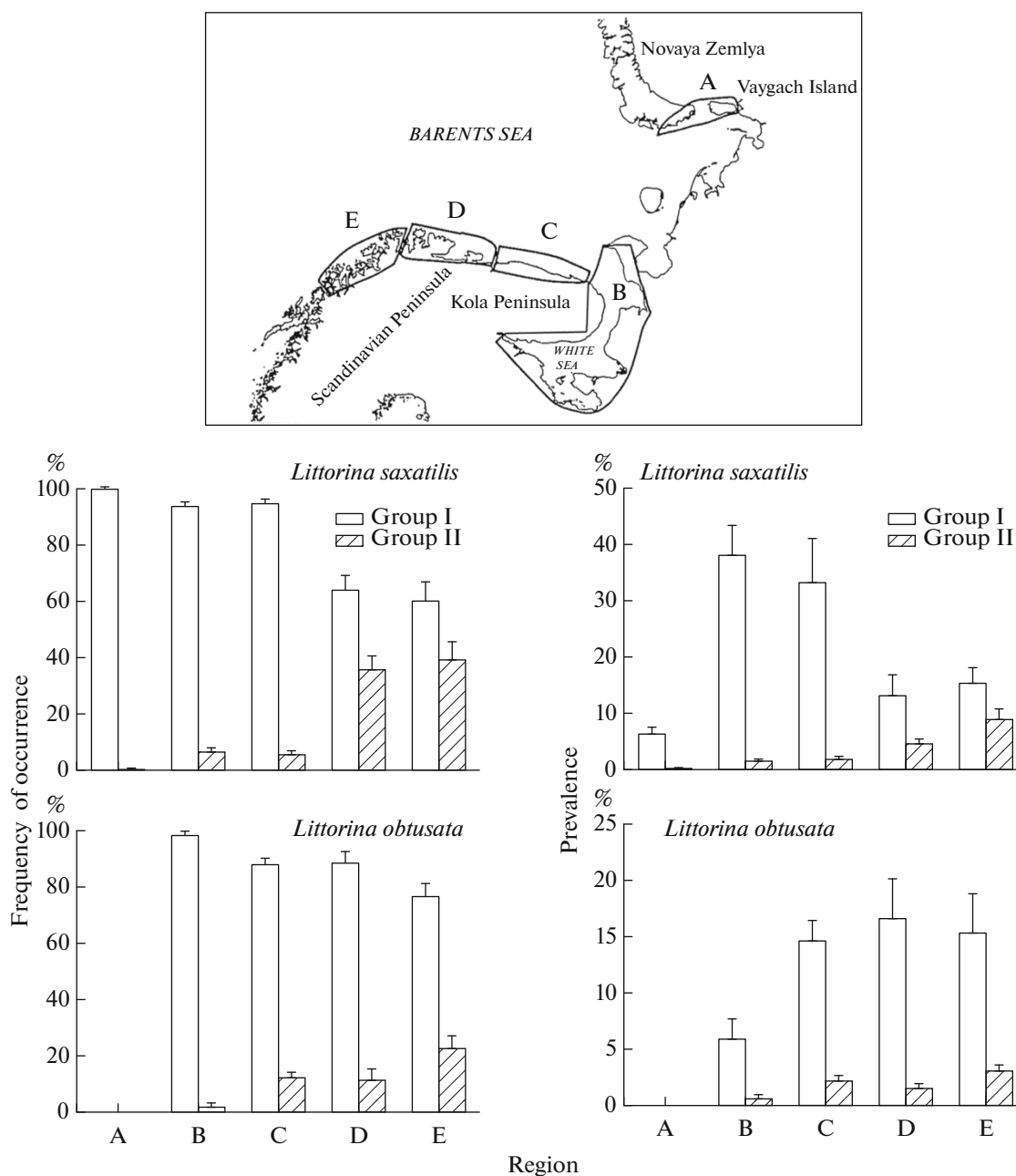
an autonomous life cycle clearly manifest themselves in ecosystems with extreme parameters of the environment, such as the Arctic coast. However, the parameters of littoral mollusk infection by trematodes with a three-host life cycle in northern Norway approach the values characteristic of species with a two-host life cycle (Fig. 2), and the parameters of infection by the two groups of trematodes in the coastal zone of Iceland are equal (Galaktionov and Bustnes, 1999; Skírnisson and Galaktionov, 2002).

In the Franz Josef Land, the rich assemblage of trematodes associated with seabirds at lower latitudes is represented by a single species, *Microphallus pseudopygmaeus* (Galaktionov et al., 1994). Its expansion to the high Arctic has been facilitated not only by the autonomous two-host life cycle but also by the biological feature unique for trematodes: the ability to use a wide range of prosobranch gastropods as the first intermediate hosts (Galaktionov, 2009). They include sublittoral mollusks *Margarites helicinus* and *M. groen-*

Fig. 2. Occurrence frequencies of parthenites and larvae of two trematode groups (percentages of hosts infected by species of a given group relative to the total number of infected hosts) and the prevalence by these trematodes (%) in littoral mollusks *Littorina saxatilis* and *L. obtusata* at the Barents Sea and White Sea coasts (according to Galaktionov and Bustnes, 1999, with modifications): A–E, regions where mollusks were sampled; group I, trematodes with two-host life cycle without free-living larval stage; group II, trematodes with three-host life cycle including at least one free-living larval stage (cercaria).

Josef Land, which prevents successful transmission of *P. botulus* (Galaktionov et al., 1994). The acanthocepalan *Polymorphus phippsi* parasitizing waterfowl and some other seabirds (see below) is common in the above regions, since its intermediate hosts are amphipods widely represented in the Arctic coastal waters.

Moreover, the parasitic fauna of birds in the high Arctic is almost completely devoid of species that are not connected with marine ecosystems. In particular,

this concerns cestodes *Aploparaksis* spp. and *Nadejdolepis* spp. and acanthocephalan *Polymorphus magnus.* Their intermediate hosts are freshwater oligochaetes, limneid mollusks, and amphipods *Gammarus lacustris,* respectively (Bondarenko and Kontrimavichus, 2006; Kuklin and Kuklina, 2013).

The circulation pathways of the majority of nematodes parasitizing seabirds in the Arctic and Subarctic (representatives of the families Capillariiae, Strepto-

caridae, Acauriidae, Anisakidae, etc.) have not yet been described in detail. It is known, however, that life cycles associated with marine ecosystems are characteristic of widespread Anisakidae species such as *Anisakis simplex*, *Pseudoterranova decipiens*, and *Contracaecum osculatum*, which use as intermediate hosts many species of invertebrates (mainly crustaceans) and fishes (including coastal fishes) (Nagasawa, 1990; Køie and Fagerholm, 1995; Andersen et al., 1995). These nematodes develop to maturity only in marine mammals but not in fish-eating birds, although their larvae are often found in the latter. It is noteworthy that single specimens of the Anisakidae in birds from the Franz Josef Land have been found only in the thick-billed murre *Uria lomvia* (our unpublished data), despite the high abundance of marine mammals in this region. This fact is apparently explained by a low proportion of fish foods in the bird diet (see below).

Spirurid nematodes *Paracuaria adunca, P. tridentata, Cosmocephalus obvelatus,* and *Streptocara crassicauda* commonly found in fish-eating seabirds use crustaceans (mysids and amphipods) as intermediate hosts and fishes as paratenic hosts (Anderson and Wong, 1982; Wong and Anderson, 1982; Marcogliese, 1992; Anderson, 2000). Similar to the Anisakidae, all these species have no free-living larvae, with the first-stage larvae hatching from the egg after its ingestion by an intermediate host (Anderson, 2000). This appears to contribute to the circulation of these nematodes in coastal ecosystems of the Arctic seas. They have been found in birds from Spitsbergen and Franz Josef Land (Kuklin et al., 2005; Kuklin and Kuklina, 2013; our unpublished data). *Stegophorus stellaepolaris* is another spirurid species found in these birds, but its life cycle is unknown.

Infection by strongylid nematodes *Amidostomum* sp. has been revealed in common eiders from Franz Josef Land (our unpublished data). The eggs of these parasites are evacuated from the bird intestines together with feces. The larvae hatched from the eggs can actively infect the final host or be ingested with food or water (McDonald, 1969; Barus et al., 1978; Anderson, 2000; Borgsteede et al., 2006). The eiders can get infected during the nesting period, when the birds remain on land for a long time. It appears that the nematodes survive the cold season within the host, with the phase of their life cycle in the external environment being accomplished during the short Arctic summer. It is unlikely that the eggs of *Amidostomum* sp. can survive long-term freezing during the Arctic winter.

ABUNDANCE AND HOSTAL RADIATION

Although the number of species in the parasitic fauna is generally reduced, the intensity of infection by cestodes and acanthocephalans in Arctic seabirds is fairly high (Baer, 1956, 1962; Threlfall, 1968, 1971; Leonov and Belogurov, 1970; Leonov et al., 1970;

Galaktionov et al., 1994; Galaktionov, 1996; Kuklin, 2001; Kuklin et al., 2005; Kuklin and Kuklina, 2005). This is explained by specific features of bird diet. The Arctic coastal waters are poor in fish, many species of boreal invertebrates are absent, while crustaceans, particularly amphipods (intermediate hosts for the above helminths) are abundant, and the birds actively utilize this readily available food resource (Belopol'skii and Shuntov, 1980; Lydersen et al., 1989; Mehlum and Gabrielsen, 1993; Weslawski et al., 1994).

This is especially true of benthophagous ducks such as the common eider (*Somateria mollissima*). The intensity of its infection (the number of parasite individuals per host) by cestodes *Microsomacanthus* spp. and acanthocephalan *P. phippsi* in the Franz Josef Land reaches 200000 and 1000 ind. (Galaktionov, 1996), compared to 19500 and 247 ind. in eastern Murman and 55000 and 57 ind. in the White Sea, respectively (Belopol'skaya, 1952; Kulachkova, 1979). This is not surprising, because amphipods are the second most important component (after mollusks *Margarites* spp.) in the diet of common eiders from the Franz Josef Land (Weslawski et al., 1994). These birds in more southern regions feed mainly on mussels and several other bivalve and gastropod species (Bianki et al., 1979; Krasnov et al., 2009).

Distinctive features of bird feeding in the High Arctic also account for the phenomenon of nonspecific parasitism (Galkin et al., 1999; Kuklin et al., 2005; Kuklin and Kuklina, 2005; Galaktionov and Atrashkevich, 2015). This term refers to the occurrence of parasites in atypical species of final hosts. These may be facultative hosts, in which the parasite can reach sexual maturity while being less adapted to them than to its specific (obligatory) hosts, or eliminative hosts in which the parasite either dies or develops without reaching the adult stage (Shul'ts and Gvozdev, 1972; Kontrimavichus and Atrashkevich, 1982; Galaktionov and Dobrovol'skii, 1998). In Spitsbergen, for example, cestodes *Microsomacanthus diorchis* and *M. microsoma*—typical parasites of anseriform birds—have been found in black-legged kittiwakes and glaucous gulls, and the same bird species proved to be infected by dilepidids *Arctotaenia tetrabothrioides*, which were previously recorded only in shorebirds (Kuklin et al., 2005). All these cestodes were sexually mature, and the intensity of their infection was considerable, especially in glaucous gulls (for *M. diorchis* and *A. tetrabothrioides,* up to 254 and 154 ind. per bird, respectively).

The acanthocepalan *Polymorphus phippsi* provides an illustrative example of nonspecific parasitism (Galaktionov and Atrashkevich, 2015). The common eider is the obligate final host of this species in the Arctic, but it has also been found in other birds phylogenetically distant from eiders, such as gulls, oaks, and the purple sandpiper *Calidris maritima*. As a rule, these birds are eliminative

hosts for *P. phippsi,* but some parasite individuals developing in the black-legged kittiwake (*Rissa tridactyla*), Arctic tern (*Sterna paradisaea*), little auk (*Alle alle*) and, possibly, Sabine's gull (*Xema sabini*) manage to reach sexual maturity. Thus, the parasite colonizes new hosts that are phylogenetically unrelated to its obligate host. The extreme living conditions in the Arctic facilitate this process: compared to southern regions, birds must expend more energy for physiological processes, including the maintenance of optimal body temperature, and this may reduce the amount of energy necessary for maintaining a high immune status, which is favorable for parasite survival and development in a nonspecific host.

It appears that a similar situation developed in the coastal zones of northern Palearctic seas during glacial periods of the Late Pliocene and Pleistocene, when marine birds and mammals concentrated in the refugia formed along the Atlantic and Pacific coasts of continents and islands, where the same food resources were available to them. Thus, parasites received new opportunities for host switching (hostal radiation), with the consequent acceleration of speciation (Hoberg, 1992, 1995; Hoberg and Adams, 1992, 2000). During interglacial periods, the hosts widely spread over ice-free water areas and coastal regions, disseminating helminths. According to Hoberg and Adams, it is these processes that provided for the formation of recent fauna of cestodes parasitizing marine birds and mammals in the North Atlantic and North Pacific. In some approximation, the recent conditions of bird parasite transmission in the high Arctic appear to be comparable to those characteristic of glacial refugia. This is why the cases of nonspecific parasitism may be regarded as a model that demonstrates different stages of the ongoing process of helminth speciation in the course of hostal radiation.

SPATIAL DISTRIBUTION OF INFECTION FOCI

The distribution of parasite infection in invertebrate populations has a mosaic pattern: sites with a high infection rate (the foci of infection) alternate with those where this rate is low of no infection occurs (Ginetsinskaya and Dobrovol'skii, 1983; Galaktionov and Dobrovol'skii, 1999). The foci of infection are usually formed at sites with a high local density of final hosts that spread infective parasite eggs and/or larvae, and their constant location is due to low mobility of invertebrate intermediate hosts. The spatial distribution of parasite infection among marine invertebrates in the littoral and sublittoral zones also has a focal pattern (Galaktionov and Marasaev, 1986, 1990; Smith, 2001; Skírnisson et al., 2004; Hechinger and Lafferty, 2005; Fredensborg et al., 2006). For example, our studies at the coasts of Franz Josef Land showed that the prevalence of *Polymorphus phippsi* acanthocephalan larvae in amphipods *Gammarus (Lagunogammarus) setosus* was very low (0−1%) in most areas sur-
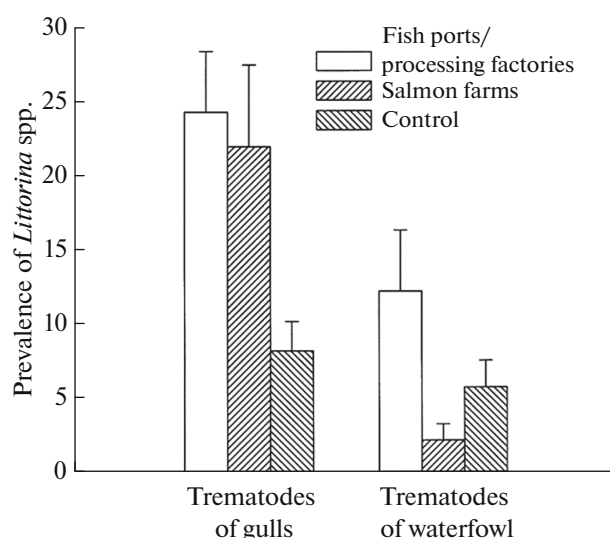

Fig. 3. Prevalence of *Littorina saxatilis* and *L. obtusata* mollusks by parthenites and larvae of trematodes that use gulls and waterfowl (primarily the common eider) as final hosts in zones of fish ports, fish-processing factories, salmon farms, and in areas unaffected by human activities (control) at the coast of northern Norway (modified from Bustnes and Galaktionov, 1999).

veyed in 1990−1993 but reached 60−90% near Etheridge and May islands inhabited by a colony of common eiders (Galaktionov et al., 1994). At the northern Norway coast, high prevalence of mollusks *Littorina* spp. and *Nucella lapillus* by parthenitae of trematodes that use gulls as final hosts were revealed in the vicinities of fish ports, fish factories, and salmon farms (Bustnes and Galaktionov, 1999; Bustnes et al., 2000) (Fig. 3). These sites attract large gulls, which concentrate there and thereby create favorable conditions for implementation of parasite life cycles.

The Arctic is crossed by flight paths of many waterfowl and shorebird species nesting on the coasts of Arctic seas and in coastal tundras, and millions of birds migrate every year along the coasts and over open sea waters (for review, see Ganter et al., 2013). Large flocks of migrating birds in stopover areas create conditions for the formation of local foci of helminth infection. Such a situation has been described in some regions of the southeastern Barents Sea (Pechora Sea), including Dolgy Island and Bolshoy Zelenets Island that are on the list of key ornithological areas of the Russian Arctic. Molting and migratory aggregations of the king eider (*Somateria spectabilis*), Steller's eider (*Polysticta stelleri*), common scoter (*Melanitta nigra*), velvet scoter (*Melanitta fusca*), and long-tailed duck (*Clangula hyemalis*) can be observed there from mid-July to mid-October (Krasnov et al., 2002, 2004). Their diet consists mainly of mussels, other mollusks, and crustaceans, which serve as intermediate hosts for bird helminths (Sukhotin et al., 2008; our unpublished data). These invertebrates from coastal zone around the

islands proved to be highly infected by the larvae of trematodes *Microphallus pseudopygmaeus*, *Tristriata anatis*, *Gymnophallus somateria* and *Renicola somateria*, cestodes *Microsomacanthus* spp., and acanthocephalans *P. phippsi*, which parasitize marine benthos-feeding ducks (our unpublished data).

In view of the above data, it is obvious that the rate of parasite infection in invertebrates can serve as a reliable indicator of both distribution and population dynamics of the final hosts of parasites. The parasitological survey in the Pechora Sea (1983−1985) revealed the foci of infection of benthic gastropods by parthenitae of trematodes whose adults parasitize birds (Galaktionov and Marasaev, 1986, 1990) (Fig. 4). These foci of molluskan infection proved to coincide with locations of summer−autumn aggregations of migrating waterfowl in the Pechora Sea, which were determined from the results of airplane observations in the 1990s (Krasnov et al., 2002, 2004) (Fig. 4).

Monitoring of infection of invertebrates with larvae of parasites can also give an idea of the long-term population dynamics of final hosts. This follows from the results of studies on the infection of littoral mollusk populations by trematode parthenitae in Chupa Bay (Kandalaksha Gulf, the White Sea). Since 1999, the prevalence of mollusks with trematodes whose final hosts are gulls and shorebirds has dropped sharply, but an increase has taken place in the infection with *Podocotyle atomon* whose adults parasitize coastal fishes (Levakin et al., 2013) (Fig. 5). This is in agreement with data on the population dynamics of final hosts: during the study period, the abundance of shorebirds in the Kandalaksha Bay has markedly decreased (Koryakin, 2012), but a population outbreak has occurred in the three-spined stickleback (*Gasterosteus aculeus*), which moves to the coast to spawn and rear (Laius et al., 2013). The abundance of these fish in the Chupa Bay alone has increased 20-fold since 2005 (Laius et al., 2011). They get infected by *P. atomon* when feeding on gammarid amphipods (the second intermediate hosts of this helminth), thereby contributing to intensification of parasite transmission in coastal ecosystems (Rybkina et al., 2016).

However, the density of final hosts is not the only factor determining the level of infection in intermediate hosts. An analysis of database on the infection of littoral mussels by trematode larvae in the North Atlantic and North Pacific has shown that the exposure of the coastal zone to wave action also has a significant effect on this parameter (Wilson et al., 2013). High wave activity interferes with host search and infection by free-swimming larvae and results in rapid removal of parasite eggs, which are washed down to deeper areas or up on the coast (James, 1968a; Galaktionov and Dobrovol'skii, 1986; Galaktionov, 1993). This, along with other factors, accounts for a low level of infection by trematode parthenitae in littoral mollusks near bird colonies in the Barents Sea coast. In

view of high bird abundance, this level should have been high as well, but the situation is different due to the location of the colonies on cliffs in coastal areas open to strong wave impact (Podlipaev and Golovkin, 1977; Galaktionov and Dobrovol'skii, 1986). Parameters of helminth infection in invertebrates along the coasts of Arctic seas reach the higher level in creeks and bays that are protected from powerful waves and frequented by birds and juvenile fish. Thus, in Yarnyshnaya Bay (the Barents Sea, eastern Murman), which projects inland for about 3 km, the prevalence of *Himasthla elongata* trematode parthenites in *Littorina saxatilis* mollusks reached 26% at the apex and gradually decreased toward the outlet, falling to zero at the bay mouth and adjacent areas of the open coast (Galaktionov et al., 1997).

The density of intermediate hosts also can have an effect on the level of their infection by parasite larvae. In the case of filter-feeder bivalves, it has been shown that an increase in their density (and, hence, total filtration activity) is accompanied by decrease in their prevalence with trematode larvae (metacercariae) (Mouritsen et al., 2003; Thieltges and Reise, 2007; Prinz et al., 2011). A probable explanation is that a finite number of cercariae in a given coastal area is distributed among greater number of hosts. This was confirmed by the results of our experiments on exposing cages with different densities of mussels in the littoral zone of Chupa Bay, the White Sea. They showed that the prevalence with metacercariae of *H. elongata* and *Renicola* sp. and their abundance (the average number of larvae per host in the total sample, including uninfected individuals) were lower in cages with higher mussel density, but the average number of larvae per unit area was found to increase in such cages. Thus, the transmission of cercariae proved to be more successful in a dense mussel settlement, despite relatively low values of standard infection indices.

The data available today show that the level of infection of invertebrate intermediate hosts in a given coastal region is determined by the interaction of many factors, with the key role being played by the abundance of final hosts. In addition to local environmental conditions, this process depends on the distribution (uniform, random, or aggregated) of potential intermediate hosts, their density and demographic composition, and specific features of the searching behavior of parasite larvae (Grosholz, 1994; Mouritsen et al., 2003; Thieltges and Reise, 2007; Prinz et al., 2011; Studer et al., 2013; Wilson et al., 2013; Galaktionov et al., 2015). All these factors should be taken into account when assessing the parasitological situation in a given region of the sea coast.

TEMPERATURE ADAPTATIONS

It is common knowledge that temperature is one of the key factors influencing vital functions of living organisms, especially poikilotherms (Precht et al.,
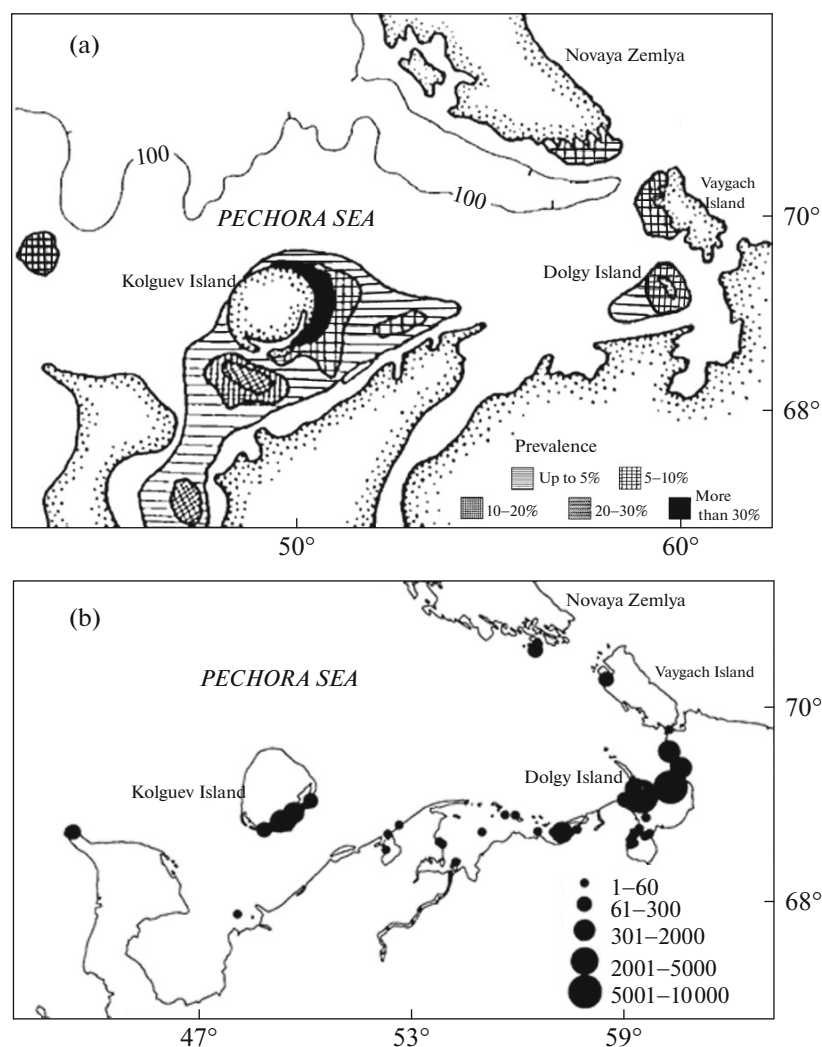
Fig. 4. Distribution patterns of (a) the prevalence by trematode parthenites and larvae in benthic mollusks of the Pechora Sea according to surveys in 1984−1985 (modified from Galaktionov, 1996) and (b) the abundance of ducks in the same regions according to airplane observations in August 1998 (modified from Krasnov et al., 2002).

1973). This category includes parasites. The highest dependence on temperature is characteristic of the stages of their life cycles that develop in poikilothermic hosts and, especially, of free-living stages (Pietrock and Marcogliese, 2003). Hence, it could be expected that the intensity of parasite transmission would decrease at high latitudes, but the actual situation is somewhat different. An analysis of original data on the infection of mussels by metacercariae of *Himastla* spp., *Renicola* spp., and *Gymnopphallus* spp. at the coasts of the northern Palearctic seas (from Ireland in the southwest to the Barents Sea in the northeast) did not reveal any significant differences in the prevalence and intensity of parasite infection along the temperature gradient (the maximum temperature of surface water layer was measured, with the difference between the extreme points reaching 14°C) (Galaktionov et al., 2015). Similar results were obtained in studies on the infection of bivalves *Austrovenus stutchburyi* by metacercariae of *Cututeria* spp. and *Acanthoparyphium* spp. along the coast of New Zealand (over about 12° of latitude, with the annual average temperature of surface water layer varying within a range of 7°C) (Studer et al., 2013).

These facts can be explained in the light of recent results of meta-analysis of cercaria production at different temperatures. They show that the daily average number of cercariae released from an infected mollusk at low latitudes (≤35° N) does not differ significantly from that at temperate latitudes (36°−60° N) (Thieltges et al., 2008; Studer and Poulin, 2014); likewise, no difference in this parameter has been revealed for the same or closely related trematode species from the White Sea (66° N) (Prokofiev et al., 2015). The reason is in the high acclimation capacity of trematodes (Morley and Lewis, 2014). It has become apparent
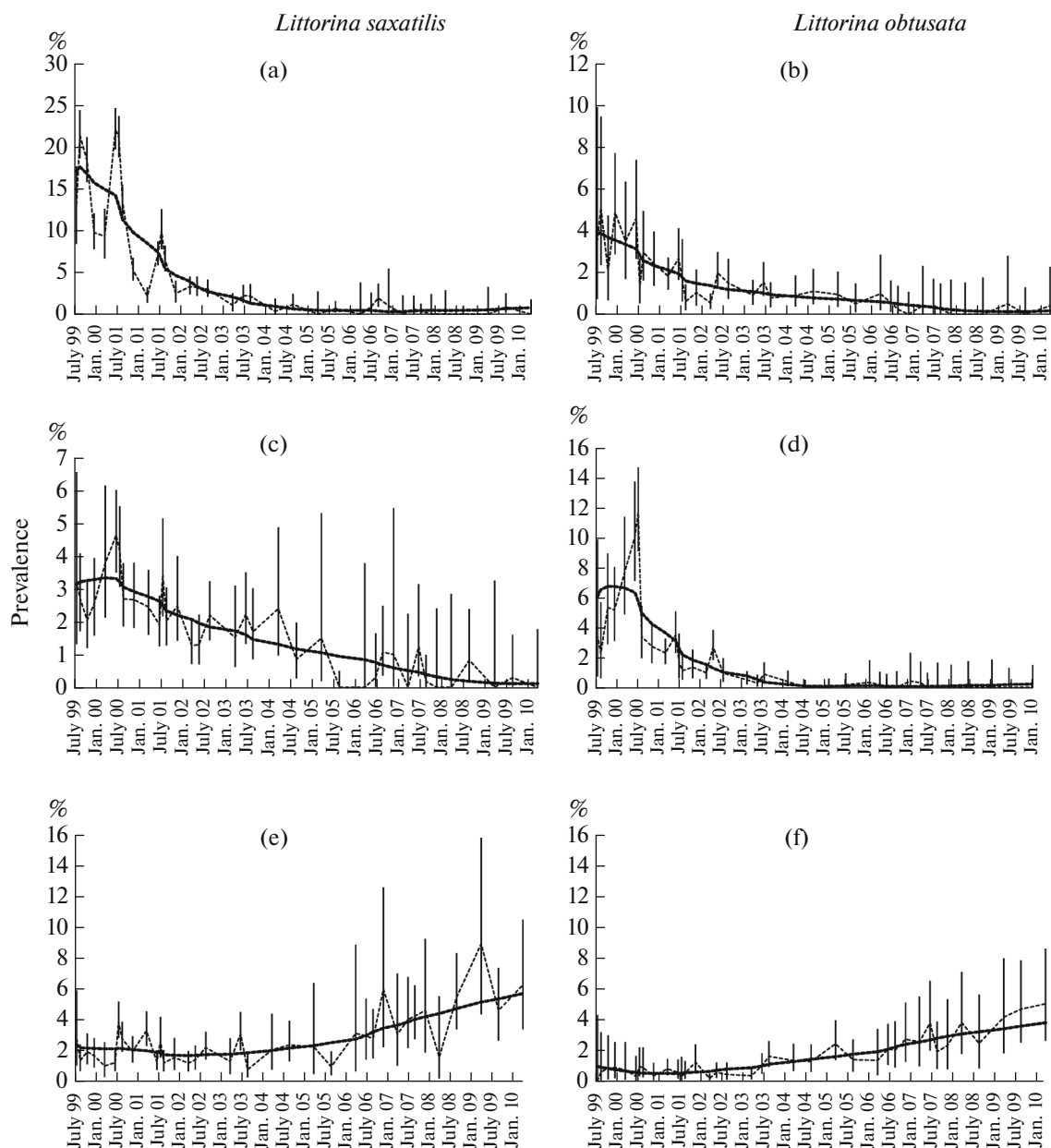
Fig. 5. Prevalence of trematode parthenitae in *Littorina saxatilis* and *L. obtusata* mollusks (broken line) and trend in its long-term dynamics revealed by singular spectral analysis (solid line) in the littoral site in Chupa Bay, the White Sea: (a–d), parasites of gulls, (e, f) parasite of fishes; (a, b) *Microphallus piriformes* with two-host life cycle; (c, d) *Renicola* sp., *Cryptocotyle lingua,* and *Microphallus similis* with tree-host life cycle; (e, f) *Podocotyle atomon.* Error bars show confidence intervals (modified from Levakin et al., 2013).

that the range of optimal temperatures for the development of cercariae in parthenitae and their emission widely varies depending on latitude. Thus, the daily average production of *Renicola* spp. cercariae from mollusks *Littorina littorea* and *Nucella lapillus* in the Barents Sea (69° N) and White Sea (66° N) is similar and does not differ significantly from this parameter for *R. roscovita* cercariae from *L. littorea* at the Danish coast of the Wadden Sea (54° N) (Prokofiev et al., 2015). However, the emission of cercariae in the Wad-

den Sea ceased completely when water temperature drops to 10°C (Thieltges and Rick, 2006), whereas this temperature in the Barents Sea is within the optimal range for the emission of *Renicola* spp. cercariae (Prokofiev et al., 2015).

In addition to acclimation, there is at least one more phenomenon related to temperature that contributes to the leveling of latitude-dependent differences in daily average cercaria production (Prokofiev

et al., 2015). Compared to the Arctic seas (e.g., the Barents Sea), the coastal zones of boreal seas and high-latitude seas with a specific hydrological regime (such as the White Sea) are characterized by greater differences between the minimum and maximum daily temperatures and illumination levels. During our studies on the rhythm of cercaria emission performed in situ in the littoral zones of White and Barents seas, the respective differences in the White Sea reached 10−15°C and tens to hundreds of thousands of lux, compared to only 3−4°C and 200 lx in the Barents Sea (Prokofiev et al., 2015). In the former case, the rapid increase in water temperature and illumination stimulated mass emission of almost all cercariae accumulated in mollusks, and this process was then interrupted (burst emission) (Fig. 6a). In the Barents Sea, the numbers of cercariae released per unit time were significantly smaller, but the period of their emission was much longer (prolonged emission) (Fig. 6b). Due to such an adaptation, trematodes implementing their life cycle in the Barents Sea can release a significantly greater number of cercariae, which is comparable to that in the boreal seas. This largely contributes to successful trematode transmission in the littoral ecosystems of northern seas.

The acclimation capacity of parasites is high, but not unlimited. The development and normal functioning of a parasitic system (the parasite population and populations of animal hosts associated with it) in the coastal waters of polar seas are possible only during the warm season (the "transmission window"), when all categories of hosts are available in the ecosystem and water temperature allows free-living stages to find and infect intermediate hosts. In the White Sea, the emission of trematode cercariae from infected mollusks is blocked when water temperature drops to 3−5°C; if the temperature remains low for a long time, the formation of embryos in the parthenitae is suspended and their groups enter hypobiosis (developmental arrest) (Galaktionov et al., 2006). This is also true of released parasite larvae enclosed in egg coats. Experiments on infecting White Sea *Hydrobia ulvae* mollusks by ingestion of *Bunocotyle progenetica* trematode eggs have shown that when the water temperature decreases to 4°C, the eggs passing through the gut remain intact and miracidia do not hatch from them (Galaktionov et al., 2006).

It should be noted that in the cold season, when birds fly away and fishes migrate from the coast, parasites do not disappear from the coastal ecosystems, although their transmission stops. Parasites at different stages of the life cycles survive in intermediate hosts and probably in the external environment (as cysts or eggs) and resume their activity and recover infectivity in spring, upon water warming and return of animals from wintering areas. Part of infected intermediate hosts die during the cold season, because the pathogenic effect of parasites makes them more vulnerable to other adverse factors. As a result, the preva-

lence of parasites in intermediate hosts is usually lower at the onset of the warm season than at the onset of the preceding cold season (Uspenskaya, 1963; Chubrik, 1966; McDaniel and Coggins, 1971; Boxshall, 1974; Pohley, 1976; Marasaeva, 1990; Galaktionov, 1992; Kube et al., 2002; etc.) (Fig. 7). The infection of intermediate hosts increases during the transmission window and, by autumn, reaches the levels characteristic of their populations in a given region. Naturally, the relevant parameters vary from year to year depending on a number of factors, both abiotic (primarily the temperature regime of the warm season) and biotic (fluctuations in the abundance of final hosts, density and age composition of intermediate hosts, etc.).

CLIMATE CHANGE AND TRANSMISSION

Until recently, it has been unequivocally accepted that climate warming will lead to intensification of parasite transmission in coastal marine ecosystems (Marcogliese, 2001; Galaktionov et al., 2006; Poulin, 2006; Studer et al., 2010; de Montaudouin et al., 2015). In trematodes, cercaria production will be intensified, with consequent increase in the infection of second intermediate hosts and then of all other hosts involved in the parasite life cycle (the so-called cascade effect; Hoberg et al., 2013). The examples of such an effect are described in the literature. Thus, the unusually high water temperature at the Wadden Sea coast in May 1990 (26°C) stimulated cercaria production in infected mollusks *Hydrobia ulvae,* which resulted in metacercarial hyperinfection and consequent mass mortality of second intermediate hosts, amphipods *Corophium volutator* (Jensen and Mouritsen, 1992; Mouritsen and Jensen, 1997). This had a serious impact on the ecosystem, because *C. volutator* amphipods (highly abundant in the region) serve as ecosystem engineers by building tubes of sand grains that form a kind of framework reinforcing the upper layer of bottom sediments. Their death resulted in substrate erosion in vast coastal shoals and changes in the structure of benthic communities, including the loss of several macrofaunal components (Mouritsen et al., 1998; Mouritsen and Poulin, 2002).

It should be noted that the disastrous consequences of the above events are explained by the fact that they were caused by a serious weather anomaly. According to recent climate models, warming in the Arctic will not be so dramatic: the predicted rise of annual average air temperature in this century will amount to 2.8−7.8°C (Kattsov and Källén, 2005; Dahl-Jensen et al., 2011; Overland et al., 2011). In the light of data on temperature acclimation of trematodes (see above), it is unlikely that the gradual rise of summer temperatures will result in appreciable intensification of their transmission. This appears to be also true of other parasitic worms, although their temperature adaptations in the coastal waters of Arctic seas have not been studied sufficiently. At the same time, the most significant
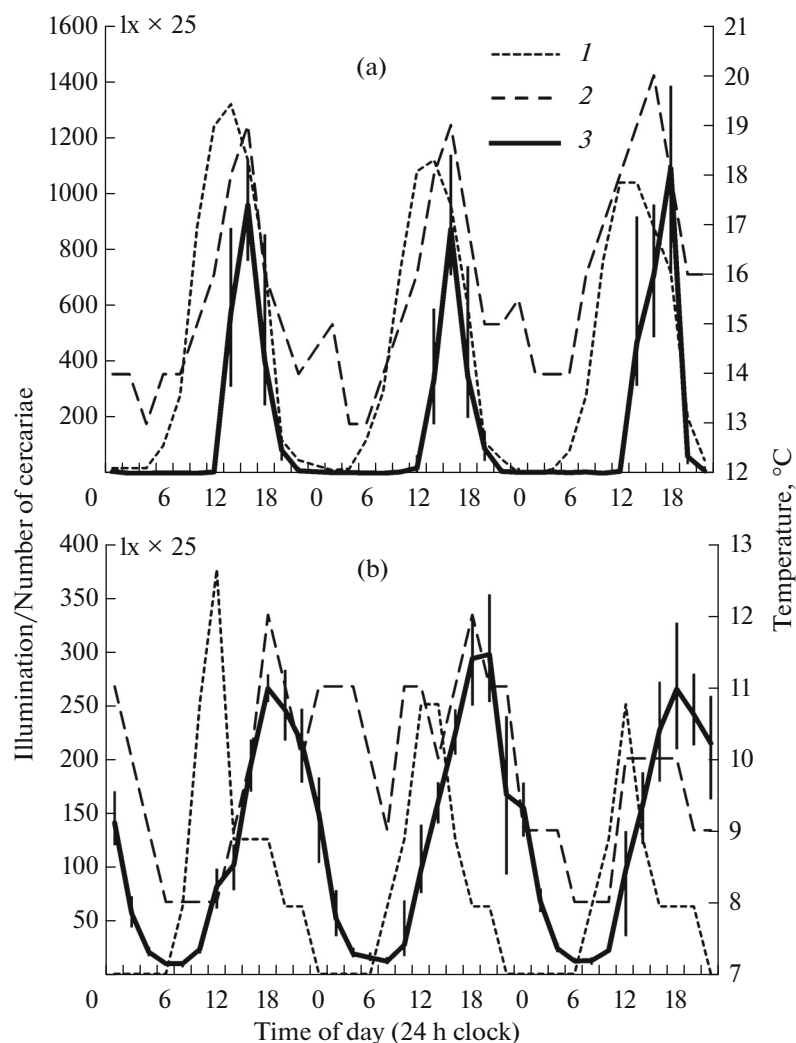
Fig. 6. Daily rhythms of emission of (a) *Renicola* sp. cercaria from *Littorina littorea* mollusks in the White Sea and (b) *R. thaidus* cercariae in the Barents Sea over 3 days at water temperatures of (a) 15.5 ± 0.5°C (13−20°C) and (b) 9.7 ± 0.4°C (8−12°C): (*1*) illumination level, lx; (*2*) water temperature, °C; (*3*) average number of cercariae released per 2 hours. Error bars show 95% confidence intervals (modified from Prokofiev et al., 2015).

warming in the Arctic is predicted for autumn and winter (Kattsov and Källén, 2005; Dahl-Jensen et al., 2011; Overland et al., 2011). This implies prolongation of the warm season (transmission window), which may well produce the aforementioned cascade effect (Hoberg et al., 2013).

Climate warming in the Arctic provides conditions for expansion of boreal species into Arctic seas, referred to as borealization (Payer et al., 2013). In particular, this concerns fishes and marine benthic animals (Denisenko, 2013; Josefson et al., 2013), including intermediate hosts of parasites circulating in the coastal waters of boreal seas. The presence of appropriate animal hosts and climate moderation will allow these parasites to implement their life cycles at high latitudes. For example, such a situation is observed in West Spitsbergen due to the influence of the warm

Spitzbergen Current (see above). In regard to trematodes, it may be expected that expansion to Arctic regions will be observed in the species that have a three-host life cycle with the free-living cercaria stage.

The final hosts of parasites also react to current climate change. Many bird species have already expanded their ranges northward, and this process will expectedly be progressing on a larger scale (Newton, 2003; Ganter et al., 2013). Conditions in Arctic ecosystems transformed under the effect of climate warming may prove favorable for some helminths carried by birds, allowing them to successfully implement their life cycle. This will facilitate the northward expansion of these parasites.

Climate warming may also lead to trans-Arctic interpenetration of the North Atlantic and North Pacific faunas, such as during the warm interglacials of

the Pleistocene (Hewitt, 1999, 2004; Avise and Walker, 1998; Briggs, 2003; Nikula et al., 2007; Newton, 2003). At present, the Taimyr Peninsula is a dividing point between the western and northern flyways of many waterfowl and shorebird species (Alerstam and Gudmundsson 1999; Petersen et al., 2006; Alerstam et al., 2007; Bustnes et al., 2010). These flyways were established after the last glaciation, and their segregation created a barrier to the circumpolar distribution of many parasites, with consequent geographic partitioning into the North Atlantic and North Pacific parasite populations and, in some cases, sister species (Hoberg, 1986, 1992, 2005; Hoberg and Adams, 2000; Galaktionov et al., 2012). Changes in bird migration routes and the expansion of intermediate hosts in the coastal zones of Siberian seas can facilitate faunal interpenetration.

A relevant example is as follows. A recent parasitological survey of common and thick-billed murres (*Uria aalge* and *U. lomvia*) in colonies on the western coast of Canada (Nunavut, Labrador, and Newfoundland) and in Greenland has revealed their infection by the cestode *Alcataenia longicervica,* which did not occur in these regions previously and was regarded as endemic to the Pacific (Hoberg, 1986; Muzzafar et al., 2005; Muzzafar, 2009). Intermediate hosts of *A. longicervica* are planktonic euphausiids *Thysanoessa* spp., which are abundant in the Bering, Chukchi, and Beaufort seas. It is these crustaceans that are considered to be responsible for the infection of Atlantic murres, since changes in the pattern of ocean currents under the effect of climate warming provided for their transfer to the seas of the Siberian Arctic and Labrador. As a result, Pacific euphausiids (including those infected by *A. longicervica* larvae) eventually entered the range of Atlantic murre populations (Muzzafar, 2009).

The above data show that our knowledge of the biodiversity, life cycles, adaptations, and ecosystem role of parasites circulating in the coastal zones of Arctic seas is far from being complete. Meanwhile, the significance of research in this field can hardly be overestimated. Parasites have a strong effect on the populations of animal hosts, are involved in the fluxes of matter and energy, and may have a role in the formation, stabilization, and transformation if communities and ecosystems (Thomas et al., 1999, 2005; Hudson et al., 2006; Poulin, 2007; Lafferty et al., 2008). All these processes in the Arctic and Subarctic obviously have certain specific features, and some of them are addressed in this review. Ecoparasitological studies are becoming increasingly important in the context of perturbations and modifications in ecosystems caused by anthropogenic impact and climate change, which is especially evident in the Arctic (Callaghan et al., 2004; Brooks and Hoberg, 2007; Hoberg et al., 2008, 2013; Burrows et al., 2011; etc.). Since Arctic ecosystems are highly vulnerable (*Arctic Biodiversity...,* 2013), any changes in the composition of parasites and the pat-
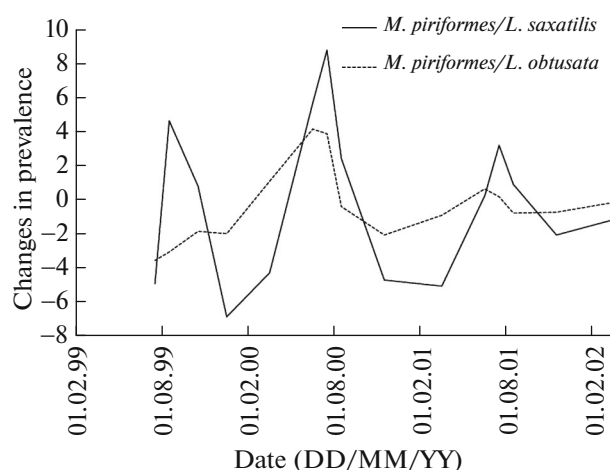

Fig. 7. Mode of singular spectrum analysis corresponding to seasonal dynamics of the prevalence by parthenitae and larvae of trematode *Microphallus piriformes* in mollusks *Littorina saxatilis* and *L. obtusata* in the littoral site in Chupa Bay, the White Sea (according to Levakin et al., 2013).

tern of their transmission under the effects of these events may have serious ecological consequences. This is why the assessment of current parasitological situation in different regions of the Arctic and Subarctic and determination of the main vectors of its development are issues of high priority. They can be resolved by performing a complex of parasitological studies aimed an analyzing not only the biodiversity of parasites but also of their transmission pathways and adaptation capacities. Long-term parasitological monitoring at different reference sites of the Arctic sea coast should be an essential component of these studies.

ACKNOWLEDGMENTS

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