Review

Impact of anthropogenous environmental factors on the marine ecosystem of trophically transmitted helminths and hosting seabirds: Focus on North Atlantic, North Sea, Baltic and the Arctic seas

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Article info

Summary

Alongside natural factors, human activities have a major impact on the marine environment and thus influence processes in vulnerable ecosystems. The major purpose of this review is to summarise the current understanding as to how man-made factors influence the marine biocenosis of helminths, their intermediate hosts as well as seabirds as their final hosts. Moreover, it highlights current knowledge gaps regarding this ecosystem, which should be closed in order to gain a more complete understanding of these interactions. This work is primarily focused on helminths parasitizing seabirds of the North Atlantic and the Arctic Ocean.

The complex life cycles of seabird helminths may be impacted by fishing and aquaculture, as they interfere with the abundance of fish and seabird species, while the latter also affects the geographical distribution of intermediate hosts (marine bivalve and fish species), and may therefore alter the intertwined marine ecosystem. Increasing temperatures and seawater acidification as well as environmental pollutants may have negative or positive effects on different parts of this interactive ecosystem and may entail shifts in the abundance or regional distribution of parasites and/or intermediate and final hosts. Organic pollutants and trace elements may weaken the immune system of the hosting seabirds and hence affect the final host's ability to control the endoparasites. On the other hand, in some cases helminths seem to function as a sink for trace elements resulting in decreased concentrations of heavy metals in birds' tissues. Furthermore, this article also describes the role of helminths in mass mortality events amongst seabird populations, which beside natural causes (weather, viral and bacterial infections) have anthropogenous origin as well (e.g. oil spills, climate change, overfishing and environmental pollution).

Keywords: Helminths; seabirds; fisheries; aquaculture; climate change; seawater acidification; microplastic; organic pollutants; trace elements

Introduction

During the last decades significant declines in the North Atlantic populations of numerous seabird species were observed, including Atlantic puffins (*Fratercula arctica*), black-legged kittiwakes (*Rissa tridactyla*), common eiders (*Somateria mollissima*) and northern fulmars (*Fulmarus glacialis*) (Anker-Nilssen *et al.*, 2019; Blew *et al.*, 2017; Mallory *et al.*, 2020). These declines are not limited to populations in the North Atlantic, but can rather be observed globally, affecting 47 % of all seabirds (Dias *et al.*, 2019). The reasons for such declines are multifactorial. One relevant stressor, which is a natural part of the marine ecosystem of sea-

birds are endoparasites, especially trophically-transmitted helminths. The complex antagonistic parasite-host relationships of helminths with their hosts are co-evolutionary in origin, and the relationship between the host's burden by the parasite and the host's defense mechanisms is crucial for the expression of pathological processes (Lucius *et al*., 2018). External confounders of these relationships may have positive or negative effects on populations of helminths, their intermediate as well as final hosts (Sure & Nachev, 2022), and may also amplify the pathological effects of helminths (Byers, 2021). While direct negative effects of environmental factors only have fatal consequences in seabirds severly infected with helminths (Galaktionov, 1996a), such environmental factors may subtly impact the parasite-host relationships of marine helminths with intermediate hosts and seabirds (Sagerup *et al*., 2000; Wayland *et al*., 2001; Muzzafar, 2009). However, evaluation of the overall impact of environmental stressors on the interaction between parasites and seabird populations are still in their infancy (Khan *et al*., 2019).

Many other factors and stressors that negatively impact the seabird's health further are related to human activities. These include
– climate change (Lindegren *et al*., 2018; Dias *et al.,* 2019),
– predation by introduced alien species such as rats (*Rattus spec.*) and cats (*Felis catus*) on breeding grounds (Dias *et al.* 2019),
– decrease in forage fish populations caused by commercial fishing of these fish species (Lindegren *et al.* 2018)
– reduction of discard quantities in fisheries caused by changed policies promoting more sustainable fisheries (Sherley *et al*., 2019),
– bycatch mortality in gillnet and pelagic longline fisheries (Cleasby *et al*., 2022; Zhou *et al*., 2020), and
– ingestion of plastic marine litter by seabirds foraging on the water surface (Van Franeker *et al*., 2021).

Organic pollutants and toxic trace elements released into the environment from human activities are additional physiological stressors for seabirds (Sonne *et al*., 2020; Dietz *et al*., 2019), because they enter the food chain and accumulate in the seabirds' prey (He & Wang, 2013; Mititelu *et al*., 2018).

Generally, the number of publications which integrate parasite-host-relationships in studies on the marine ecosystem is scarce (Poulin *et al*., 2014), particularly with regard to how the biocenoses of parasites and hosts are influenced by anthropogenous environmental factors. This review focuses on anthropogenic stressors that could affect parasite-host systems of seabirds, namely fisheries, aquaculture, temperature and seawater acidification, plastic marine litter, organic pollutants and trace elements released by human activities. The article explores whether these factors also influence the helminths and the health of their intermediate and final hosts. Furthermore, the impact of these stressors on the interaction between the parasites and their intermediate as well as their final hosts is also discussed. Moreover, the present review tries to elucidate major existing gaps of knowledge.

Infections with trophically transmitted helminths are widespread in long-lived seabirds, i.e. offshore, pelagic and coastal birds, whose normal habitat and food source is the sea (Harrison *et al*., 2021). The parasitic worms which have been isolated from seabirds belong to the three common phyla of the polyphyletic group of helminths: platyhelminthes (cestodes and trematodes), nemathelminthes (nematodes) and acanthocephalans (Galaktionov & Bustnes, 1999; Mallory *et al*., 2007; Kuklin, 2017). Prevalence and intensity of helminth infestation vary, but in some cases both prevalence among a population and/or intensity per seabird may reach extremely high numbers (Galaktionov, 1996b; Mallory *et al*., 2007; Muzaffar, 2009). Many seabird helminths have complicated life cycles, often involving more than one intermediate host, as well as free-living stages (Galaktionov, 1996b). As far as their life cycles are known digenea species found in seabirds of the North Atlantic and adjacent seas always use molluscs as their first intermediate host. Insofar as they parasitize a secondary intermediate host they can use molluscs, polychaetes or fishes (Table 1). Cestodes and nematodes primarily parasitize different crustacean species and fishes as their intermediate host, though they occasionally also use polychaetes and, in the case of cestodes, even insect larvae (Tables 2 and 4). The acanthocephala detected in the seabirds analysed by the studies exclusively use crustacean species as intermediate hosts (Table 3). The infection of seabirds normally occurs through ingestion of the intermediate hosts as prey (Born-Torrijos *et al*., 2016; Lucius *et al*., 2018).

The presence of intermediate and final hosts is a necessary condition for trophically transmitted helminths to complete their life cycles. Infestations of first and second intermediate hosts may vary depending on seasonal and environmental factors (Nikolaev *et al*., 2020; Lafferty *et al.,* 1999; Koprivnikar *et al*., 2010). For example, Periwinkles (Littorinidae) exhibit a wide range of infection prevalences with larval trematodes of up to 77 % (Laukner, 1984). These snails serve as first intermediate host for several seabird trematodes (Table 1). Infection rates with trematode larvae were particularly high for the following second intermediate hosts: blue mussels (*Mytilus edulis*) 95 %, sandeels (*Ammodytes tobianus)* 90 %, and European sprats (*Sprattus sprattus*) 90 % (Galaktionov *et al*., 2015; Thieltges *et al*., 2006a; Groenewold *et al*., 1996; O'Connell & Fives, 2004; Kleinertz *et al*., 2012).

As shown for the trematode genera *Gymnophallus*, *Himasthla* and *Renicola,* infection rates of the second intermediate host *Mytilus edulis* correlate with local bird incidence, mussel age and mussel density (Galaktionov *et al*., 2015). It can thus be assumed that the prevalence of helminth infections in seabirds will vary depending on the abundance of infected first or second hosts (if any). This assumption is supported by two studies, which showed that the abundance (Bommarito *et al*., 2020) or the prevalence and abundance (Thieltges & Reise 2007) of infections with trematode species in secondary intermediate hosts, is dependent on the density of infected initial intermediate hosts.

Considering the substantial decline in seabird populations,

Table 1. Marine digenean species (Trematoda) determined in seabirds of the North Atlantic, the Barent Sea, as well as the Baltic and the North Sea. Only those species are listed for which at least one intermediate and one final host are known.

Digenea	First intermediate host	Second intermediate host	Final host
Gymnophallidae			
Gymnophallus deliciosus	?	Blue Mussel (Mytilus edulis)[16]	European Herring Gull (Larus argentatus)[15]
Gymnophallus bursicola	Unknown[18]	Mytilus edulis[18]	Common Eider (Somateria mollissima)[18] Velvet scoter (Melanitta fusca)[30]
Gymnophallus choledochus	Bivalvia: Cestoderma edule[12]	Polychaeta[1] (Hediste diversicolor, Arenicola marina etc.)[12] or alternatively Cestoderma spec. [12]	Common Eider (Somateria mollissima)[3,26]
Parvatrema spec.	Unknown[2]	Littorina saxatilis[2,11], Littorina obtusata[2,11]	Common Eider (Somateria mollissima)[3] Long-tailed Duck (Clangula hyemalis)[10] Velvet Scoter (Melanitta fusca)[10] Common Scoter (Melanitta nigra)[10]
Microphallidae			
Microphallus triangulus	Littorina saxatilis[2,5,20], Littorina obtusata[2,5]	None[2]	Common Eider (Somateria mollissima)[3]
Microphallus pygmaeus	Littorina saxatilis[2,5,11,20], Littorina obtusata[2,5,11], Littorina littorea[2]	Littorina spec.[24]	Common Eider (Somateria mollissima)[3,20] Great Black-backed Gull (Larus marinus)[4] European Herring Gull (Larus argentatus)[4,15]
Microphallus pseudopygmaeus	Littorina saxatilis[2,5,11,20], Littorina obtusata[2,5,11], Onoba aculeus[2], Margarites helicinus[2], Margarites groenlandicus[2,20], Lacuna vincta[2]	None[2]	Common Eider (Somateria mollissima)[3,19] Glaucous Gull (Larus hyperboreus)[27]
Microphallus piriformes	Littorina saxatilis[2,5,11,20], Littorina obtusata[2,5,11]	None[2]	Common Eider (Somateria mollissima)[3] Great Black-backed Gull (Larus marinus)[4], European Herring Gull (Larus argentatus)[4,15]
Microphallus similis	Littorina saxatilis[2,11], Littorina obtusata[2,11], Littorina littorea[2]	Crustacea: Carcinus maenas[2], Hyas araneus[2]	Great Black-backed Gull (Larus marinus)[4] European Herring Gull (Larus argentatus)[4,15]
Maritrema arenaria	Littorina saxatilis[2,11]	Crustacea: Semibalanus balanoides[2]	Great Black-backed Gull (Larus marinus)[4] European Herring Gull (Larus argentatus)[4] Glaucous Gull (Larus hyperboreus)[3]

	First intermediate host	Second intermediate host	Final hosts
Opisthorchidae			
Cryptocotyle lingua	*Littorina littorea*[2], *Littorina saxatilis*[2,11], *Littorina obtusata*[2,11]	Pisces (*Ammodytes tobianus, Gadus* spec.*, Sprattus sprattus, Salmo* spec.,, Pleuronectiformes)[2,17,23]	Common Guillemot (*Uria aalge*)[4] Brünnich's Guillemot (*Uria lomvia*)[4,6] Black-legged Kittiwake (*Rissa tridactyla*)[4,6] Great Black-backed Gull (*Larus marinus*)[4] European Herring Gull (*Larus argentatus*)[4,15] Glaucous Gull (*Larus hyperboreus*)[3,27] Northern Fulmar (*Fulmarus glacialis*)[21]
Cryptocotyle concavum	*Hydrobia ventrosa*[8], *Hydrobia ulvae*[9]	Pisces (*Platichthys flesus*[9], *Pomatoschistus microps*[10], *Pungitius pungitius*[10], *Gasterosteus aculeatus*[10])	Black-headed Gull (*Chroicoceohalus ridibundus*)[10] Black-legged Kittiwake (*Rissa tridactyla*)[4,6] Northern Fulmar (*Fulmarus glacialis*)[21]
Diplostomidae			
Diplostomum nordmanni	Gastropoda[7]	Pisces[7]	Black-legged Kittiwake (*Rissa tridactyla*)[4,6]
Notocotylidae			
Notocotylus spec.	*Littorina saxatilis*[2,11], *Littorina obtusata*[2,11], *Skeneopsis planorbis*[2]	None[2]	Seaducks[13] European Herring Gull (*Larus argentatus*)[4,15] Oystercatcher (*Haematopus ostralegus*)[14]
Renicolidae			
Renicola spec.	*Littorina saxatilis*[2,11], *Littorina obtusata*[2,11], *Littorina littorea*[2]	*Mytilus edulis*[2], *Littorina* spp.[2]	Common Eider (*Somateria mollissima*)[3] Common Gull (*Larus canus*)[10] Velvet Scoter (*Melanitta fusca*)[10] Long-tailed Duck (*Clangula hyemalis*)[10] Cormorant (*Phalacrocorax carbo*)[10] Shelduck (*Tadorna tadorna*)[10] Manx Shearwater (*Puffinus puffinus*)[25]
Himasthlidae			
Himasthla spec.	*Littorina saxatilis*[2,11], *Littorina obtusata*[2,11], *Littorina littorea*[2]	*Mytilus edulis*[2]	Great Black-backed Gull (*Larus marinus*)[4] European Herring Gull (*Larus argentatus*)[4,15] Glaucous Gull (*Larus hyperboreus*)[3]
Echinochasmidae			
Mesorchis pseudoechinatus	unknown	Pisces[29]	Black-legged Kittiwake (*Rissa tridactyla*)[28] Cormorant (*Phalacrocorax carbo*)[29]

Data from: [1]Frank, 1969; [2]Galaktionov & Bustnes, 1999; [3]Kuklin, 2015; [4]Kuklin, 2017; [5]Sergievsky et al., 1997; [6]Kuklin et al., 2020; [7]Faltýnková et al., 2014; [8]Probst & Kube, 1999; [9]Zander et al., 1984; [10]Reimer, 2002; [11]Galaktionov, 1996; [12]Magalhães et al., 2020; [13]Galaktionov & Bustnes, 1996; [14]Borgsteede et al., 1988; [15]Kuklin, 2011; [16]Ching, 1991; [17]Heuch et al., 2011; [18]Galaktionov et al., 2015; [19]Galaktionov et al., 2021; [20]Galaktionov et al., 2019; [21]Kuklin et al., 2019; [22]O'Connell & Fives, 2004; [23]Groenwold et al., 1996; [24]Thieltges et al., 2006a; [25]De Matos et al., 2020; [26]Thieltges et al., 2006b; [27]Sagerup et al., 2009; [28]Kuklin & Kuklina, 2022; [29]Kanarek et al., 2003.

clarifying the influences of anthropogenic environmental factors on the parasite-host systems of marine helminths and the effects on seabird populations is of general interest. Fisheries, aquaculture, global warming and ocean acidification, plastic waste, persistent organic pollutants and heavy metal inputs were chosen as human-induced environmental factors, as they affect various aspects of the marine environment. However, the large number of complex parasite-host systems makes it necessary to limit this review regionally to seabirds and their parasitizing helminths living in the North Atlantic, North Sea, Baltic Sea, and Barents Sea. Thus, the list of final hosts is limited to seabirds of the orders Procellariiformes (petrels, shearwaters and fulmars), Gaviiformes (divers), Anseriformes (seaducks), Charadriiformes (auks, phalaropes, gulls, skuas, terns, plover-like waders) and Suliformes (cormorants, gannets). The nomenclature and taxonomy of the helminth species described here follows that given in the World Register of Marine Species (WoRMS Editorial Board, 2022).

The Influence of Fisheries

Decrease of forage fish stock, such as those of sandeels and European sprats, is a stressor for both ichthyophagous seabirds and helminths because breeding success of seabirds depends on the availability of forage fish (Matthew *et al*., 2017; Guillemette *et al*., 2018). Thus, reduced abundance of such fishes as intermediate hosts may impair the chances of helminths to complete their life cycle successfully (Wood *et al*., 2010). Different studies described that long-term intensive fishing lead to a reduced parasitisation of fishes by helminths and to a decreased diversity of parasite species (Lafferty & Kuris, 1999; Marzoug *et al*., 2012; Wood *et al*., 2014; Vidal-Martinez *et al*., 2019). Heavy fishing results not only in a reduced parasitisation level on the fish stocks but also in the intermediate hosts, such as snails and mussels (Wood *et al*., 2014). On the other hand, the discarding of fishery waste leads to an increase in parasite numbers in the immediate surroundings. In areas with intensive fishing activities the highest prevalence of the trematode *Cardiocephaloides longicollis* occurred in fish captured close to harbours frequented by vessels with high fish hold capacities (Born-Torrijos *et al*., 2016). For many seabirds fish waste represent a relevant food source (Sherley *et al*., 2020). Herring gulls (*Larus argentatu*s), great black-backed gulls (*Larus marinus*), cape gannets (*Morus capensis*), and procellarids such as great shearwaters (*Ardenna gravis*), sooty shearwaters (*Ardenna grisea*) or northern fulmars, seem to use fishery discard particularly when availability of their natural prey declines (Tew Kai *et al*., 2016; Maynard *et al*., 2020). Fishery discard thus brings the potential intermediate hosts and the final host particularly closely together, and thus improves the chances for helminths to complete their life cycle. Changes in fishery waste policies, such as the European Union's Landing Obligation, which drastically reduce the practice, will thus decrease the availability of fish waste for scavenging seabirds (Sherley *et al*., 2020) and may consequently reduce inflated seabird communities that feed on fishery discard (Sherley *et al*., 2020) and negatively impact the hosted parasites (Tables 1 – 4). Fisheries management measures should lead to reduced competition for seabird forage fishes such as sandeels (Tasker & Sydeman, 2022) and reduced seabird bycatch (Melvin *et al*., 2022). Protection of marine habitats (Ronconi *et al*., 2022) should also have a positive impact on seabird populations and thus on the parasite-host relationships of helminths and seabirds.

The Influence of Aquaculture

On helminths – Aquaculture of non-native fish species may entail the introduction of helminth species to new regions which they did not previously inhabit. This intensifies the ecological effects of the parasites, insofar as the native fish species are susceptible to the introduced parasites (Soler-Jiménez *et al*., 2017). Examples of non-native fish-farmings are aquacultures of salmonids in the southern hemisphere (Blanco *et al*., 2015): Atlantic salmon (*Salmo salar*), coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*), all native in the northern hemisphere, are frequently bred in marine fish farms in South America (Soler-Jiménez *et al*., 2016). In these farmed salmonid species infections with monogeneans, larval forms of digeneans, nematodes, cestodes and acanthocephalans – at least some of which are not native in the region – were recorded (Soler-Jiménez *et al*., 2016). In fact, Soler-Jiménez *et al*. (2016) assessed that more than 90 % of the helminths affecting fishes in aquaculture conditions in Latin America are non-native. However, data on the influence of non-native endoparasites originating from marine aquaculture on the ambient native fish species is rather limited and requires further analysis.

Aquacultures may additionally increase the importance of avian fish predators for the life-cycles of digeneans, nematodes, cestodes and acanthocephalans, aside from merely serving as final hosts (Murugami *et al*., 2018). Seabirds gather near fish farms (Buschmann *et al*., 2006; Aguado-Giménez *et al*., 2018; Surman & Dunlop, 2015) which will lead to a more concentrated release of seabird faeces into the aquaculture's immediate surroundings. Larvae of helminths contained in the faeces are thereby brought into more concentrated contact with their primary intermediate hosts (e.g. snails), which increases the local infection success rate. In turn, more infected first intermediate hosts release more cercariae, which may then increase the infection rate of the second intermediate hosts (Studer *et al*., 2013; Galaktionov *et al*., 2015) and thus drive the life cycles of helminths (Fig. 1).

On seabirds – Unprotected aquaculture may have positive impacts on at least some seabirds. The high fish density in marine aquaculture is attractive for ichthyophagous birds, such as gulls and cormorants (Buschmann *et al*., 2006; Aguado-Giménez *et al*., 2018; Barret *et al*., 2019; Surman & Dunlop, 2015). The additional food resources can result in improved breeding success of these

Table 2. Cestodes determined in seabirds of the North Atlantic, the Barent Sea as well as the Baltic Sea and the North Pacific. In addition, intermediate hosts are named as far as known.

Cestoda (Tapeworms)	Intermediate hosts	Final host
Dilepididae		
Alcataenia armillaris	Crustacea, Euphausiids of the genus *Thysanoessa*[6]	Common Guillemot (*Uria aalge*)[2,3] Brünnich's Guillemot (*Uria lomvia*)[2,3,5,10] Black-legged Kittiwake (*Rissa tridactyla*)[3,5,10]
Alcataenia dominicana	Crustacea, Euphausiids of the genus *Thysanoessa*[6]	Black-legged Kittiwake (*Rissa tridactyla*)[3,10] Great Black-backed Gull (*Larus marinus*)[3] European Herring Gull (*Larus argentatus*)[3] Glaucous Gull (*Larus hyperboreus*)[4,7,22]
Alcataenia larina	Crustacea, Euphausiids of the genus *Thysanoessa*[1,6]	Atlantic Puffin (*Fratercula arctica*)[1] Black Guillemot (*Cephus grille*)[1] Black-legged Kittiwake (*Rissa tridactyla*)[1,3,5,10] Great Black-backed Gull (*Larus marinus*)[1,3] European Herring Gull (*Larus argentatus*)[1,3] Glaucous Gull (*Larus hyperboreus*)[4] Northern Fulmar (*Fulmarus glacialis*)[1,21]
Alcataenia longicervica	Crustacea, Euphausiids of the Genus *Thysanoessa*[20]	Common Guillemot (*Uria aalge*)[20] Brünnich's Guillemot (*Uria lomvia*)[20]
Neovalipora spec.	Pisces[8]	Brünnich's Guillemot (*Uria lomvia*)[3,10]
Paricterotaenia porosa	*Chironomus* spec.[9]	Great Black-backed Gull (*Larus marinus*)[3] European Herring Gull (*Larus argentatus*)[3] Black-legged Kittiwake (*Rissa tridactyla*)[10]
Paricterotaenia sternina	?	European Herring Gull (*Larus argentatus*)[3]
Anomotaenia microcantha	1. Crustacea[16] 2. Pisces[16]	Black-legged Kittiwake (*Rissa tridactyla*)[3,10] European Herring Gull (*Larus argentatus*)[3] Common Gull (*Larus canus*)[16] Glaucous Gull (*Larus hyperboreus*)[5,22]
Lateriporus teres	Amphipoda (*Amphitoe rubricata*)[4]	Common Eider (*Somateria mollissima*)[4,20]
Hymenolepididae		
Microsomacanthus ductilis	Gammaridae[12]	Common Guillemot (*Uria aalge*)[3], Brünnich's Guillemot (*Uria lomvia*)[5,10] Great Black-backed Gull (*Larus marinus*)[3] European Herring Gull (*Larus argentatus*)[3] Black-legged Kittiwake (*Rissa tridactyla*)[10] Common Gull (*Larus canus*)[16] Glaucous Gull (*Larus hyperboreus*)[22] Common Eider (*Somateria mollissima*)[20]
Microsomacanthus diorchis	Gammaridae[12]	Common Eider (*Somateria mollissima*)[4,20] Black-legged Kittiwake (*Rissa tridactyla*)[10]
Microsomacanthus microsoma	Gammaridae[12] (*Gammarus setosus*)[20]	Common Eider (*Somateria mollissima*)[4,20] European Herring Gull (*Larus argentatus*)[17] Long-tailed Duck (*Clangula hyemalis*)[16] Velvet Scoter (*Melanitta fusca*)[16] Northern Fulmar (*Fulmarus glacialis*)[21]
Microsomacanthus jaegerskioeldi	Gammaridae[12]	Common Eider (*Somateria mollissima*)[4,20]
Fimbriarioides intermedia	Copepoda[18], Ostracoda[18], *Semibalanus balanoides*[4] *Balanus balanoides*[20]	Common Eider (*Somateria mollissima*)[4,20]

Laricanthus lateralis	?	European Herring Gull (*Larus argentatus*)[3]
Nadejdolepsis nutidulans	?	Black-legged Kittiwake (*Rissa tridactyla*)[3,5,10]
Wardium cirrosa	Nereidae[13]	Great Black-backed Gull (*Larus marinus*)[3] European Herring Gull (*Larus argentatus*)[3] Glaucous Gull (*Larus hyperboreus*)[4] Common Gull (*Larus canus*)[16] Northern Fulmar (*Fulmarus glacialis*)[21]
Wardium fryei	Nereidae[15]	Great Black-backed Gull (*Larus marinus*)[3] European Herring Gull (*Larus argentatus*)[3] Glaucous Gull (*Larus hyperboreus*)[4]
Wardium fusa	Crustacea (Branchiopoda[14])	Great Black-backed Gull (*Larus marinus*)[3] Purple Sandpiper (*Calidris maritima*)[4]
Wardium manubriatum	Crustacea (Branchiopoda[14])	Black-legged Kittiwake (*Rissa tridactyla*)[10]
Aploparaksis crassirostris	Oligochaeta[19]	European Herring Gull (*Larus argentatus*)[3]
Diphyllobotriidae		
Diphyllobotrium dendriticum	1. Copepoda[11, 16] 2. Pisces[11]	Great Black-backed Gull (*Larus marinus*)[3] European Herring Gull (*Larus argentatus*)[3] Cormorant (*Phalacrocorax carbo*)[16]
Tetrabothriidae		
Tetrabothrius erostris	1. Planktonic Crustacean[6] 2. Arctic cod? (*Boreogadus saida*)[5]	Brünnich's Guillemot (*Uria lomvia*)[5,10] Great Black-backed Gull (*Larus marinus*)[3] European Herring Gull (*Larus argentatus*)[3] Black-legged Kittiwake (*Rissa tridactyla*)[3,10] Glaucous Gull (*Larus hyperboreus*)[5,22]
Tetrabothrius cylindraceus	1. Planktonic crustacean[6] 2. Arctic cod? (*Boreogadus saida*)[5]	Black-legged Kittiwake (*Rissa tridactyla*)[10] European Herring Gull (*Larus argentatus*)[16]
Tetrabothrius jaegerskioeldi		Common Guillemot (*Uria aalge*)[3] Brünnich's Guillemot (*Uria lomvia*)[10]
Tetrabothrius morschtini		Black-legged Kittiwake (*Rissa tridactyla*)[5,10] Glaucous gull (*Larus hyperboreus*)[5]
Tetrabothrius immerinus		Great black-backed Gull (*Larus marinus*)[3] European Herring Gull (*Larus argentatus*)[3] Black-legged Kittiwake (*Rissa tridactyla*)[3,10]
Tetrabothrius bassani		Atlantic Gannet (*Morus bassani*)[23]

Data from: [1]Muzzaffar *et al*., 2007; [2]Hoberg, 1984; [3]Kuklin, 2017; [4]Kuklin, 2015; [5]Galaktionov, 1996; [6]Hoberg, 1996; [7]Sagerup *et al*., 2000; [8]Ortega-Olivares & Garcia-Varela, 2018; [9]Krasnoshchekov & Tomilovskaia, 1978; [10]Kuklin *et al*., 2020; [11]de Marval *et al*., 2013; [12]Kuklin & Maslich, 2011; [13]Greben *et al*., 2019; [14]Maksimova, 1990; [15]Bondarenko, 1997; [16]Reimer, 2002; [17]Kuklin, 2011; [18]McDonald, 1996; [19]Jarecka, 1961; [20]Galaktionov *et al*., 2021; [21]Kuklin *et al*., 2019; [22]Sagerup *et al*., 2009; [23]Mendes *et al*., 2013.

birds and thus lead to increasing populations in the surrounding area. The increased competition may however detrimentally impact other regional seabirds less assertive than the benefiting species (Surman & Dunlop, 2015). One smaller negative impact is that these piscivore seabirds may be entangled in the mesh of the walls of the cages and drown (Surman & Dunlop, 2015). However, in order to avoid losses of farmed fish, many farmers prevent the seabirds' access to the marine aquaculture through nets (Quick *et al*., 2004).

On the ambient fauna – Marine aquacultures attract wild fishes from the surrounding area which leads to cross-contagion of parasites between wild and farmed fish species (Bouwmeester *et al*., 2021; Callier *et al*., 2018; Arechavala-Lopez *et al*., 2013). While a lot of data exists on the occurrence and pathologic role of different monogeneans in finfish aquacultures (Hoai, 2020) and their possible transfer from wild to farm fish (Arechavala-Lopez *et al*., 2013), data on the infection densities of trophically transmitted parasites (larval nematodes, digenean metacercariae, cestodian plerocer-

coids) in farm-associated wild-fishes (Barret *et al*., 2019), or the infection of farmed fish by wild farm-associated fishes is scarce.

In general, severe infections of aquaculture fish stocks with the second larval forms of cestodes (metacestodes) or with metacercariae of digenea can result in increased morbidity, weight loss, as well as reduced quality and market value of the cultured fishes (Norbury *et al*., 2022; Soler-Jiménez *et al*., 2017). These larval forms occur in the body cavity, encyst in the viscera or migrate through the muscle and internal organs (Scholz *et al*., 2021). Naturally, farmers take measures in order to reduce such damage as much as possible.

Heuch *et al*. (2011) compared the prevalence of trophically transmitted helminths in a) wild, b) sea-caught and subsequently farmed, as well as c) hatchery-reared Atlantic cods (*Gadus morhua*). The prevalence of most of these helminths was significantly lower in sea-caught and subsequently farmed cods and especially in hatchery-reared cods compared to wild caught cods of the same area (though not caught in the immediate surroundings of investigated fish farms). Sea-caught farmed fish only exhibited frequently 3 of the 10 digenean species, 2 of 4 eucestodean species and 3 of 8 nematodean species typical for wild cods (digenea*: Derogenes varicus, Hemiurus levinseni*, metacercarian stage of *Cryptocotyle lingua;* eucestoda: *Tetraphyllidea spp*., *Diphyllobothrium phocarum;* nematoda: *Anisakis simplex, Hysterothylacium aduncum,*

Pseudoterranova decipiens). In contrast, in hatchery-reared cod only two species, *Cryptocotyle lingua* and *Hysterothylacium aduncum,* were found in relevant numbers (Heuch *et al*., 2011). Brooker *et al*. (2012) showed that in fish farms infections with parasitic nematodes can be reduced even further when fish, such as Atlantic halibut (*Hippoglossus hippoglossus*) and rainbow trout (*Oncorhynchus mykiss*), are prevented from consuming natural prey. A reduced number of helminth species were also found in rainbow trout from marine cage culture in Denmark when compared to wild fish caught in the marine area connected to the aquaculture farms (Karami *et al*., 2022). However, in the latter study only a different fish species (Atlantic cod) was used as comparator group. Considering all these study results leads to the conclusion that feeding formulated food and preventing the farmed fish by the cage net from foraging on bottom fauna decreases infections of the fishes with many helminths (Heuch *et al*., 2011; Karami *et al*., 2022).

Another question relates to the potential impact of antihelminthic treatments of marine aquaculture fishes on the helminth communities of the surrounding fish and parasite fauna. However, in contrast to the treatment of ectoparasitic monogeneans the availability of active substances for pharmaceutical treatment of trophically transmitted helminths in aquacultures is limited (Buchmann 2022) and, moreover, they are not suitable for all helminth infections. Thus, treatment of fish whose internal organs are heavily infested

Table 3. Acanthocephalans determined in seabirds of the North Sea, the Barent Sea and the Baltic Sea, as well as their intermediate hosts.

Acanthocephala	Intermediate hosts	Final hosts
Polymorphidae		
Corynosoma strumosum	*Spinulogammarus ochotensis*[5], *Gammarus setosus*[7]	Common Eider (*Somateria mollissima)*[7] Brünnich's Guillemot (*Uria lomvia*)[1] Black-legged Kittiwake (*Rissa tridactyla*)[1] Glaucous Gull (*Larus hyperboreus*)[13] Cormorant (*Phalacrocorax carbo*)[4] Northern Fulmar (*Fulmarus glacialis*)[8]
Polymorphus phippsi	*Gammarus setosus*[7], *Gammarus oceanicus*[3,7]	Common Eider (*Somateria mollissima)*[2,7] Black-legged Kittiwake (*Rissa tridactyla*)[7] Glaucous Gull (*Larus hyperboreus*)[13] Arctic Terns (*Sterna paradisea*)[7] Brünnich's Guillemot (*Uria lomvia*)[7] Black Guillemot (*Cepphus grille*)[7] Northern Fulmars (*Fulmarus glacialis*)[14]
Polymorphus magnus	*Gammarus* spec.[4]	Purple Sandpiper (*Calidaris maritima*)[2] Common Scoter (*Melanitta nigra*)[4] Long-tailed Duck (*Clangula hyemalis*)[4] Steller's Eider (*Polysticta stelleri*)[4]
Polymorphus minutus	*Gammarus* spec.[10]	Common Eider (*Somateria mollissima)*[9]
Proficollis botulus	Decapoda*: Carcinus maenas*[6,11], *Hyas araneus*[7], *Pagurus pubescens*[7]	Common Eider (*Somateria mollissima*)[2,7,11,12], Purple Sandpiper (*Calidaris maritima*)[2]

Data from: [1]Kuklin *et al*., 2020; [2]Kuklin, 2015; [3]Kuklin & Maslich, 2011; [4]Reimer, 2002; [5]Skorobrekhova & Nikishin, 2019; [6]Neal & Pizzolla, 2008; [7]Galaktionov *et al*., 2021; [8] Kuklin *et al*., 2019; [9]Garbus *et al*., 2018; [10]Hynes & Nicholas, 1957; [11]Camphuysen *et al*., 2002; [12]Thieltges *et al*., 2006b; [13]Sagerup *et al*., 2009; [14]Mallory *et al*., 2008.
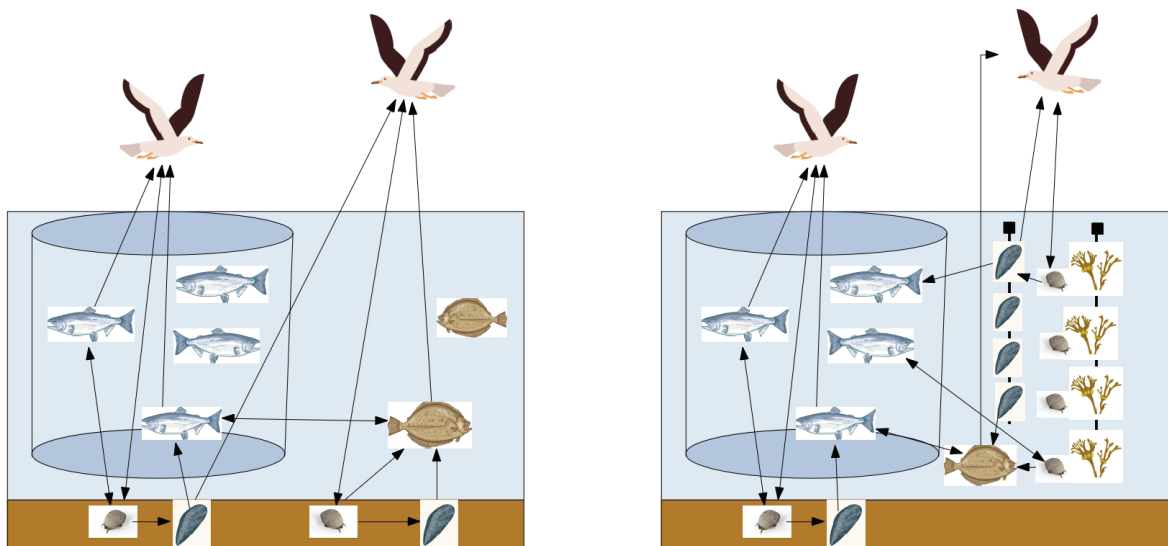
Fig. 1. **Left**: Possible routes of helminth infections in marine aquaculture of fish when foraging on the bottom fauna is not prevented and the plant is not protected from seabirds with nets. **Right:** Possible additional routes of helminth infections when fishes, filter-feeders and kelp are farmed together (integrated multi-trophic aquaculture, IMTA). Likelihood of infection may be increased when first intermediate hosts (Littorina) populate on kelp and second intermediate hosts (mussels) are farmed close to farmed fishes to clear environmental input from fish-aquaculture (Parts of the graphics licensed from stock.adobe.com).

with nematodes may result in immunopathological reactions triggered by the dying worms (Buchmann 2022). In some countries praziquantel got marketing authorization under certain conditions for the use in aquacultures to treat specific endoparasitic helminths (Norbury *et al*., 2022) while in others it can only be used off-label (Bader *et al*., 2019). Due to the chosen route of application (bath or oral), by excretion of the active metabolite, but also due to overfeeding with feed loaded with the active substance praziquantel can enter the surrounding environment (Norbury *et al*., 2022). Because praziquantel kills both parasitic and free-living flatworms as well as some protozoa, its availability in the environment and potential accumulation of the substance in marine sediment will likely impact surrounding fauna as well as the parasite-host relationships of wild fishes living near aquaculture operations (Norbury *et al*., 2022). However, clear and definite conclusions thereon cannot be drawn as of now, due to the partly contradictory results of the available investigations (Norbury 2022).

Besides fish, aquacultures are also used to breed bivalves. Blue mussels (*Mytilus edulis*) farmed in estuarine tidelands are consumed by common eiders and oystercatchers (*Haematopus ostralegus*) (Dunthorn 1971; Caldow *et al*., 2003). Mussels serve as second intermediate hosts for several trematode species of the genera *Gymnophallus*, *Himasthla* and *Renicola.* The final hosts of *Himasthla* and *Renicola* species are gulls and waders, whereas *Gymnophallus bursicola* parasitises common eiders (Galaktionov *et al*. 2015, 2021). Moreover, clusters of blue mussels are areas with high densities of primary hosts, such as grazing *Littorina* snails (Cornelius & Buschbaum, 2020). The increased density of first and second intermediate hosts in aquaculture of bivalves may therefore be an additional driver of infestation of seabirds with hel-

minths. Since damage to unprotected shellfish farms by sea ducks can have severe economic consequences, many farmers attempt to avoid this by using protective nets (Varennes *et al*., 2013).
The descending organic waste from marine fish farms as well as the fall-off of mussels from bivalve farms positively influence the fauna beneath the aquaculture, including polychaetes, bivalves, echinoderms and crabs (Callier *et al*., 2018; Kutti *et al*., 2007). Considering the aforementioned impacts of aquaculture on their immediate surroundings, this may locally lead to an increased abundance of different helminth development stages. However, specific investigations would be needed to further clarify the relevance of such effects.

Integrated multi-trophic aquaculture (IMTA) – In some cases, IMTAs, where two or more marine species from different trophic levels are farmed together, are used to reduce environmental impacts (Kim *et al*., 2022). Alongside the desired farm fishes, for example steelhead trout (*Oncorhynchus mykiss irideus*) or Atlantic salmons, some IMTAs cultivate filter-feeding species - like mussels and oysters - and kelp to 'clear' fish feed as well as fish faecal particulates and to reduce the fish derived nitrogen (Sanz-Lazaro & Sanchez-Jerez, 2017; Buck *et al*., 2018; Reid *et al*., 2010). Kelp is the preferred habitat of the gastropod genera *Littorina* and *Lacuna* as well as of amphipods (Nakata *et al*., 2006; Christic *et al*., 2003). The snails are first intermediate hosts of different digenean species (Galaktionov & Bustnes, 1999) and the amphipods can be part of some cestodes' life cycle (Table 2). IMTAs may therefore bring primary, secondary and final host even closer together than conventional fish farms. However, there is no data on the abundance of helminths in IMTA-systems (Fig 1).

Table 4: Nematodes determined in seabirds of the North Atlantic, Barent Sea and the Baltic Sea as well as their intermediate hosts.

Nematoda	Intermediate host	Final hosts
Acuariidae		
Stegophorus stellapolaris	Unknown (pisces)[7]	Common Guillemot (*Uria aalge*)[9] Brünnich's Guillemot (*Uria lomvia*)[1,9] Razorbill (*Alca torda*)[18] Little Auk (*Alle alle*)[18] Common Eider (*Somateria mollissima*)[10] European Herring Gull (*Larus argentatus*)[9] Common Gull (*Larus canus*)[9] Black-legged Kittiwake (*Rissa tridactyla*)[1] Glaucous Gull (*Larus hyperboreus*)[17] Arctic Skua (*Stercorarius parasiticus*)[9] Long-tailed Skua (*Stercorarius longicaudus*)[9] European Storm-petrel (*Hydrobates pelagicus*)[9] Northern Fulmar (*Fulmarus glacialis*)[9,11]
Stegophorus crassicauda	Unknown	Brünnich's Guillemot (*Uria lomvia*)[1] Black-legged Kittiwake (*Rissa tridactyla*)[1]
Cosmocephalus obvelatus		Brünnich's Guillemot (*Uria lomvia*)[1]
Paracuaria adunca	Amphipoda (i.e. *Gammarus duebeni*)[5]	Glaucous Gull (*Larus hyperboreus*)[2, 17] Northern Fulmar (*Fulmarus glacialis*)[11] Black-legged Kittiwake (*Rissa tridactyla*)[20]
Streptocara formosensis		Common Eider (*Somateria mollissima*)[16]
Streptocara crassicauda	Gammaridae[6]	Common Eider (*Somateria mollissima*)[2] Common Scoter (*Melanitta nigra*)[3] Velvet Scoter (*Melanitta fusca*)[3] Glaucous Gull (*Larus hyperboreus*)[17]
Anisakidae		
Anisakis spec.	1. Krill crustaceans (Euphausiacea)[4] 2. Pisces[4] (*Gadus morhua*[8] *Sprattus sprattus*[12], *Sardina pilchardus*[13], *Engraulis encrasicolus*[13]) or Cephalopods[12]	Brünnich's Guillemot (*Uria lomvia*)[1] Black-legged Kittiwake (*Rissa tridactyla*)[1] Northern Fulmar (*Fulmarus glacialis*)[11]
Contracaecum spec.	1. Copepoda / Amphipoda 2. Pisces	Common Scoter (*Melanitta nigra*)[3] European Herring Gull (*Larus argentatus*)[3] Common Gull (*Larus canus*)[3] Black-legged Kittiwake (*Rissa tridactyla*)[1] Brünnich's Guillemot (*Uria lomvia*)[1] Cormorant (*Phalacrocorax carbo*)[3] European Shag (*Phalacrocorax aristotelis*)[19] Northern Fulmar (*Fulmarus glacialis*)[11]
Capillariidae		
Capillaria contorta		European Herring Gull (*Larus argentatus*)[3] Common Gull (*Larus canus*)[3] Black-legged Kittiwake (*Rissa tridactyla*)[1]
Capillaria laricola		Common Gull (*Larus canus*)[3]
Raphidascaididae		
Hysterothylacium aduncum	Sandeels (*Ammodytes tobianus, Hyperoplus lanceolatus*)[14], Clupeidae (*Sprattus sprattus*)[12]	Brünnich's Guillemot (*Uria lomvia*)[1] Northern Fulmar (*Fulmarus glacialis*)[11] Glaucous Gull (*Larus hyperboreus*)[17]

Cyatholaimidae		
Seuratia spec.		Brünnich's Guillemot (*Uria lomvia*)[1]
		Black-legged Kittiwake (*Rissa tridactyla*)[10]
Dioctophymatidae		
Eustrongylides mergorum	1. Oligochaeta[7]	Brünnich's Guillemot (*Uria lomvia*)[1]
	2. Pisces[7]	
Amidostomidae		
Amidostomum anseri	None[3]	Common Eider (*Somateria mollissima*)[2]
		Long-tailed Duck (*Clangula hyemalis*)[3]
		Common Scoter (*Melanitta nigra*)[3]
		Velvet Scoter (*Melanitta fusca*)[3]
Amidostomum acutum		Common Eider (*Somateria mollissima*)[15]

Data from: [1]Kuklin *et al*., 2020; [2]Kuklin, 2015; [3]Reimer, 2002; [4]Pravettoni *et al*., 2012; [5]Anderson & Wong, 1982; [6]Garkavi, 1949; [7]Leszek *et al*., 1999; [8]Heuch *et al*., 2011; [9]Nagasawa *et al*., 1998; [10]Galaktionov *et al*., 2021; [11]Kuklin *et al*., 2019; [12]Kleinertz *et al*., 2012; [13]Dessier *et al*., 2016; [14]Groenewold *et al*., 1996; [15]Thieltges *et al*., 2006b; [16]Borgsteede *et al*., 2005; [17]Sagerup *et al*., 2009; [18]Muzzafar & Jones, 2004; [19]Abollo *et al*., 2001; [20]Kuklin & Kuklina, 2022.

Influence of Temperature and Seawater Acidification

Climate change as well as commercial fishing have altered marine ecosystems (Halpern *et al*., 2008). Ocean acidification caused by anthropogenic carbon dioxide (CO_2) emissions (Doney *et al*., 2020) and rising temperatures led to (1) reduced abundance of habitat-forming species such as mussels, (2) shifts in species distribution, (3) altered food web dynamics, and (4) decreased productivity of the seas (Hoegh-Guldberg & Bruno, 2010). Besides industrial fishery increasing water temperature seems to be a substantial driver for the decreased productivity of the lesser sandeel (*Ammodytes marinus*) in the North Sea, one of the most important forage fish species of seabirds in the North-East Atlantic (Lindegren *et al*., 2018). A corresponding decline of sandeels in seabird chick diets was observed, usually substituted with Clupeidae, such as European sprats (Wanless *et al*., 2018). The issue is whether such changes in the seabirds' diet has any impact on the trophically transmitted parasites?

The digenean *Cryptocotyle lingua* and the nematodes *Contracaecum* spec., *Anisakis simplex* and *Hysterothylacium aduncum,* – all of which have seabirds as their final hosts – were found in both sandeels as well as European sprats (Groenwold *et al*., 1996; Kleinertz *et al*., 2012) (Table 1 and 4). Infections with these nematode species were also observed in sardines (*Sardina pilchardus*) and anchovies (*Engraulis encrasicolus*) (Gutiérrez-Galindo *et al*., 2010; Dessier *et al*., 2016). These warmwater preferring forage fish species are already more prevalent in the southern North Sea (Heessen *et al*., 2015; Petitgas *et al*., 2012). Therefore, switches in the forage fish of seabird chicks do not necessarily lead to changes in the helminth community of seabirds.

Influences on helminths – There seems to be a relation between the average annual surface seawater temperature and the number of trematode species parasitizing in intertidal molluscs (*Littorina*

spp. and *Hydrobia* spp.). The number of trematode species in these molluscs declines with decreasing temperatures in European seas, from the French Atlantic coast to the arctic waters of the Kara Sea at Vaygach Island and the Barents Sea at Franz Josef Land (Galaktionov, 2017; Galaktionov *et al*., 2021). Possible reasons for the lower number of trematode species in the high Arctic include the lack of suitable intermediate hosts in coastal waters or the low density of the hosts' populations, as well as difficulties in the completion of life cycles, especially for trematodes with free-living larvae (Galaktionov, 1996b; Galaktionov *et al*., 2015, 2019, 2021). For example, only one of the six trematodes of the *Microphallus* "*pygmaeus*" group commonly using molluscs as first intermediary hosts were determined in the high Arctic. Only the trematode species (*Microphallus pseudopygmaeus*) found there is able to use other molluscs as first intermediate host (Galaktionov *et al*., 2021), whereas the other trematodes of this group specifically use molluscs of the genus *Littorina* as first intermediate host which do not occur in in the Arctic Sea. Furthermore, neither gastropods of the genus *Nucella* nor blue mussels occur in the high Arctic Seas of Franz Josef Land. This means that the first and the second intermediate hosts are not available for the trematodes *Renicola somateria* and *Gymnophallus* spec. Consequently, in contrast to subarctic parts to the Barents Sea, these trematodes were not found in common eiders in this region (Galaktionov, 2017; Galaktionov *et al*., 2021). Comparably, some cestodes (*Fimbriarioides intermedia* and *Lateriporus teres*) and the acanthocephalan *Profilicollis botulus* did not occur in common eiders at Franz Josef Land as their intermediate hosts (Tables 2 and 3) are missing here (Galaktionov *et al*., 2021).

In the high Arctic helminths which use amphipods as intermediate host have a competitive advantage to complete their life cycle, because amphipods are trophically more important for seabirds there than fishes (Galaktionov *et al*., 2021).

Increase of ambient temperature and related changes in salinity

and pH seem to have also direct impacts on the development of the larval stages of some trematode species. However, recent studies have lead to diverging results: from an increase of cercarial output from snails, as their primary hosts, with decreased survival time (Poulin, 2006; Selbach & Poulin, 2020) to a decrease in cercarial activity (Koprivnikar *et al*., 2010) and emergence (Morley & Lewis, 2013). These inconsistent findings may be caused by species-specific adaptation of the parasite, seasonal and circadian influences and competition between parasites in the primary host (Morley & Lewis, 2013; Selbach & Poulin, 2020; Kiatsopit *et al*., 2014; Carpenter *et al*., 2021; Soldánová *et al*., 2022), as well as possibly the nutritional status of the cercariae (Fokina *et al*., 2018). However, in the trematode *Himasthla elongata* a decrease of salinity seems to be more important for the emergence, activity, survival and infectivity of cercariae than an increase of temperature (Bommarito *et al*., 2020).

Intestinal helminths, for their part, are often hosts of bacterial communities, to which symbiotic functions are also attributed. Morley (2016) discusses whether changes in the composition and function of their bacterial community caused by environmental changes could have an indirect negative impact on helminth health. As has been shown in fishes and snails, changes in the salinity of the surrounding water led to changes in the gastrointestinal microbiome (Dulski *et al*., 2020; Kivistik *et al*., 2022). If such changes in the gastrointestinal microbiome were associated with a shift away from a symbiotic community and toward a pathogenic community, lack of symbiotic functions could have negative effects on gastrointestinal helminths (Morley, 2016).

Influences on intermediate hosts – Temperature increases in the Arctic Ocean lead to borealisation of the biota (Polyakov *et al*., 2020). This means, helminths using boreal invertebrates and fishes as intermediate hosts to complete their life cycles may appear in the high Arctic (Galaktionov, 2017; Galaktionov *et al*., 2021), if the corresponding species migrate to this region (Galaktionov *et al*., 2021). Early example can be observed in the northwest Atlantic, where current parasite communities differ from those reported in the 1960s. The Pacific tapeworm *Alcataenia longicervica* is present there since 2006 and affects common guillemots (*Uria aalge*) and Brünich's guillemots. It is assumed that its planktonic intermediate host, the crustacean *Thyanoessa* spec. (Euphausiid krill), spread into that region through the mixing of water between the North Pacific and the North Atlantic (Muzzafar, 2009). Moreover, prevalence of some trematodes of the microphallid "pygmaeus" group increased in periwinkles along the coast of the subarctic island Vaygach, while one species (*Microphallus piriformes*) even expanded northward when comparing data of the 1980s and 2000s (Galaktionov *et al*., 2019).

Long-term, the increase of carbon dioxide in the atmosphere may influence the physical vitality of helminths' intermediate hosts, and thus may lead to reduced food availability for seabirds. Ocean acidification is occurring more rapidly in coastal and estuarine areas, which are less buffered (Waldbusser *et al*., 2011) but simultaneously characterised by an abundance of molluscs. For example, the snail *Lacuna vincta,* a common grazer in coastal kelp forests and intermediate host for *Microphallus pseudopygmaeus*, shows decreased grazing activity when experimentally exposed to increased CO_2 in the ambient seawater (Young *et al*., 2021). Scientists concluded that further acidification of the ocean waters together with eutrophication may reduce herbivore grazing of the *Lacuna* snail (Young *et al*., 2021). Acidification of seawater (pH 7.4 and pH 7.6 vs. pH 8.1 as control) also leads to reduced shell growth and strength as well as increased shell dissolution in the mud snail *Zeacumantus subcarinatus* (MacLeod & Poulin, 2015).

Table 5. Studies on the helminth population of individual seabird species and their geographical localization.

Seabirds species	Number of helminth species identified	Geographic area	Authors
Common Guillemot	7	Murman coast	Kuklin 2017
Brünnich´s Guillemot	8	Murman coast	Kuklin 2017
	6	Novaya Zemlya	Kuklin *et al*. 2020
Black-legged Kittiwakes	24	Murman coast	Kuklin 2017
	11	Murman coast	Kuklin & Kuklina 2022
	5	Novaya Zemlya	Kuklin *et al*. 2020
Great Black-backed Gull	30	Murman coast	Kuklin 2017
European Herring Gull	38	Murman coast	Kuklin 2017
Northern Fulmar	14	Murman coast	Kuklin *et al*. 2019
Common Eider	13	North sea	Thieltges *et al*. 2000
	10	Franz Josef Land	Galaktionov *et al*. 2021
Velvet Scoter	60	Southern Baltic + literature	Rolfes 2023
Great Cormorant	9	Southern Baltic sea	Kanarak *et al*. 2003

Similar changes in biocalcification rates of juvenile oysters (*Crassostrea virginica*) described Waldbusser *et al*. (2011) under experimental conditions. Interestingly, infections of molluscs with trematodes may alter the response of the intermediate host's organism to seawater acidification depending on the parasite species. At pH 8.1 and 7.6 mud snails infected with *Maritrema novazealandensis* showed significantly higher shell growth than uninfected mud snails (MacLeod & Poulin, 2015). As gastropods infected by trematodes are typically sterilised during the parasites' growth, the energy consumed by the trematodes may be less than that required for reproduction (MacLeod & Poulin, 2015) and may be used for shell growth. This aspect warrants further investigation.

Temperature effects on seabirds – Global warming affects seabirds in many ways and may in consequence also affect the hosted helminths (Gilg *et al*., 2012). Especially arctic seabirds are suffering from direct and indirect changes of their environment. For example, Brünich's guillemots (*Uria lomvia*) display reduced heat tolerance relative to bird species originating from hot and arid climates. When incubating on sun exposed cliffs, Brünich's guillemots show signs of heat stress and a low evaporative cooling efficiency (Choy *et al*., 2021). As stress in general, high temperatures influence the bidirectional relation of the birds' immune and the nervous systems (Calefi *et al*., 2017). Heat stress increases the release of corticosterone, decreases food intake, entails mild multifocal acute enteritis (Quinteiro-Filho *et al*., 2015), and increases mortality (Quillfeldt *et al*., 2004). As the host's immune system plays an important role in the control of endoparasitic helminths (Moreau & Chauvin, 2010), a weakened immune system generally facilitates infections with parasites (Quillfeldt *et al*., 2004).

Even short period heat waves in arctic regions can lead to a lack of seabird food. Piatt *et al*. (2020) observed mass mortality of common guillemots caused by starvation in the Gulf of Alaska and the North American West Coast during heat waves.

As shown in the extensively investigated model species *Gallus gallus*, short periods of starvation lead to changes in the bird's neuroendocrine system which regulates the functions of the adrenal cortex, the gonades and the thyroid gland (Tanabe *et al*., 1981; Van der Geyten *et al*., 1999; Wrońska & Szpregiel, 2021). These physiological stress responses are comparable to those described for heat-stress (Quinteiro-Filho *et al*., 2015), resulting in a weakened immune system (Quillfeldt & Möstl, 2003; Quillfeldt *et al*., 2004) which improves the conditions for the infestation with helminths.

Environmental changes, such as heat stress as well as starvation caused by high temperatures may therefore have consequences for both, helminths and seabirds.

Ingestion of Plastic Marine Litter

Drifting plastic litter represents a well-known problem in the marine environment even for seabirds. Long-term investigations showed that even in arctic areas 87.5 % of northern fulmars have plastic pieces in their stomachs (Trevail *et al*., 2015). Procellariformes
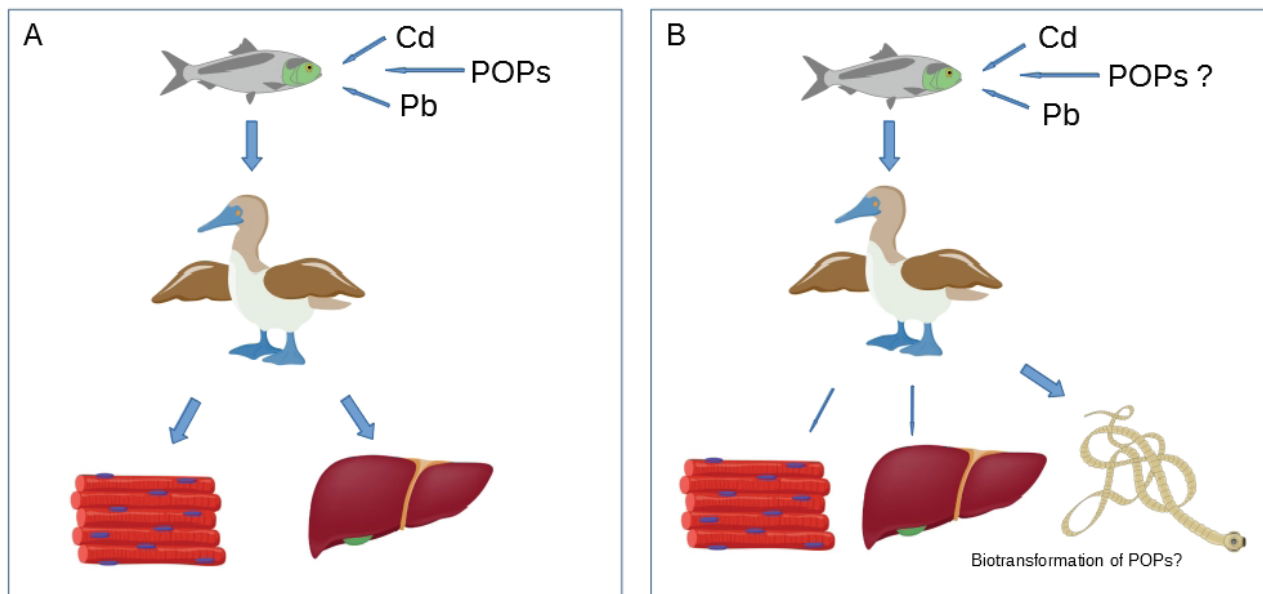

Fig. 2. Illustration of the potential role of intestinal helminths as a sink for the trace elements cadmium (Cd) and Lead (Pb).
Some digenea, cestoda, or acanthocephala show higher concentration of trace elements than the hosts' tissues. Clues are still missing today whether helminths are also able to accumulate and/or metabolise POPs in seabirds as shown for parasite host relationships of other vertebrates.
A: accumulation of Cd and Pb as well as POPs in seabirds' tissues (muscle and liver) not infested with helminths; **B**: greater bioaccumulation of Cd, Pb, and hypothetically POPs, in helminths compared to the seabirds' tissues (Parts of the graphics licensed from istockphoto.com).

ingest plastic debris drifting at the sea surface. Most members of this order are not able to regurgitate plastic pieces, meaning that these particles remain in the bird's stomach (Schwantes 2023).

Moreover, seabirds may passively ingest microplastic, i.e. plastic particles smaller than 5 mm, together with prey, soil adhering to the prey or with sea- and freshwater. Microplastic is globally found in marine fauna, and even invertebrates and fish in Arctic Seas are contaminated (Collard & Ask, 2021). Microplastic are ingested by deposit feeders, filter-feeders and suspension feeders such as amphipods, holothurians, polychaetes as well as mollusc and copepod species (Wright *et al.*, 2013). It accumulates in these invertebrates (Saley *et al.*, 2019) and thus enters the food chain. Depending on exposure time, in blue mussels polyethylene particles cause histological changes, inflammatory responses such as formation of granulocytomas and lysosomal membrane destabilization (von Moos *et al.*, 2012).

Microplastics (e.g. polyethylene, polypropylene, polystyrene polyvinyl chloride) are typically mixed with additives (i.e. plasticizers, flame retardants, antioxidants, UV stabilizers), which can trigger various toxic effects (Liu *et al.*, 2020; Gruber *et al.*, 2022). Moreover, pieces of microplastic have sorption affinities, which means they accumulate organic pollutants as well as heavy metals from the environment. Thus, microplastic can carry an additional vector effect, by transporting toxic chemicals, organic pollutants and heavy metals into the gastrointestinal tract of organisms (Fackelmann & Sommer, 2019), where they may be absorbed into the blood and/or accumulate in body organs and tissues of vertebrates. In a small sample of seabirds (2 sawbill ducks, 1 common guillemot), Haave *et al.* (2021) found the polymers polystyrene and polyvinylchloride in the birds' stomach, intestine and liver. Tanaka *et al.* (2012) detected polybrominated diphenyl ethers (PBDEs), which are used as flame retardants, in plastic pieces extracted from the stomachs, as well as in the abdominal adipose tissue of short-tailed shearwaters (*Puffinus tenuirostris*), but not in their natural prey (pelagic fishes).

Kühn *et al.* (2020) showed that additives from plastic litter ingested by northern fulmars can leach into the birds' stomach oil, and may consequently be absorbed systemically. Such additives, especially PBDEs, have been found in liver and muscle-tissue and eggs of northern fulmars in the high arctic (Sühring *et al.*, 2022). Increased blood concentrations of uric acid, amylase and plasma cholesterol in relation to the number of ingested plastic pieces were measured by Lavers *et al.* (2019) in flesh-footed shearwaters (*Ardenna carneipes*). The authors discuss whether these changes of uric acid concentration are signs of renal failure, and whether the increase of cholesterol may indicate stress caused by plastic debris. Unfortunately, only a few studies investigated whether molecular components of ingested plastic appear in seabird tissues and in which way they influence the seabirds'health. Further analysis would be desirable here.

Research in literature databases did not provide any information on whether such plastic debris has any impact on the infestation of seabirds with helminths. In this context Hernandez-Milian *et al.* (2019) hypothesized that aggregation of microplastic in the intestinal tract of grey seals (*Halichoerus grypus*) may be related to the aggregation of helminths (mostly acanthocephalans). Pennino *et al.*, (2020) found a positive relationship between parasites and microplastic in the Mediterranean fish species, anchovy and sardine, which are already more common in the southern North Sea (Heesen *et al.*, 2015; Petigas *et al.*, 2012).

Ingestion of microplastic can generally lead to (1) mechanical disruption and inflammation of the gastrointestinal tract, (2) changes in the gut microbiome enabling pathogens to enter the organism, and (3) disruption of the endocrine system impacting immune response (Liu *et al.*, 2020; Fackelmann & Sommer, 2019; Gruber *et al.*, 2022; Schwantes 2023). Considering these potential consequences, the relevance of ingested microplastic on the infestation of seabirds with helminths should be subject of targeted studies, to investigate whether this impairs the host´s defense mechanisms against parasites.

In fulmars and Cory's shearwaters, a correlation was found between the amount of microplastic ingested and the diversity and composition of gut bacteria, with commensal microbiota decreasing and pathogenic germs increasing (Fackelmann *et al.*, 2023). The decrease in symbiotic bacteria could have indirect negative effects on helminth health, as already described in the case of altered salinities (Morley, 2016).

Burden with persistant organic pollutants (POPs) and halogenated natural products (HNPs)

In the marine environment HNPs biosynthesised by marine bacteria, macroalgae, phytoplankton, tunicates, corals, worms, sponges and other invertebrates are common (Bidleman *et al.*, 2019). Several HNPs with higher molecular weight bioaccumulate and have similar toxic properties as anthropogenic POPs (Bidleman *et al.*, 2019). HNPs were detected in eggs of common eiders, common guillemots, black guillemots and herring gulls, in tissues of northern fulmars, and in tissues and eggs of glaucous (*Larus hyperboreus*) gulls and shags (Bidleman *et al.*, 2019). Thus, HNPs have to be taken into account as part of the total burden of organic pollutants impacting the marine ecosystem.

Marine ecosystems represent major sinks for xenobiotic POPs, where they accumulate in various compartments like seawater and sediments (Avellan *et al.*, 2021) as well as the tissues of wildlife (Harmon, 2015). They possess various sublethal, insidious toxic effects including the potential for endocrine disruption and carcinogenesis (Harmon, 2015). In birds, both in laboratory tests and in wildlife including seabirds, side effects of POPs have been observed which affect the endocrine and neuronal systems, as well as the immune system, reproduction, development and growth (Hao *et al.*, 2021). Since the immune system plays an essential role in the infestation of helminths, the following will focus on the influence of POPs on the immune system of seabirds.

Impairment of seabirds' immune system – POPs, such as organic halogenated contaminants (OHCs), were detected in different tissues and/or eggs of black-legged kittiwakes, northern fulmars, glaucous gulls, great and lesser black-backed (*Larus fuscus*) and herring gulls as well as common eiders (Letcher *et al.*, 2010). Even when birds were exposed to low quantities of OHCs, sub-clinical toxicity may lead to relevant physiological changes. A randomised controlled study in American kestrels showed that long-lasting dietary exposition of polychlorinated biphenyls (PCBs) provoke an increase in total white blood cell counts associated with a decrease in the ratio of heterophiles to lymphocytes (Smits *et al.*, 2002) which indicates a suppressed immune system. In another controlled study, Sagerup *et al.* (2009b) investigated the influence of a naturally occurring mixture of POPs fed to newly hatched glaucous gulls and compared the results with those of a control group fed an almost uncontaminated diet. At the end of the study period, when self-production of antibodies was established, the control group showed higher levels of immunoglobulin M (IgM) and IgG. In addition, the ability to produce antibodies against influenza viruses was impaired in the experimental group after appropriate immunization.

This data corresponds to the wildlife observations of Bustnes *et al.* (2004), who found increased white blood cells and a lower immune response in breeding glaucous gulls affected by high OHC-concentrations in relation to birds with lower levels. A decrease in lymphocytes and an increase in heterophiles depending on the blood concentration of OHCs was also observed in the chinstrap penguin *Pygoscelis antarctica* (Jara-Carrasco *et al.*, 2015), and a significant correlation of PCB-138 and PCB-153 compared to the respective concentration of the immunoglobulin IgY could be shown in the blood of Antarctic penguins (Jara *et al.*, 2018). Furthermore, a clear relationship between the level of exposure to OCHs and suppressed T-cell mediated immunity was observed by Grasman *et al.* (1996) in contaminated juvenile herring gulls and Caspian terns. In contrast, great skuas on the Shetland Islands had the lowest immunoglobulin levels compared to birds from Iceland and Bjørnøya, although exposure to POPs was lowest there (Bourgeon *et al.*, 2012). The authors suggest that other stressors were prominent in Shetland at that time. However, there is evidence that the composition of ingested organic pollutants, as well as species-dependent sensitivities to individual POPs, play a role in the expression of toxic effects. Hoffman *et al.* (1998) demonstrated in a comparative controlled study different sensitivities to defined PCBs of common tern (*Sterna hirundo*), American kestrel and chicken (*Gallus gallus*) embryos. In contrast to kestrels and chickens, common terns were less sensitive to PCB 126. In the latter malformations or edemas were only observed at such high PCB concentrations which affected hatching success. Additionally, the authors reported different toxicities of miscellaneous investigated PCBs in chicken and kestrels.

The egg-injection concentrations of PCB 126, which resulted in low-level toxic effects in common terns during this study, were comparable to the highest concentrations of PCB 126 found in wild Great Lakes common terns and Forster's terns. In these wild terns reduced hatching success, edema and malformation were observed. (Hoffmann *et al.*, 1998). The authors concluded that other chemicals must also contribute to the malformations and decreased hatching success observed in the wild terns.

In addition to the negative changes of the immune responses, exposure to OCHs also becomes histologically visible in structural changes of lymphoid tissues. Fernie *et al.* (2005) observed in nestlings of American kestrels, structural changes in spleen, thymus and bursa fabricius after experimental administration of polybrominated diphenyl ethers compared to the control.

Burden by parasitic load – Birds with high OHC-burden may become more susceptible to parasites and diseases due to weakened immune defences. Sagerup *et al.* (2000) described a significant correlation of intestinal nematode intensity and PCBs in glaucous gulls, though further investigations did not confirm these findings (Sagerup *et al.*, 2009a). These differing results may be caused by the fact that the latter group of glaucous gulls were in good condition and seemed to exhibit significantly lower PCB-levels than the birds in the first study (Sagerup *et al.*, 2000). In breeding ring-billed gulls (*Larus delawarensis*) which were exposed to high concentrations of OHCs, Marteinsson *et al.* (2017) found a relation between parasite load and the birds' spleen mass: the mass of the lymphoid organ, which is important for avian immune systems, was lower in gulls which had a greater helminth load. Similar results were reported for lesser snow geese (*Chen caerulescens*) by Shutler *et al.* (1999). Two other studies found no association between helminth load and spleen mass in grey geese (Figuerola *et al.*, 2005) and double-crested cormorants (Robinson *et al.*, 2008), but these studies did not consider OHCs. In northern fulmars spleen size was not significantly affected by either OHCs or the presence of helminths (Mallory *et al.*, 2007). The authors discussed that the OHC-concentration in northern fulmars were comparatively low and might not be high enough to impact the birds' immune system.

In summary, data on the influence of OHCs on the immune system and the helminth infestation in seabirds are inconsistent. This may be explained by:
• different seasonal exposures to OHCs,
• variable concentrations of OHCs in birds of the wildlife studies,
• different sensitivities of the analysed seabird species towards OHCs,
• varying mixtures of environmental pollutants with different modes of action (independent, additive, synergistic, antagonistic) (Heys *et al.*, 2016).

Another aspect of the pollution with POPs is resulting from the observation that some helminths are able to accumulate POPs and even to metabolise POPs, affecting the partition of these pollutants in their hosts (Le *et al.*, 2014; Schäfer *et al.*, 2009; Henríquez-Hernández *et al.*, 2017; Molbert *et al.*, 2020). The impact

of such a bioaccumulation and biotransformation of pollutants in parasites on the burden of the hosts is discussed in the next chapter together with similar observations with trace elements.

Burden with trace elements

Burden on seabirds – When assessing the total burden of anthropogenous pollution on seabirds the load of trace elements must also be taken into account. Beside trace elements of natural origin, trace elements derived form human activities are released into the marine environment (Ansari *et al*., 2004). Potentially toxic trace elements e.g. copper (Cu), lead (Pb), zinc (Zn), mercury (Hg), arsenic (As) and cadmium (Cd) are of particular concern. Seabirds, especially top-predators of the described marine ecosystem, accumulate high levels of such elements in their tissues, and sometimes suffer from lower reproductive success (Ackerman *et al*., 2014; Whitney & Cristol, 2017). For example, northern fulmars and brünnich's guillemots in the Bering Sea (Ishii *et al*., 2017) as well as leach's storm petrels, black guillemots, double-crested cormorants (*Nannopterum auritum*) and common eiders in the Gulf of Maine (Pollet *et al*., 2017; Stenhouse, 2018) accumulate high concentrations of Hg in tissues and blood, respectively. Chronic exposure to Hg and Pb apparently has a negative effect on the immune system of birds and decreases their immune responses (Whitney & Cristol, 2017; Vallverdú-Coll *et al*., 2019). Wayland *et al*. (2001) found that common eiders showed a positive correlation between the intensity of parasitic infestation with nematodes and the concentration of hepatic mercury within the birds. In glaucous gulls a positive correlation between the gastrointestinal intensities of cestodes and selenium levels (Se), as well as between the intensities of acanthocephalans and Hg levels are described by Sagerup *et al*. (2009a). In contrast, chronic Pb-intoxication decreased helminth species richness and infection intensity in mallards (*Anas platyrhynchos*) (Prüter *et al*., 2018).

Load in helminths – Higher bioaccumulation of chrome (Cr), Cd, As, Zn and manganese (Mn) in the cestode *Tetrabothrius bassani* than in different tissues of its final host, the Atlantic gannet (*Morus bassanus*) were described by Mendes *et al*. (2013). Al Quraishy *et al*. (2019) found comparable results for a cyclophillidean cestoda parasitizing in the domestic pigeon (*Columba livia domestica*). In cormorants (*Phalacrocorax carbo*), which were severely infected with the nematode *Contracaecum rudolphii* (Anisakidae), the Pb concentration in the parasites was significantly higher than in the birds' pectoral muscle and liver, whereas the accumulation of Cd was higher in the tissues of cormorants than in the parasites (Baruš *et al*., 2001). Carravieri *et al*. (2020) reported that female shags with high Hg and low Se levels had higher loads of *Contracaecum rudolphii* than those with a higher ratio of Se to Hg. However, this relationship could not be confirmed in male shags, despite their higher Hg and lower Se concentrations and higher parasite loads compared to females. The authors discussed different susceptibil-

ity to Hg and/or parasites between males and females as well as the complexity of the antagonistic interactions of Hg and Se (Heinz & Hoffmann, 1998). When it comes to Hg detoxification in seabirds the potential role of selenoneine, the Se-analogue of ergothioneine should also be considered, because El Hanafi *et al*. (2022) found a dramatic decrease of selenoneine with the increase of Hg concentration in the liver of giant petrels (*Macronectes* spec.).

Sures *et al*. (2017) reviewed a large number of studies which show that numerous species of digenea, cestoda, acanthocephala and nematoda accumulate organic pollutants and trace elements to a high extent. In particular, digenean, cestodes and acanthocephalans, are able to accumulate trace elements and OHCs to a much higher degree than their hosts (Sures *et al*., 2017), and some helminths are apparently able to metabolise OHCs via Cytochrome P450 (Schäfer *et al*., 2009; Henríquez-Hernández *et al*., 2017). Whether helminths in seabirds can act as pollutant sinks in the host-parasite system in a manner comparable to rats, dogs and fish (Al-Bayati, 2018; Molbert *et al*, 2020; Hassanine & Al-Hasawi, 2021; Henríquez-Hernández *et al*., 2017) requires further investigations (Fig 2). Contrasting results were described in other host-parasite relationships, like the impact of Cd on cormorants (Baruš *et al*., 2001), where increased pollutant burdens were observed in the hosts' tissues as compared to those in the parasites. However, in the majority of investigated relationships it was evident that acanthocephalans and cestodes were able to reduce trace elements in different tissues of their hosts (Sures *et al*., 2017).

Helminth species and their developmental stages seem to respond to different trace elements and/or varying concentrations of heavy metals in different ways. For example, the viability of cestode eggs (*Schistocephalus solidus*) is negatively affected by increasing Zn concentrations in the aquatic environment, whereas the free-living stage coracidia of this cestode was not negatively affected by Zn. The growth of the procercoids in copepods, which are the first intermediate hosts, accelerates when Zn concentration elevates. Similarly, the total mass of plerocercoids in three-spined sticklebacks (*Gasterosteus aculeatus*) increased when the fish were fed with copepods reared in media containing high Zn concentrations (Ismail, 2018).

In summary, some POPs and trace elements of industrial origin seem to play an important role in the infestation of seabirds with helminths as well as in the interaction of parasites with their final hosts. However further studies are required to, for one settle inconsistent data and secondly verify specific relations.

Mass mortality of seabirds and the role of helminths

Besides weather events (i.e. storms, calm), viral and bacterial infections, oil spills, poisoning with shellfish toxins as a consequence of algal blooms, and starvation, are regarded as the main causes of mass mortality events among seabird populations (Clairbaux *et al*., 2021; Camphuysen *et al*., 1999; Starr *et al*., 2017; Anker-Nils-

sen *et al*.; 2002; Shearn-Bochsler *et al*., 2017; Descamps *et al*., 2012; Thieltges *et al*., 2006b). Northern fulmars, seaducks, kittiwakes, common guillemots, razorbills (*Alca torda*), Atlantic puffins and little auks (*Alle alle*), are most frequently affected by mass mortality events in the North-Atlantic and adjacent seas (Camphuysen *et al*., 1999).

As presented in this article, an interplay of different natural and anthropogenous stressors impact seabirds which, taken together, may negatively influence the birds' immune system to such an extent that the immune defence is no longer able to sufficiently control pathogens like helminths.

In common eiders, which were studied thoroughly in events of mass mortality, a high parasitic load with helminths, particularly acanthocephalans, nematodes and trematodes of different families, including *Gymnophallidae*, *Bucephhalidae*, *Echinostomidae*, *Notocotyluridae* and *Levinsinella,* was reported (Borgsteede *et al*., 2005; Camphuysen *et al*., 2002; Garbus *et al*., 2018, 2019; Garden *et al*., 1964). Garbus *et al*. (2018, 2019) described the dissected eiders as emaciated with depleted fat resources, severe atrophy of the breast muscles and a completely empty gastrointestinal tract except for the parasites. Haematological investigations revealed an increased ratio of heterophils and lymphocytes compared to reference values pointing towards stress response and immune suppression (Garbus *et al*., 2019).

As most studies of eiders affected by mass mortality events investigated beached corpses or sick birds, the number of examined reference birds with good body condition is rather low. Occurence rates of helminths in healthy eiders were diverse. Garbus *et al*. (2018, 2019) described moderate to heavy load of the acanthocephalan *Polymorphus minutus* in all investigated eiders of the mortality events (i.e. range: 115 – 3.839 individuals/male bird) and significantly lower infestations in healthy birds. Other investigators found high loads of the acanthocephalan *Proficollis botulus* in healthy juvenile eiders, whereas the abundance was lower in healthy adult birds (Garden *et al*., 1964; Liat & Pike, 1980; Thieltges *et al*., 2006b). This indicates a different susceptibility of age groups, acquired immunity in older birds, or age-dependent food preferences (Thieltges *et al*., 2006b). Similarly, Camphuysen *et al*. (2002) reported significantly higher infection levels with *Proficollis botulus* in young eider ducks compared to adult birds when investigating beached corpses during a mass mortality event in the Dutch Wadden Sea.

Generally, helminth infestation in the gastrointestinal tract does not only result in physiological changes correlating with the parasitic density, for example an increase of the proteolytic activity as shown for cestodes (*Alcataenia larina*) in kittiwakes (Kuklina & Kuklin, 2011), but also in macroscopically or in histopathologically visible damages. In anatidae ducks, inflammatory reactions (granuloma) of the mucosa were associated with the occurence of nematodes in the proventriculus, trematodes in the cecum, and acanthocephalans in the small intestine (Padilla-Aguilar *et al*., 2020). Acanthocephalans inserted their proboscis into the intes-

tinal subserosa and caused the formation of granulomas, along with giant cells, epithelioid cells as well as heterophiles, and even systemic necrotic areas (Padilla-Aguilar *et al*., 2020). Lymphocytic interstitial infiltrate, ductal ectasia and tubular necrosis have been observed in kidneys of manx shearwaters infected with the digenean *Renicola sloanei*, and renal lesions were significantly associated with parasite infection (de Matos *et al*., 2021).

It is obvious that a heavy load of helminths constitutes a significant health burden for seabirds, regardless of whether additional stressors affect the animals or not. Results of two controlled studies suggest that parasitic load with helminths has negative effects on the birds physical fitness, especially when other stressors exist simultaneously: A placebo-controlled study using oral pharmacological treatment with the anti-helminthic drug fenbedazole demonstrated a positive effect on nesting success in breeding male glaucous gulls, which are present at the nest significantly longer (80 % compared to 35 %) and consequently more engaged in the protection of the nesting site than females (Bustnes *et al*., 2006). Eider duck females, which arrived late or were in poor condition, showed increased nesting propensity after oral anti-helminthic treatment as compared to the placebo-group, while birds arriving early and in good condition exhibited no positive effect from treatment (Provencher *et al*., 2017). Based on the results of their microscopical and chemical investigations in herring gulls from Sweden and Iceland, Jansson *et al*. (2018) concluded that it seems unlikely that infections with helminths alone explain the higher mortality observed in the Baltic Sea population of herring gulls. Rather, other factors must contribute to the seabirds' higher mortality. In that respect the interplay of the anthropogenous stressors described in this overview may be of relevance.

Existing studies on Helminth Populations in Seabirds

Analysis of the literature data shows that the helminth fauna was thus far only studied in a few seabird species and typically focussed on specific geographic areas (e.g. Arctic and Baltic Sea). The seabird species that have been extensively studied in term of helminth populations are listed in Table 5. Very little data is available on changes in helminth populations in seabirds over time, due to climate change, seasons, winter migration or external factors such as salinity or temperature. A little more data is already available on this at the intermediate host level. Further comprehensive studies in seabirds on seasonal influences, changes over time and during migration would be welcome.

Conclusions

Generally, the anthropogenous stressors described here can further aggravate natural factors and may thus jointly impact the life of and interaction between helminths, their intermediate hosts and seabirds. However, the specific interaction of the different man-made factors with this ecosystem is complex and in large parts not

clear. Further detailed investigations are necessary to determine more precisely how and to what extent these stressors impact the endoparasites, their intermediate hosts, the seabirds as well as their interaction.

Statements & Declarations

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