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PROJECT REPORT

Diversity and prevalence of
seabird parasites in intertidal zones
of the southern Barents Sea coast

Kirill Galaktionov
Jan Ove Bustnes

The Joint Norwegian - Russian Commission on
Environmental Cooperation
The Seabird Expert Group
Report No. 5: 1994/96



NINA • NIKU

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Abstract

Galaktionov, K. & Bustnes, J. O. 1996. Diversity and prevalence of seabird parasites in intertidal zones of the southern Barents Sea coast. - NINA•NIKU Project report 04: 1-27.

In the Barents Sea region there is little knowledge about seabird parasites, especially at the Norwegian side, and the aim of this project was to map the distribution of such parasites in this area. In addition, we investigated how factors such as longitude, exposure and human activities influenced the species composition and the distribution of the different parasite species. To avoid killing seabirds we investigated the intermediate hosts of the parasites, such as gastropods and gammarids. The dominant part of the seabird parasite fauna in this area are the trematodes. Different species of trematodes have life-cycles of varying complexity, that may consist of one intermediate host and no free-living larval stages (autonomic life-cycles), two intermediate hosts and one free-living stage, and two intermediate hosts and two free-living larval stages. Different species also have different final hosts, such as gulls and common eiders. We collected three species of periwinkles (*Littorina saxatilis*, *L. obtusata*, *L. littorea*), and *Nucella lapillus* in the area from Novaya Zemlya to Tromsø, totally 37 575 snails from 180 different sampling stations. The material was collected between 1978 and 1994. We divided the area into 5 different regions (figure 6), and compared the fauna among these regions. We found 14 species of trematodes in the gastropods, of which 13 have marine birds as final hosts. In periwinkles the number of species per sampling station increased westwards (except for *L. obtusata*). The frequency of trematodes with more than one intermediate host increased westwards, that is they became more important in the species composition. The trend for the prevalence showed the same pattern, and more snails were infected by trematodes with complicated life-cycles in the western regions. The causes

of this are probably that the climate in the east is harsher, thus reducing the probability of successful transmission of trematodes with complicated life-cycles, and the distribution of final hosts. The only exception from this was the autonomic *Microphallus piriformes*, which has gulls as main final hosts. Overall, the trematodes of the common eider was more common in the eastern regions, while gull trematodes became increasingly important in the western regions. The reason for this is probably that the large number of fishery villages along the Norwegian coast leads to a clumped distribution of gulls, which again leads to high prevalence of gull trematodes. Along the Norwegian coast we investigated the prevalence of trematodes around fishery villages and fish farms, and found higher prevalence of gull trematodes close to human settlements than at natural sites. Fishery activities therefore lead to a higher level of parasite infection in the environment. We also collected the amphipod *Gammarus oceanicus* at 38 stations along the Norwegian Barents Sea coast, and found totally five species of parasites, two of which have seabirds as final hosts. These two were the cestode *Microsomacanthus microsoma* (fam. Hymenolepididae), and the acantocephalan *Polymorphus phippisi* (fam. Polymorphidae). However, they were only found at a very low density. The fauna of seabird parasites which use *Gammarus oceanicus* as intermediate hosts seems to be rather uniform in the Barents Sea region.

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Galaktionov, K. & Bustnes, J. O. 1996. Artsammensetning og prevalens av sjøfuglparasitter i fjæresoner langs den sørlig Barentshavkysten. - NINA•NIKU Project report 04: 1-27.

Et sentralt problem innen studier av parasitter i fugl er at det trenges store utvalg av for å få et klart bilde av faunaen i et område, noe som fører til at man må avlive mange fugler. En vei rundt dette problemet er å kartlegge forekomsten av forskjellige parasittarter på mellomvertsstadiene, som for de fleste parasitter på sjøfugl inkluderer snegler og krepsdyr. Selv om man ikke kan overføre funn på mellomvertsstadiene direkte til nivåer i sluttverte (sjøfugl), så vil det gi en meget god indikasjon på hvordan den parasitologiske situasjonen er i et område. I Barentshavregionen er kunnskapen om sjøfuglparasittenes utbredelse og hvor stor del av vertsbestandene som er infisert, begrenset, særlig i den norske delen av området. I tillegg mangler mye kunnskap om hva som påvirker artsammensetningen av faunaen og utbredelsen av de enkelte artene. Hensikten med dette prosjektet har vært å skaffe tilveie kunnskap om parasitter som har sjøfugl som sluttverter gjennom studier av mellomverter i strandsonen (snegler og krepsdyr). De mest utbredte sjøfuglparasittene er iktene, som for det meste har snegler som mellomverter. Forskjellige ikter har ulike livsykler som kan omfatte en mellomvert og ingen frittlevende larvestadier (autonomske livssyklus), to mellomverter og ett frittlevende stadium og to mellomverter og to frittlevende stadier (figur 1-3). Vi samlet inn spiss-, butt-, og stor strandsnegl (*Littorina saxatilis*, *L. obtusata*, *L. littorea*), samt purpurnegl (*Nucella lapillus*) i området fra Novaja Zemlja til Tromsø, tilsammen 37 575 snegl fra 180 lokaliteter. Materialet ble samlet inn i tidrommet 1978-1994. Vi delte området inn i 5 regioner (figur 6), og sammenlignet parasittfaunaen i de forskjellige regionene. Vi fant 14 forskjellige ikter (13 med sjøfugl som sluttvert). Hos strandsneglene viste det seg at

antall arter per lokalitet økte i vestlig retning (untatt for butt strandsnegl). Frekvensen av ikter med mer enn en mellomvert økte også i vestlig retning, noe som betyr at disse artene ble viktigere i artsammensetningen. Trenden for hvor stor prosent av sneglene som var infisert (prevalensen) viste det samme mønsteret, og flere var infisert med ikter med kompliserte livssykluser i de vestlige regionene (Norskekysten). Årsaken til dette mønsteret er sannsynligvis at klimaet i de østlige, arktiske områdene er mye hardere noe som gjør overføringen av kompliserte ikter vanskelig, samt at fordelingen av sluttverter (sjøfugl) er andeledes. Det eneste unntaket fra dette ser ut til å være den autonome ikten *Microphallus piriformes*, som har måker som hovedsluttvert. Det viste seg videre at ærfuglikter var vanligere i øst, mens måseikter var vanligere i vest. Grunnen til dette ligger sannsynligvis i at bosetningsmønstret på Norskekysten, med fiskevær og fiskeoppdrett, fører til at måser klumper seg sammen og parasittene spres lettere. Det viste seg også at lokaliteter med fiskeindustri og fiskeoppdrett hadde mere ikter enn naturlige lokaliteter langs Norskekysten. Slik aktivitet fører tydeligvis til at overføringen av parasitter går raskere, fordi fuglene beiter svært lokalt. Vi samlet også inn marflo på 38 stasjoner langs den norske Barentshavkysten, og fant tilsammen fem arter av parasitter. Av disse var det to arter; bendelormen *Microsomacanthus microsoma* (fam. Hymenolepididae), og krasseren *Polymorphus phippii* (fam. Polymorphidae) som har sjøfugl som sluttvert. Disse ble bare påvist i små mengder. Det ser ut til å være en relativ uniform fauna av parasitter som bruker marflo som mellomvert over det meste av det sørlige Barentshavet.

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Preface

This report is the result of a cooperation between Murmansk Institute of Marine Biology and Norwegian Institute for Nature Research (NINA), Department of Arctic Ecology. The aim of this joint project has been to combine the taxonomical knowledge that the Russian scientific community have with the more statistical oriented ecology in Norway. This was done to map a little known part of the biodiversity, the seabird parasites, of the northern seas, and to investigate factors that influence the level of infection of such parasites in the environment.

The financial support for this project came from the Norwegian Directorate for Nature Management, the Roald Amundsen center in Tromsø and The Norwegian Research Council.

We wish to thank Dag Atle Lysne for commenting on earlier drafts of the report, and Rob Barrett for improving the English.

Jan Ove Bustnes
Project leader

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1 Introduction

The Barents sea is one of the most productive seas in the world, and large numbers of seabirds inhabit this area. In the last 30-40 years many studies have been carried out on these seabird populations. However, there have been few detailed studies of seabird parasites, although some data exist from northwestern Russia. In northern Norway, very few studies have reported the distribution of seabird parasites, especially those linked to the intertidal zones (but see Kristoffersen 1991 and Galaktionov & Bustnes 1995).

Most seabird parasites have complicated life-cycles that involve one or several intermediate hosts. This makes it possible to study the distribution of such parasites without killing large numbers of seabirds. The aim of this study has been to investigate the distribution of such organisms on the southern coast of the Barents Sea, which is also the northern coast of mainland Europe, by investigating intermediate hosts.

1.2 Seabird parasites in the intertidal zones

Seabirds are the final hosts of many helminth parasites (Trematoda, Cestoda, Nematoda and Acanthocephala), which have intertidal invertebrates and fishes as intermediate hosts. Such parasites may have a large influence on individual hosts, and intestinal helminthes often kill seabirds (Hill 1952,1954, Thom & Graden 1955, Clark et al. 1958, Garden et al. 1964, Grenquist 1970, Itamies et al. 1980, Kulachkova 1979, Karpovich 1987). However, the effects on populations of seabirds are not well established (Lauckner 1985), but a high parasitic burden among individuals in a population will make them vulnerable to other environmental constraints (Lauckner 1985, Krasnov et al. 1995). Evidence of mass death from parasites has been found in common eiders in the Kandalaksha reserve, White sea, where close to 90% of the ducklings may have died as a result of trematode infection (Kulachkova 1979, Karpovich 1987). Skorping & Warelus (unpublished manuscript) also found that high trematode infection correlated with poor body condition in prelaying common eider females.

Among the parasites of seabirds, the Trematoda clearly predominate (Lauckner 1985). Most trematodes use the gastropods of the littoral and upper sublittoral zone as intermediate hosts. Among these gastropods the periwinkles (*Littorina* spp.) play an important role as the first intermediate host (Chubrick 1966, James 1968, 1969, Werdning 1969, Podlipajev 1979, Lauckner 1980, Irwin 1983, Matthews et al. 1985, Galaktionov & Dobrovolskij 1986, Kristoffersen 1991, Galaktionov 1993). Trematodes are distributed unevenly within populations of periwinkles and areas with high infestation (focus of infection) alternate with seashores with low infestation (Galaktionov & Dobrovolskij 1986, Galaktionov 1993).

There are many different species of seabird trematodes that use intertidal gastropods as intermediate hosts, and there is a large variation in life-histories. A central group of species are the Microphallids of the "pygmaeus" group (*Microphallus pygmaeus*, *M. piriformes* etc.) which have so-called autonomic life-cycles. This means that they have only one intermediate host - mostly periwinkles - and no free-living larval stages (figure 1). Another life-history involves two intermediate hosts, first a gastropod (periwinkle), then another gastropod, bivalve, crab or fish. Common species of this type in the northeastern Atlantic are *Microphallus similis*, *Cryptocotyle lingua* and *Renicola* sp. (figure 2). A third type of life-history involves two intermediate hosts and two free-living larval stages. Relatively common species having this life-cycle are *Himastha* spp. (figure 3). These parasites can be divided into two groups; those that have predominantly sea ducks such as the common eider *Somateria mollissima*, and those that have gulls *Larus* spp. as final hosts.

Crustaceans are important intermediate hosts for some seabird parasites such as Cestodes and Acanthocephalans (Uspenskaya 1963, Marasaeva 1990). Among these species *Microsomacanthus microsoma* (Cestoda) (figure 4) and *Polymorhus phippisi* (Acanthocephala) (figure 5) are common in the northern areas. These have predominantly eiders as final hosts.

The aim of this study was to map the fauna composition and the prevalence (degree of infection) of the seabird trematodes which use periwinkles (*Littorina saxatilis*, *L. obtusata*, *L. littorea*) and *Nucella lapillus* as intermediate hosts, in the area from Novaya Zemlya to Tromsø. We also wanted to investigate how factors such as exposure and longitude influence the frequency and prevalence of trematodes with different life-histories. Of special interest for this study was how the human activities - fishery activities and fish farming - along the Norwegian coast influence the distribution of different trematode species. From the Norwegian part of the area, we also report the fauna composition and prevalence of the seabird parasites that use the amphipode *Gammarus oceanicus* as intermediate hosts.

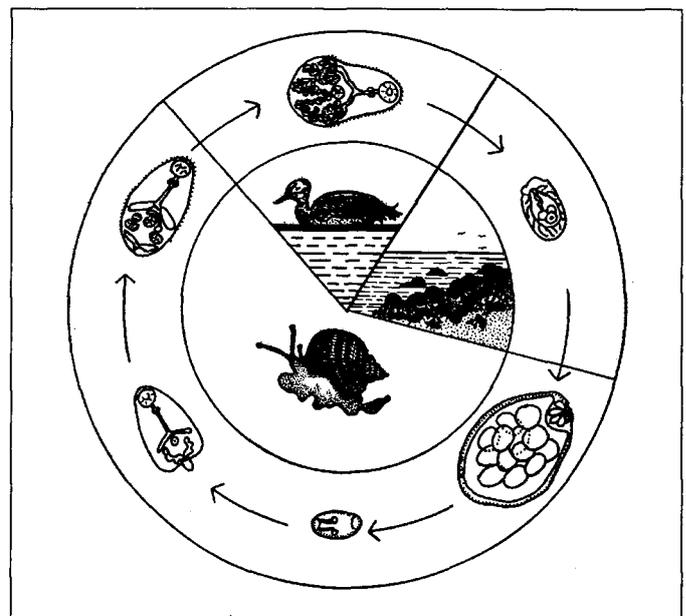


Figure 1

The autonomic life-cycle of microphallids of the "pygmaeus" group, with two hosts and no free-living larval stages- Livssyklus hos ikter med to verter og ingen frittlevende larvestadier (Microphallider av "pygmaeus" gruppen).

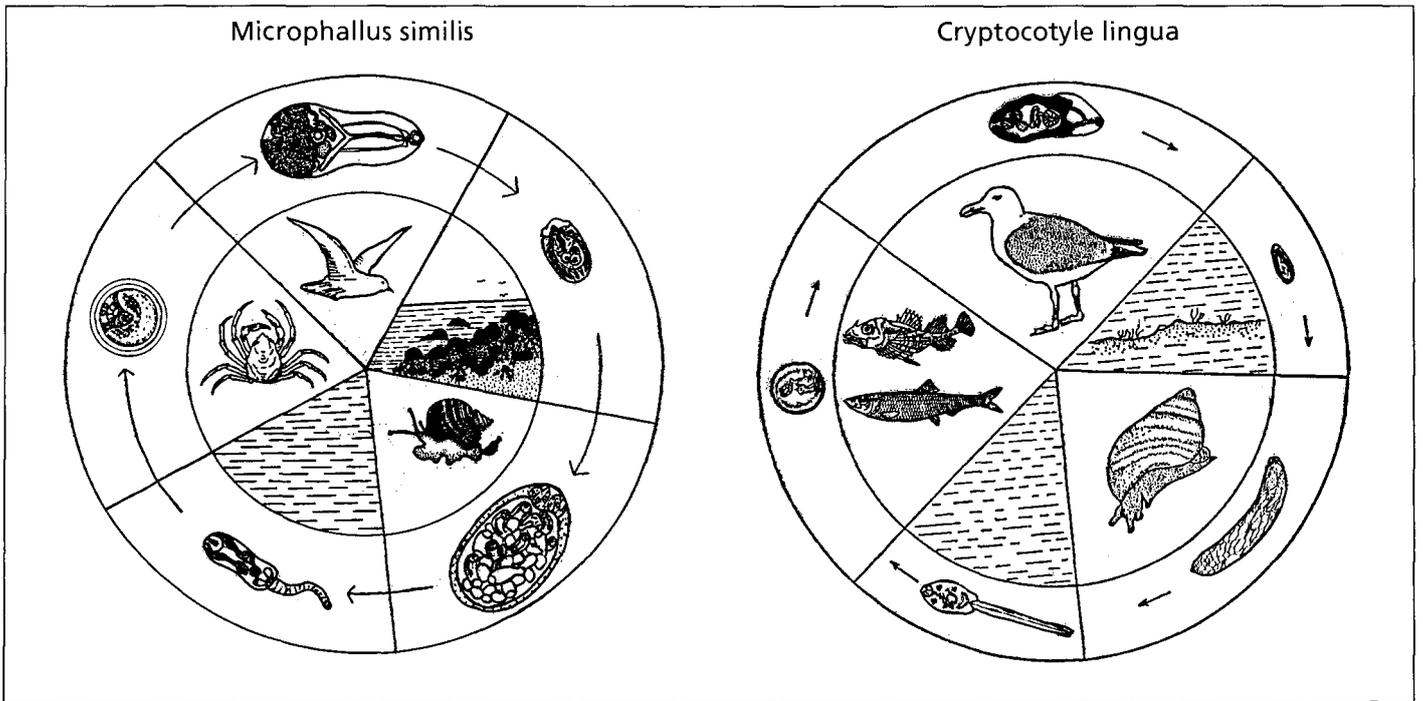


Figure 2
 Life-cycles of trematodes with three different hosts, and one free-living larval stage (Examples *Microphallus similis*, *Cryptocotyle lingua*).
 - Livssyklus hos ikter med tre forskjellige verter og et frittlevende larvestadium (Eksempler *M. similis*, *C. lingua*).

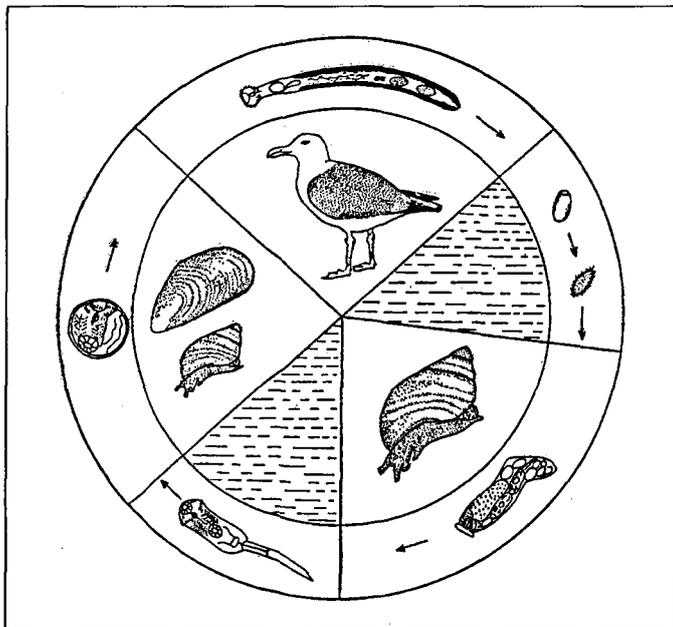


Figure 3
 The life-cycle of *Himasthla elongata*, with three hosts and two free-living larval stages. - Livssyklus hos ikten *Himasthla elongata*, med to mellomverter og to frittlevende larvestadier.

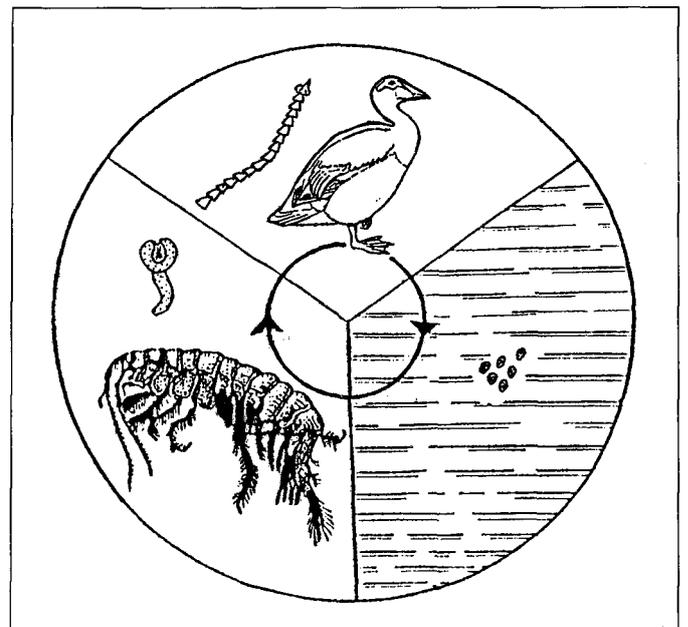


Figure 4
 The life-cycle of the cestod *Microsomachanthus microsoma*.
 - Livssyklus hos bendelmarken *Microsomachanthus microsoma*.

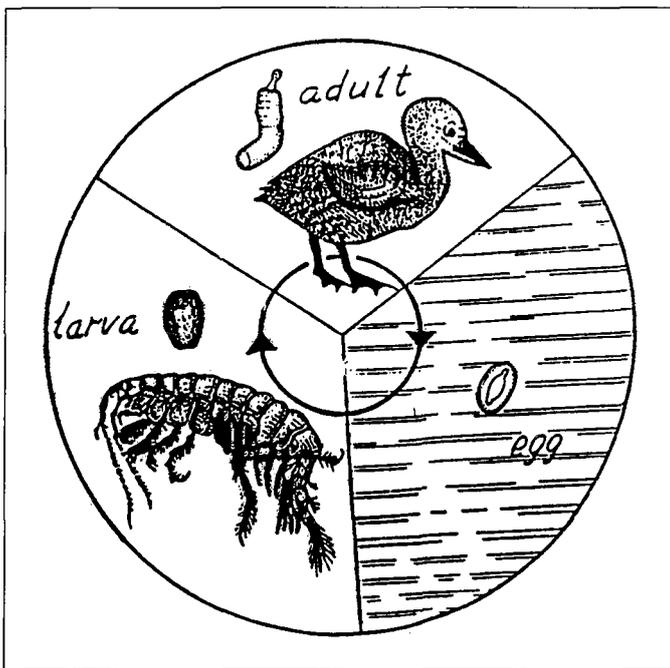


Figure 5
Life-cycle of the acanthocephalan *Polymorphus phippsi*. -
Livssyklus hos krasseren Polymorphus phippsi.

2 Study area and methods

2.1 Study area

The coastline that was investigated stretched from Novaya Zemlya to Tromsø, including the White sea. This coast has a very harsh climate, especially the arctic eastern parts. We divided the coastline into 5 different regions which could be naturally distinguished. Region A was Novaya Zemlya and the Vaygatch island. Region B was the White Sea and the tip of Kanin peninsula (Cape Kanin nose). Region C was the eastern Kola coast to the Kola fjord (eastern Murman). Region D was the western Murman and Finnmark east of the Porsanger fjord. Region E was western Finnmark and Troms (**figure 6**).

The areas surrounding Novaya Zemlya and Vaygatch have an arctic climate with very low temperatures during the whole year. Sea ice dominate from October until June, and intertidal zones are covered by ice. The climate in the White Sea is milder, but the sea is frozen in winter (November-April). The seawater in this region has a low salinity. The eastern Kola coast is usually not frozen in winter. There are no big fjords in this region, and the intertidal zones are exposed to wave action. The western Murman and eastern Finnmark have more fjords and the water is warmer, somewhat influenced by the North-Atlantic drift. Nevertheless the prevalent wind directions are more easterly than further west. Troms and western Finnmark are dominated by western winds, and are relatively mild compared to the other regions.

2.2 Material and methods

The collection of the material was carried out from 1978 to 1990 in Russia, and in 1992 and 1994 in Norway. For logistic reasons, the sampling stations in Russia were more clustered in specific areas, while in Norway they were distributed more evenly along the coastline (**figure 7**). In northern Norway we collected material close to ports where there was a fish industry or fish farms, and on nearby control sites with similar environmental conditions. Totally 180 stations were visited, and 37 575 gastropods were collected.

We distinguished 5 degrees of exposure to wave action on the sea shores. 1 = most sheltered parts of fjords and bays, 5 = open sea shore, while 2-4 were ranked between the two extremes.

Of the gastropod species collected, *L. saxatilis* is the most common and widely distributed in the study area and only this species is able to survive under the severe conditions in the arctic littoral zone of Novaya Zemlya and Vaygatch Island (region A). However the distribution of this species stops at the southern part of Novaya Zemlya (Karmakulskaja Bay). *L. saxatilis* inhabits all types of intertidal zones except sand marshes. It is therefore absent (as all other representatives of the macrobenthic flora and fauna) in the intertidal zone of the Pechora Sea (south-eastern part of the Barents Sea) from the strait of Yugorsky Shar in the

east to the Cape Kanin Nose in the west. In the rest of the southern Barents Sea, *L. saxatilis* occurs throughout the intertidal zone, but the greatest density is found in the upper-middle littoral. In region B, C, D and E, *L. obtusata* is common in the middle and lower levels of the seaweed fronds. The environment in the eastern Murman coast (region C) and also in the western Murman (the eastern part of the region D) is unfavourable for *L. littorea*. Here it is found in extremely low densities and only in the lowest parts of the intertidal zone. Along the northern coast of Norway, *L. littorea* is distributed more widely in the low littoral. *Nucella lapillus* is totally absent in region A and B. In region C, D and E this species inhabits the low and partly middle zones of the rocky shores.

Molluscs were collected by hand at low tide. The sampling was done in the same period of the year- August and September. In this season the infestation of intertidal snails by trematode larvae in the Arctic areas is at its highest (Chubrick 1966, Podlipajev 1979, Galaktionov & Dobrovolskij 1986). Snails were dissected under a stereomicroscope, and the trematode larvae were determined in vivo. For the analyses we recorded the presence of different trematode species in each mollusc.

In 1994 we collected amphipodes *Gammarus oceanicus* along the coast of Troms and Finnmark. These specimens were fixed in 70% alcohol and dissected in the laboratory in Murmansk in 1995. 50 specimens from 38 stations were dissected.

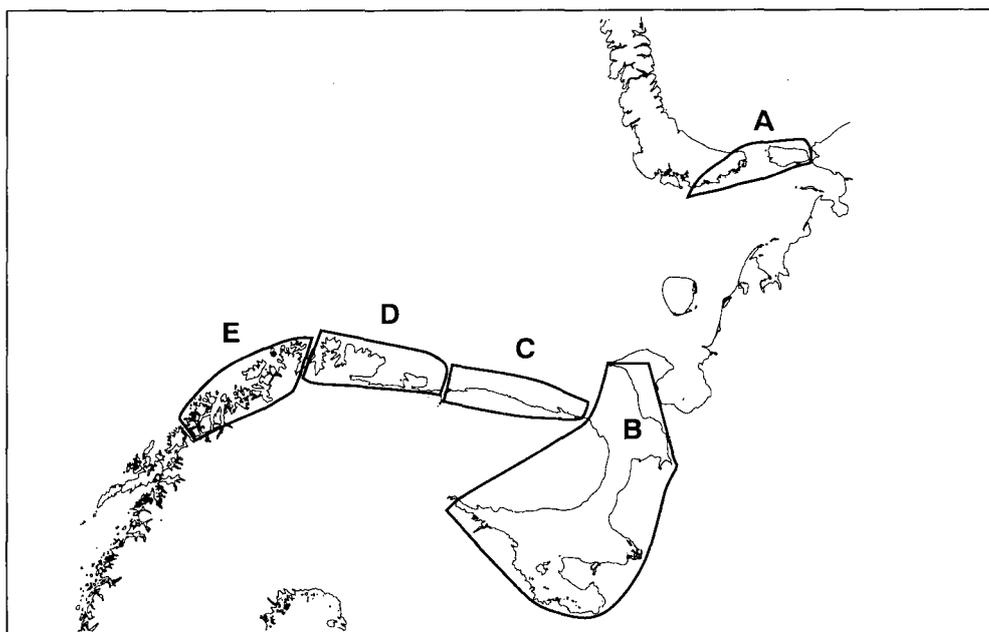


Figure 6
The study area divided into different regions (A-E) (see method chapter).- Studieområdet indelt i forskjellige regioner (A-E).

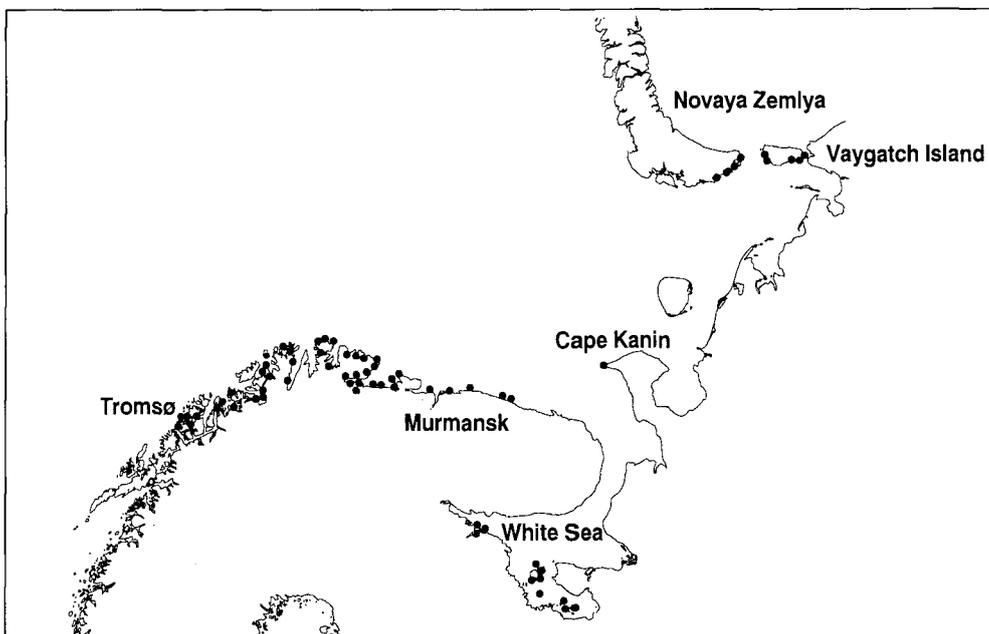


Figure 7
The distribution of sampling stations (black dots) along the southern Barents Sea Coast.- Fordeling av innsamlingsstasjoner (punkter) langs den sørlige Barentshavkysten.

2.2.1 Species composition and prevalence

In order to determine the importance of different trematode species, or groups of species in the fauna composition in different regions, we calculated the *frequency of occurrence* of each trematode species (group of species) among the infected snails. That is the percentage of snails infected with each trematode species.

We also calculated prevalence as the percentage of gastropods or gammarids infected by particular parasite species or groups of species. This was done for all regions.

When calculating the frequency and prevalence, we divided the trematode species into four groups (Group I= microphallids of the "pygmaeus" group, which have autonomic life-cycles. Group II= common seabird trematodes with more than one intermediate host and free-living larval stages: *M. similis*, *C. lingua*, *Renicola* sp. *Himasthla* sp. Group III= very rare seabird- and wader trematodes. *P. atomon*, which has fishes as final hosts, was classified in a fourth group).

2.2.2 Statistical methods

Statistical calculations were carried out using SAS (SAS 1990, 1993). Because of lack of normality, we used the GENMOD procedure (SAS 1993) to test how the number of species at different stations were influenced by longitude and exposure. For comparisons of prevalence between regions, in relation to exposure and influence of human activities we ranked the data using the SAS procedure PROC RANK (SAS 1990). This was done to overcome the lack of normality (Conover & Iman 1981, Potvin & Roff 1993, Schmutz 1994). We then tested the effects of the different factors on the prevalence of trematodes by using general linear models (PROC GLM). All tests used here allowed to test for effects of both discrete and continuous variables. Interactions between independent variables were tested for, and removed when not significant.

3 Results

3.1 Composition of trematode fauna in intertidal gastropods

3.1.1 Number of trematode species

In this study we found the parthenithes and larvae of 14 trematode species in the intertidal gastropods (**table 1**). Thirteen of these have marine birds as final hosts. The exception was *P. atomon* which uses fishes as a definitive host.

When controlling for exposure, we found a significant decrease eastwards in the number of trematode species per sampling station in *Littorina saxatilis* (White Sea excluded). This was due to the low number of trematode species in the easternmost region. The same trend was found in *L. littorea*, but not in *L. obtusata* (**figure 8, table 2**). The lowest number of trematode species (n=6) in *L. saxatilis* was found in Novaya Zemlya (region A) (**table 3**), but the number of trematode species increased to seven at the Cape Kanin Nose, and to 11 on the coast of the Onega- and the Kandalaksha Bays in the White Sea (region B). On the eastern Murman coast (region C) we found 12 species, and 14 and 13 species in western Murman/eastern Finnmark (region D) and western Finnmark and Troms (region E), respectively. The most diverse trematode fauna in *L. obtusata* was also recorded in the western regions (D and E), the least diverse in the eastern Murman (region C) (**table 3**).

The main difference in the composition of the trematode fauna between regions, in both *L. saxatilis* and *L. obtusata* was the number of species with free-living larval stages (1 or 2) in their three-host life cycles. The number of these species was highest in the western regions (**table 3**), while in the easternmost region (A) no such seabird trematode were found, except one snail infected with *Notocotylus* sp. *Podocotyle atomon* was common also in region A. Microphallids of the "pygmaeus" group, with autonomic, two-hosts life-cycles (without free-living larvae), were found everywhere.

There was no trematode infection in *L. littorea* in the intertidal zone of the eastern Murman (region C). The number of species in the region D and E were the same (5) in *L. littorea*, but only *C. lingua* and *M. pygmaeus* were common in these regions. *Nucella lapillus* was infected by only *Renicola* sp. in all regions, and a few *Himasthla* sp. in region E (**table 3**).

3.1.2 Frequency of different trematode species in different regions

In all regions, microphallids of the "pygmaeus" group (Group I) occupied a central place among the trematodes in both *L. saxatilis* and *L. obtusata* (**figure 9**).

In the intertidal zone of Novaya Zemlya and Vaygatch, 50% of all parasitized snails were infected with Group I trematodes (frequency=50%). The value for *P. atomon* in *L. saxatilis* was also about 50%.

Table 1. List of trematode species found in the study area. Ikkearter funnet i studieområdet.

Trematode species	First intermediate host (main)	Second intermediate host (main)	Definitive host (main)	No. of free living stages
<i>Microphallus pygmaeus</i> (Levinsen, 1881) (fam. Microphallidae)	<u><i>L. saxatilis</i></u> , <i>L. obtusata</i> , <i>L. littorea</i>	absent	<u>Common eider</u> , other eiders and seaducks	0
<i>M. piriformes</i> (Odhner, 1905) Galaktionov, 1983	<u><i>L. saxatilis</i></u> , <i>L. obtusata</i>	absent	<u>Large Gulls</u> , Common Gull, Eider	0
<i>M. pseudopygmaeus</i> Galaktionov, 1980, (probably several subspecies)	<i>L. saxatilis</i> , <i>L. obtusata</i> <u><i>Onoba aculeus</i></u> , <u><i>Margarites helicina</i></u> , <u><i>M. groenlandicus</i></u> <i>Epheria vincta</i>	absent	<u>Common eider</u> , probably some other seaducks	0
<i>M. triangulatus</i> Galaktionov, 1984	<u><i>L. saxatilis</i></u> <i>L. obtusata</i>	absent	<u>Common eider</u> , probably some other seaducks	0
<i>M. similis</i> (Jagerskiöld, 1900)	<u><i>L. saxatilis</i></u> , <u><i>L. obtusata</i></u> <i>L. littorea</i>	<u><i>Carcinus maenas</i></u> <i>Hyas araneus</i>	Gulls (all species in the area studied)	1 (cercaria)
<i>Maritrema arenaria</i> Hadley & Castle, 1940	<i>L. saxatilis</i>	<i>Semibalanus balanoides</i>	Waders (<u><i>Arenaria interpres</i></u>)	1 (cercaria)
<i>M. murmanica</i> Galaktionov, 1989	<i>L. saxatilis</i>	absent	unknown	0
<i>Cryptocotyle lingua</i> (Creplin, 1825) (fam. Heterophiidae)	<u><i>L. littorea</i></u> , <i>L. saxatilis</i> , <i>L. obtusata</i>	Seafish, different species (cod, flatfish salmon, etc.)	Gulls (all species in the area studied)	1 (cercaria)
<i>Himasthla</i> sp. Podlipayev, 1979 (fam. Echinostomatidae)	<u><i>L. saxatilis</i></u> , <i>L. obtusata</i> , <i>L. littorea</i>	<i>Mytilus edulis</i>	Gulls (<u>herring gull</u> , great black-backed gull)	2 (miracidium, cercaria)
<i>Renicola</i> sp. Podlipayev, 1979 (possible 2-3 different species) (fam. Rencolidae)	<u><i>Nucella lapillus</i></u> <i>L. saxatilis</i> , <i>L. obtusata</i> , <i>L. littorea</i>	<u><i>Mytilus edulis</i></u> <i>Littorina</i> spp.	Gulls (?)	1 (cercaria)
<i>Parapronocephalum symmetricum</i> Belopolskaya, 1952 (fam. Pronocephalidae)	<u><i>L. saxatilis</i></u> , <i>L. obtusata</i>	absent	Waders (<u>sandpipers</u> , oystercatcher)	0
<i>Notocotylus</i> sp. Podlipayev, 2-3 different species) (fam. Notocotilidae)	<u><i>L. saxatilis</i></u> , <i>L. obtusata</i> <i>Sceneopsis planorbis</i>	absent (cercaria)	Seaducks	1
<i>Parvatrema</i> sp. Podlipayev, 1979 (fam. Gymnophallidae)	<i>Turtonia minuta</i>	<i>Margarites helicinus</i> , <i>L. saxatilis</i> <i>L. obtusata</i> <i>Lacuna neritoides</i>	Common eider	1 (cercaria)
<i>Podocotyle atomon</i> (Rudolphi, 1802) (Opecoelidae)	<u><i>L. saxatilis</i></u> , <i>L. obtusata</i> , <i>L. littorea</i>	Intertidal gamma ids (<i>Gammarus</i> spp. <i>Marinogammarus obtusatus</i>)	Seafishes (122 species)	1 (cercaria)

Table 2. Analysis testing the effect of eastern longitude, controlled for environmental exposure, on the number of trematode species in different periwinkles (all species also include *L. littorea*) at sampling locations along the Barents Sea coast (PROC GENMOD, SAS 1993). - Analyse som tester sammenhengen mellom østlig lengdegrad og eksponeringsgrad på antallet av iktearter i forskjellige arter av strandsnegl (spiss- og butt strandsnegl (Alle arter omfatter også stor strandsnegl) på forskjellige innsamlinglokaliteter langs Barentshavkysten (PROC GENMOD, SAS 1993).

Host species Vertsart	Exposure - eksponering			Longitude -lengdegrad		
	DF	χ^2	p	DF	χ^2	p
<i>L. saxatilis</i>	4	4.45	ns	1	43.92	***
<i>L. obtusata</i>	4	8.79	*	1	0.29	ns
All species- Alle arter	4	11.71	**	1	19.88	***

*** : p<0.001, **: p<0.05, *: p<0.1, ns: p>0.1

Table 3. Occurrence of trematode parthenithes and larvae in intertidal molluscs in the different regions (A-E) (see study area) of the southern Barents Sea and the White Sea.- Forekomst av larver av forskjellige iktearter i forskjellige regioner av Barentshavet og Kvitsjøen.

Trematode species- Iktearter	First intermediate host - første mellomvert																			
	<i>L. saxatilis</i>					<i>L. obtusata</i>					<i>L. littorea</i>					<i>N. lapillus</i>				
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
<i>Microphallus pygmaeus</i>	+	+	+	+	+	0	+	+	+	+	0	*	-	+	+	0	0	-	-	-
<i>M. piriformes</i>	+	+	+	+	+	0	+	+	+	+	0	*	-	-	-	0	0	-	-	-
<i>M. pseudopygmaeus</i>	+	+	+	+	+	0	+	+	+	+	0	*	-	-	-	0	0	-	-	-
<i>M. triangulatus</i>	+	+	+	+	+	0	+	+	+	+	0	*	-	-	-	0	0	-	-	-
<i>M. similis</i>	-	+	+	+	+	0	+	+	+	+	0	*	-	+	-	0	0	-	-	-
<i>Maritrema arenaria</i>	-	-	-	+	+	0	-	-	+	+	0	*	-	-	-	0	0	-	-	-
<i>M. murmanica</i>	-	-	-	+	-	0	-	-	-	-	0	*	-	-	-	0	0	-	-	-
<i>Cryptocotyle lingua</i>	-	+	+	+	+	0	+	-	+	+	0	*	-	+	+	0	0	-	-	-
<i>Renicola</i> sp.	-	+	+	+	+	0	+	-	-	+	0	*	-	-	+	0	0	+	+	+
<i>Himasthla</i> sp.	-	+	+	+	+	0	-	-	+	+	0	*	-	-	-	0	0	-	-	+
<i>Parvatrema</i> sp.	-	+	+	+	+	0	-	+	+	+	0	*	-	-	-	0	0	-	-	-
<i>Notocotylus</i> sp.	+	+	+	+	+	0	-	-	+	+	0	*	-	-	-	0	0	-	-	-
<i>Parapronocephalum symmetricum</i>	-	-	+	+	+	0	+	-	+	+	0	*	-	-	-	0	0	-	-	-
<i>Podocotyle atomon</i>	+	+	+	+	+	0	+	+	+	+	0	*	-	+	-	0	0	-	-	-

0 absence of molluscs in region; * absence of data; - absence of trematode species in mollusc; + presence of trematode species in mollusc

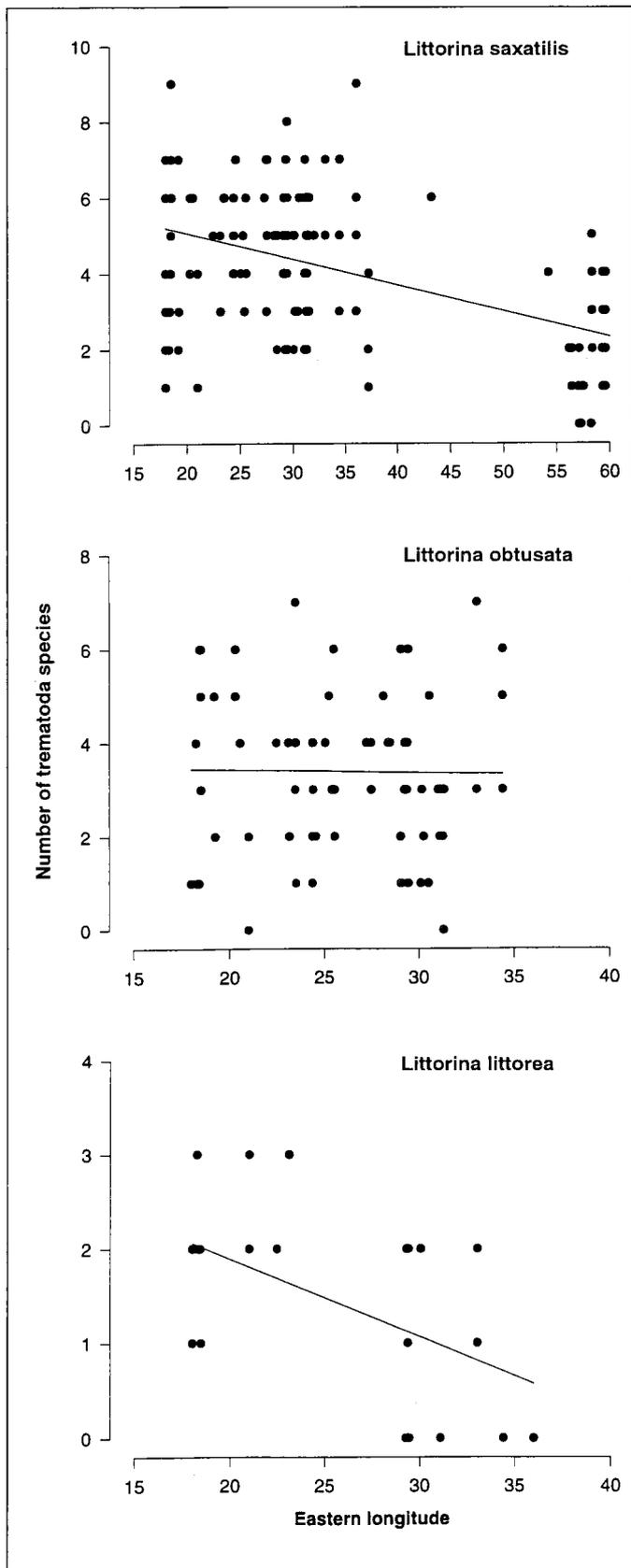


Figure 8
 Number of trematode species per sampling stations in three species of periwinkles, versus eastern longitude. Data from the southern Barents Sea region. - Antall iktarter per lokalitet hos tre arter av strandsnegl plottet mot østlig lengdegrad. Data fra det sørlige Barentshavet.

In region B and C the frequency of Group I trematodes was about 90% in both *L. saxatilis* and *L. obtusata* (figure 9). In the two westernmost regions (D and E), the frequency of such trematodes decreased drastically in *L. saxatilis* (to 50%) and *L. obtusata* (to about 65%) (figure 9). This was because the frequency of Group II trematodes increased steadily westwards; in *L. saxatilis* from 0% in region A to about 45% in region E, and in *L. obtusata* from about 5% (region B) to about 25% (region E) (figure 9). The trends were less pronounced for Group III trematodes, of which the frequency were low (figure 9).

The trend found for the trematode groups was caused by the decrease westwards in the frequency of *M. pygmaeus* (which occupy a dominante position in Group I). Moreover, the frequency of Group II trematodes such as *M. similis*, *C. lingua*, *Himasthla* sp. and *Renicola* sp. generally increased westwards in both *L. saxatilis* and *L. obtusata* (figure 10). The second most important species in Group I, *M. piriformes* shows a clear increasing trend in frequency westwards, along the the Barents Sea coast and in region B (figure 10). In region E, this parasite was more common in *L. saxatilis* than *M. pygmaeus*. The pattern of *M. piriformes* was similar to that found for trematode species classified in Group II (figure 10).

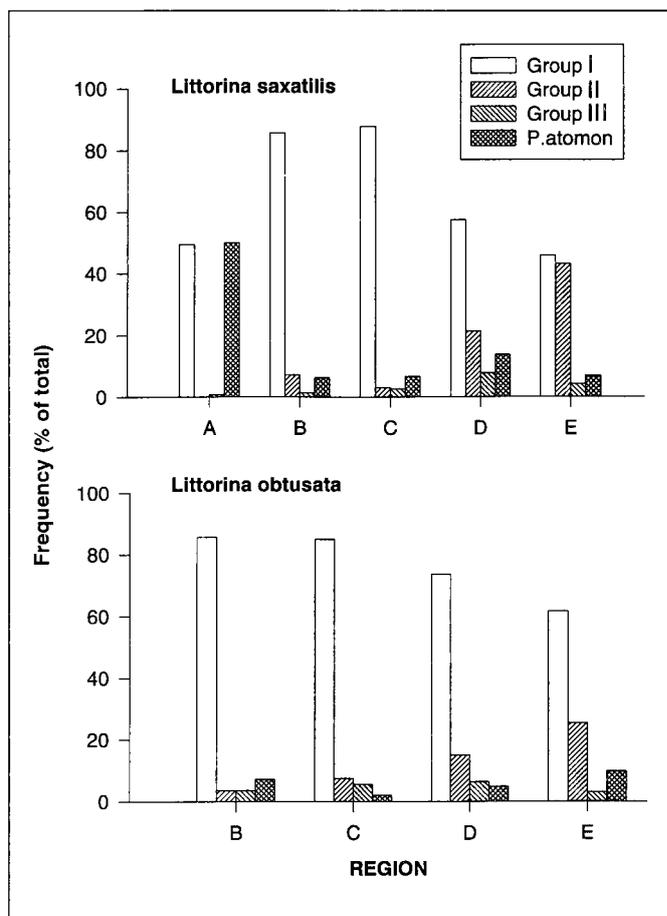
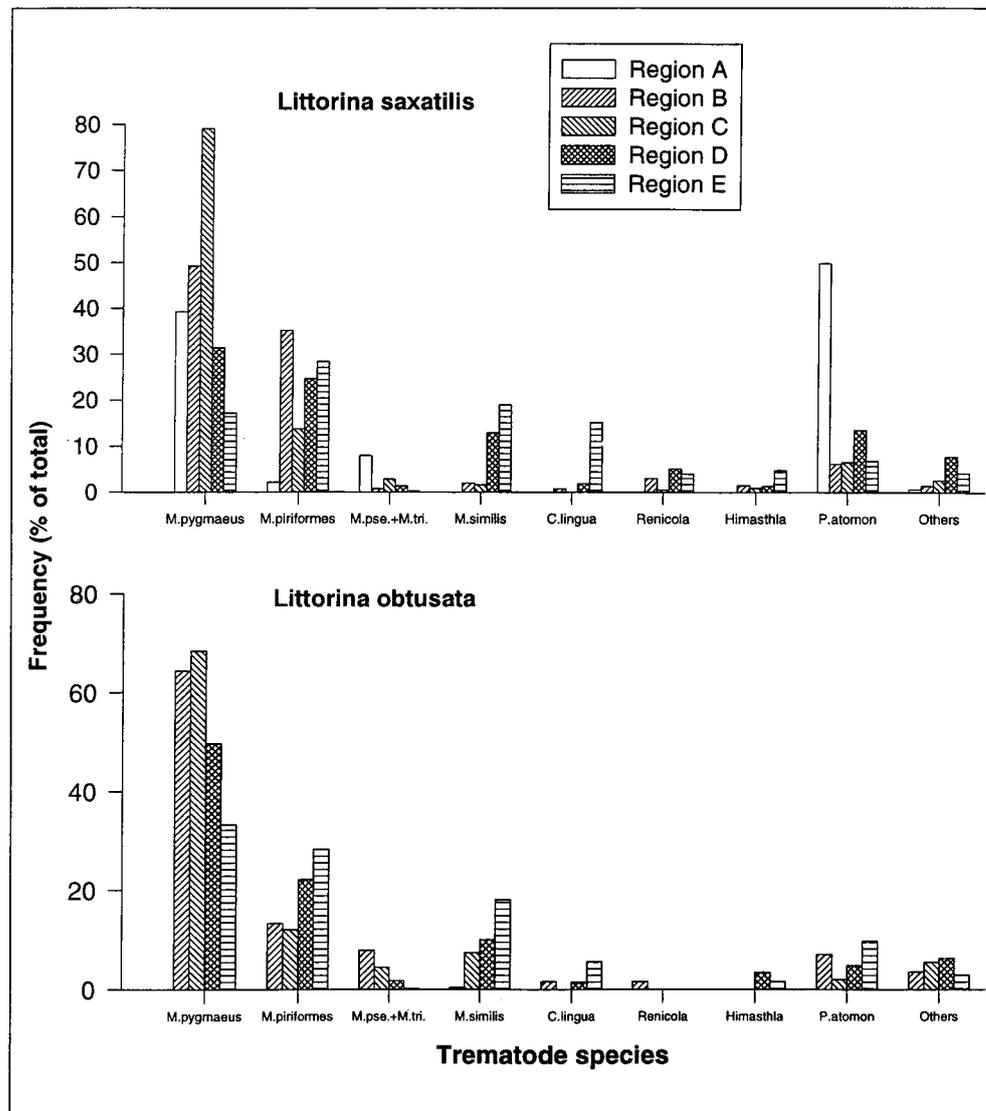
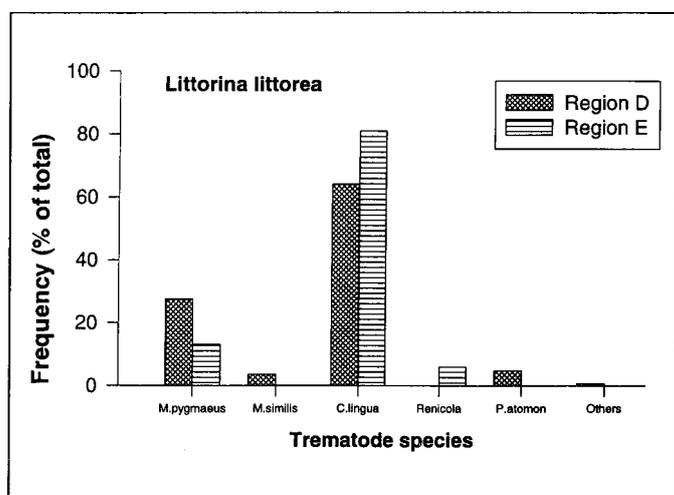


Figure 9
 Frequency of different trematode groups (see text) in two species of periwinkles (infected individuals) in different regions of the Barents Sea and the White Sea. - Forekomst av forskjellige iktgrupper i spiss- og butt strandsnegl blandt totalt antall infiserte snegler i forskjellige regioner av Barentshavet og Kvitesjøen.



Figur 10
Frequency of different trematode species in two species of periwinkles (infected individuals) in different regions of the Barents Sea and the White Sea. - Forekomst av forskjellige iktearter blant totalt antall infiserte snegler (spiss- og butt strandsnegl) i forskjellige regioner av Barentshavet og Kvitesjøen.



Figur 11
Frequency of different trematode species in *L. littorea* (infected individuals) in different regions of the Barents Sea - Forekomst av forskjellige iktearter blant totalt antall infiserte individer av stor strandsnegl i forskjellige regioner av Barentshavet.

In all regions, except region A, the frequency of *P. atomon* varied between from 5 to about 15% both in *L. saxatilis* and *L. obtusata* (figure 10). We recorded trematode infection in *L. littorea* in the western regions (D and E), and *C. lingua* predominated in this mollusc, and to a lesser extent *M. pygmaeus* (figure 11).

In conclusion, trematodes with simple autonomic life-cycles dominated in the eastern regions, while those with more complex life-cycles increased in their importance in the western regions. The exception was *M. piriformes*.

3.2 Prevalence (% of snails infected)

3.2.1 Prevalence of different trematode species in different regions

In *L. saxatilis* the prevalence of all trematode species (pooled) was lowest in region A, where 10% of the snails were infected, and highest in region B where 40% of the snails were infected. In the two westernmost regions the prevalence was about 30% (table 4). For the other snail species, there was an increase in the percentage of infected snails westwards (table 4).

The differences in the prevalence of trematode species (groups of species) in periwinkles between regions, showed a similar pattern as the *frequency of occurrence*. That is a westward decrease in the prevalence of autonomic trematodes (Group I) and increase in prevalence of trematodes with complicated life-cycles (Group II) (**figure 12**). Our statistical analyses showed that this trend was significant for all common trematode species and groups of species that infected *L. saxatilis* (**table 5**), and for most representatives of trematodes in *L. obtusata* (**table 6**), when controlling for exposure. In *L. obtusata*, the prevalence of *C. lingua*, *Himasthla* sp. and trematode species in Group III was not significantly different between regions (**table 6**).

Exposure had a significant effect on the prevalence of *M. piriformes* and *Himasthla* sp. in *L. saxatilis* and *L. obtusata*, but not for other trematodes (**table 5-6**).

The lowest prevalence of trematodes was recorded in *L. saxatilis* on the coast of Novaya Zemlya and Vaygatch in region A (9.3%). In this region microphallids of the "pygmaeus" group predominated, through the high prevalence of *M. pygmaeus* (4.6%). The prevalence of *M. piriformes* was very low in this region (0.16%) (**figure 13**). The highest prevalence of *M. pygmaeus* was found in region C (eastern Murman) in both *L. saxatilis* (23.6%) and *L. obtusata* (11%), while further west it decreased to 5.3% and

Table 4. Total prevalence (% snails infected) of trematodes in different species of intertidal gastropodes in different regions (A-E) (see study area) on the coast of the southern Barents and White Sea. - Prosent av undersøkte snegler infisert med ikter i forskjellige regioner (se studieområde) langs den sørlige Barentshavkysten og Kvitsjøen.

Host- Vertsart	Region				
	A	B	C	D	E
<i>Littorina saxatilis</i>	10.2	40.4	35.4	28.1	29.6
<i>L. obtusata</i>	-	6.1	17.0	20.9	20.2
<i>L. littorea</i>	-	-	0.4	8.3	26.0
<i>Nucella lapillus</i>	-	-	2.7	11.4	15.6

Table 5. Analysis testing the regional effect, controlled for environmental exposure, on the prevalence (% of snails infected) of different trematode species in *L. saxatilis* along the Barents Sea coast and White Sea (PROC GLM, on ranked data PROC RANK, SAS 1990). - Analyse som tester den regionale effekten, kontrollert for eksponeringsgrad, på prevalensen (% av snegler infisert) av forskjellige iktesarter i spiss strandsnegl *L. saxatilis* på Barentshavkysten og Kvitsjøen (PROC GLM, på rankede data PROC RANK, SAS 1990).

Trematode species Iktesarter	Exposure - eksponering			Region - region		
	DF	F	p	DF	F	
<i>Microphallus pygmaeus</i>	4	1.44	ns.	4	11.51	****
<i>M. piriformes</i>	4	5.48	***	4	22.41	****
<i>M. similis</i>	4	1.05	ns.	4	25.34	****
<i>Cryptocotyle lingua</i>	4	1.12	ns.	4	27.81	****
<i>Renicola</i> sp.	4	1.10	ns.	4	6.32	****
<i>Himasthla</i> sp.	4	2.29	*	4	4.60	**
Group I	4	5.09	***	4	15.09	****
Group II	4	1.32	ns.	4	47.31	****
Group III	4	0.81	ns.	4	2.54	**
<i>Podocotyle atomon</i>	4	0.66	ns.	4	4.87	***

**** : p<0.0001, ***: p<0.01, ** p<0.05, *: p<0.1, ns: p>0.1

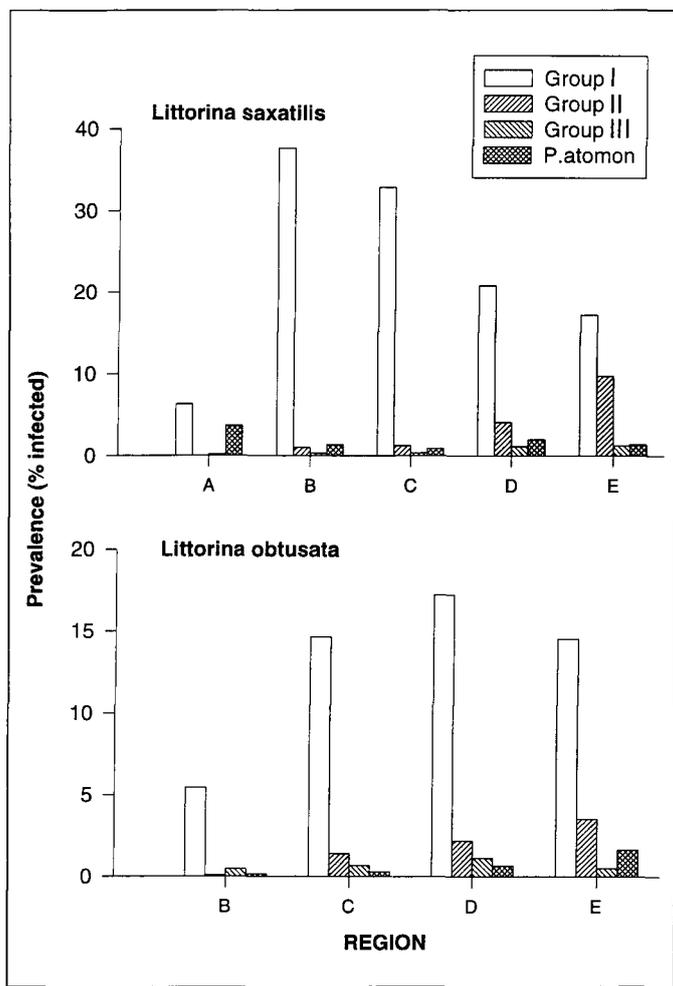


Figure 12

Prevalence of different trematode groups in two species of periwinkles (% of snails infected) in different regions of the Barents Sea and the White Sea.- Prevalens (% infiserte snegler) artsgrupper av ikter i spiss- og butt strandsnegl (% infiserte snegler) i forskjellige regioner

8.4% in region E in both snail species, respectively. In contrast, the prevalence of *M. piriformes* increased westwards (figure 13), and was also high in *L. saxatilis* in region B (White Sea) (15.9%) (figure 13). The prevalence of *M. similis*, *C. lingua*, *Renicola* sp. and *Himasthla* sp. in *L. saxatilis* increased significantly in the western regions (table 5, figure 13). In *L. obtusata* it was significant only for *M. similis* (table 6, figure 13). We also noticed a trend toward increased prevalence of trematodes in Group III in the western regions (figure 12), but it was significant for *L. saxatilis* only (table 5-6). The same trend was found in the prevalence of *C. lingua* in *L. littorea* and of *Renicola* sp. in *N. lapillus* (figure 14-15), but the interregional differences were not significant.

3.3 Prevalence of parasites in northern Norway in relation to human activities

Only material collected in Norway in 1994 was used for this comparison. Gastropods were sampled in fishing villages, close to fish processing factories (n=27), at sites near fish farms (n=14) and at natural sites (controls) within a few km of the fishery activities (n=25) with similar environmental conditions. Since we found regional effects on the species composition and prevalence, we controlled for longitude in our statistical analyses.

3.3.1 Differences at the species level

For this analysis, the stations near the two types of human activities (fish industry and farms) were pooled. Seven species of trematodes were sufficiently abundant to be analysed individually in relation to the human activities (*M. pygmaeus*, *M. piriformes*, *M. similis*, *C. lingua*, *Renicola* sp., *Himasthla* sp. and *P. atomon*). All these species were analysed for *L. saxatilis* and *L. obtusata*, while for *L. littorea* only *C. lingua* and for *Nucella lapillus* only *Renicola* sp., were analysed.

In *L. saxatilis* the prevalence of *M. piriformes*, *M. similis* and *C. lingua* was significantly higher close to fish industry and farms than in control sites (table 7, figure 16). For *M. piriformes* the prevalence was 14% close to fish industry and farms, compared to 5.7% at control sites. The respective values for *M. similis* were 4.1% vs. 1.1%, and for *C. lingua*, 3.2% vs 0.7%. For *M. pygmaeus*, longitude played a much more important role than the fish activities (table 7, figure 16).

The situation was very different for *L. obtusata*, and the prevalence of *M. pygmaeus* was slightly higher at control sites than on sites with human activities (6.4% vs. 4.5%, p=0.03). For *M. piriformes* there was no significant difference (7.4% vs. 6.5%, p=0.83), while for *M. similis*, sites with human activities tended to have a higher prevalence, but the significance was marginal (3.3% vs. 1.3%) (table 7, figure 16)

For *L. littorea* the prevalence of *C. lingua* was higher at sites with human activities (15.5% vs. 5.5%), but the difference was not significant, and longitude explained much of this difference (table 7, figure 17). In *N. lapillus*, *Renicola* sp. tended to be more prevalent at sites with human activities, but the tendency was not significant (table 7, figure 18).

In conclusion, it seems that stations with human activities had a higher prevalence of most trematodes, even if all our results were not significant. A clear exception was prevalence of *M. piriformes* in *L. obtusata*.

Figure 13

Prevalence of different trematode species in two species of periwinkles (% of snails infected) in different regions of the Barents Sea.- Prevalens av ikter i spiss- og butt strandsnegl (% infiserte snegler) i forskjellige regioner av Barentshavet og Kvitsjøen.

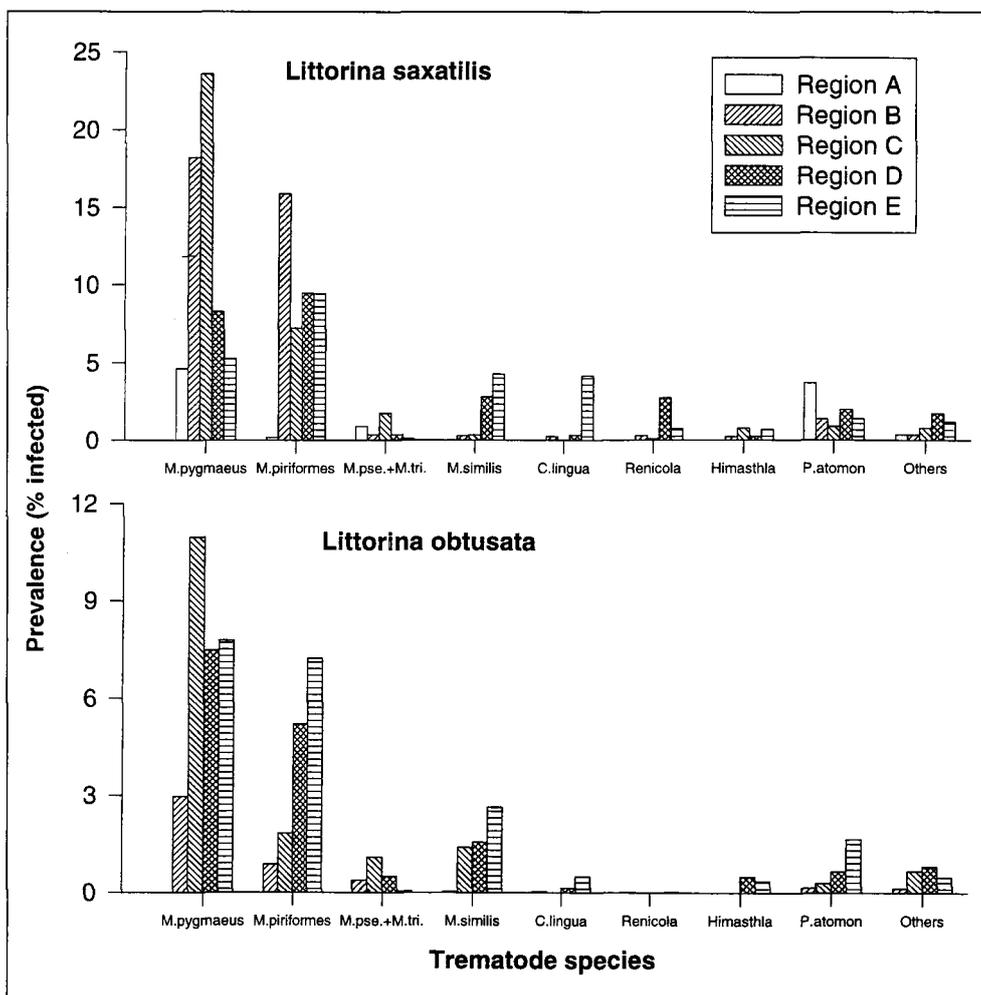


Table 6. Analysis testing the regional effect, controlled for environmental exposure, on the prevalence (% of snails infected) of different trematode species in *L. obtusata* along the Barents Sea coast and white Sea (PROC GLM, on ranked data PROC RANK, SAS 1990). - Analyse som tester den regionale effekten, kontrollert for eksponeringsgrad, på prevalensen (% av snegler infisert) av forskjellige iktearter i butt strandsnegl *L. obtusata* på Barentshavkysten og Kvitsjøen (PROC GLM, på rankede data PROC RANK, SAS 1990).

Trematode species Iktesarter	Exposure - eksponering			Region - region		
	DF	F	p	DF	F	
<i>Microphallus pygmaeus</i>	4	0.47	ns.	4	3.50	**
<i>M. piriformes</i>	4	3.30	**	4	2.12	ns.
<i>M. similis</i>	4	1.44	ns.	4	3.80	**
<i>Cryptocotyle lingua</i>	4	0.97	ns.	4	1.54	ns.
<i>Himasthla</i> sp.	4	3.74	***	4	1.01	ns.
Group I	4	1.50	ns.	4	4.35	**
Group II	4	2.14	*	4	4.41	***
Group III	4	0.59	ns.	4	0.53	ns.
<i>Podocotyle atomon</i>	4	0.49	ns.	4	0.86	ns.

**** : p<0.0001, ***: p<0.01, ** p<0.05, *: p<0.1, ns: p>0.1

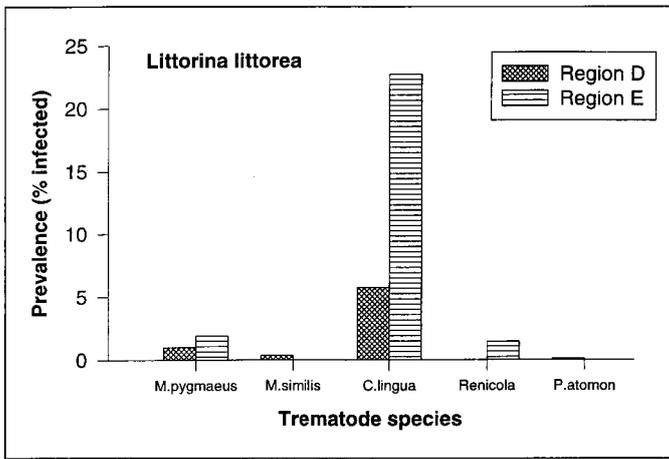


Figure 14
Prevalence of different trematode species in *L. littorea* (% of snails infected) in southwestern part of the Barents Sea.- Prevalens av ikter i stor strandsnegl (% infiserte snegler) i forskjellige regioner av Barentshavet.

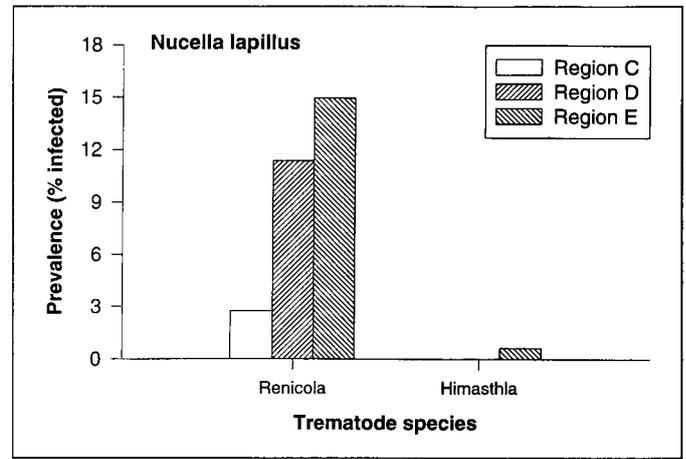
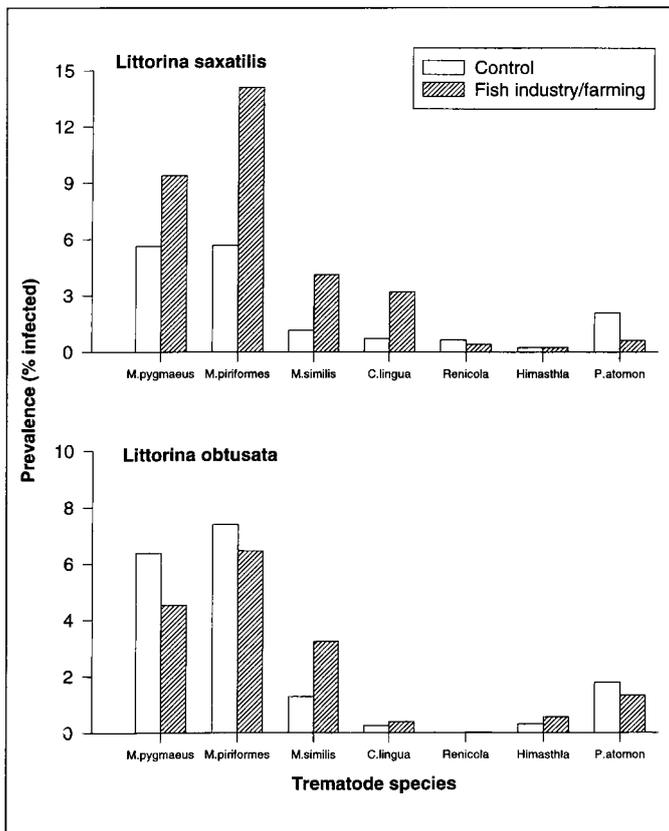


Figure 15
Prevalence of different trematode species in *Nucella lapillus* (% of snails infected) in southwestern part of the Barents Sea.- Prevalens av ikter hos purpurnegl (% infiserte snegler) i det sørvestlige Barentshavet.



Figur 16
Prevalence of different trematode species in two species of periwinkles (% of snails infected) in relation to fish industry and farms along the Norwegian Barents Sea coast.- Prevalens av forskjellige iktearter i spiss- og butt strandsnegl (% infiserte snegler) i forhold til fiskeindustri og fiskeoppdrett langs den norske

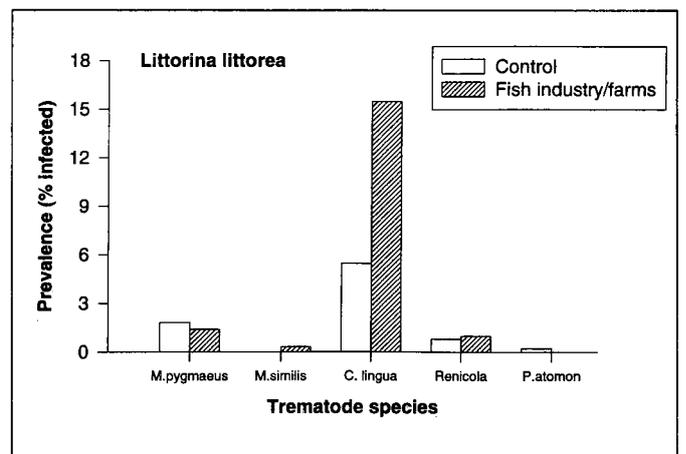


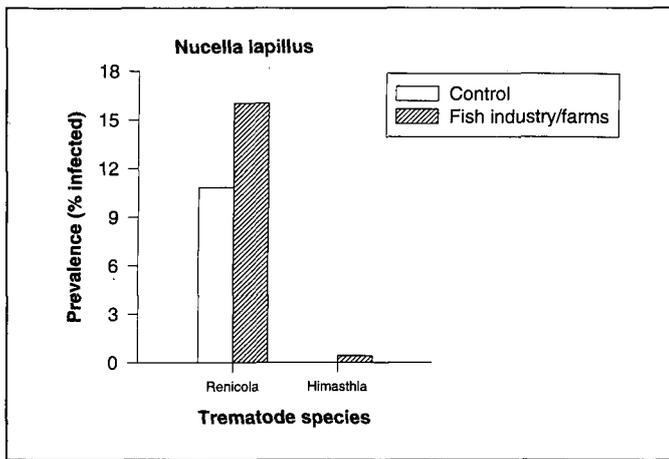
Figure 17
Prevalence of different trematode species in *L. littorea* (% of snails infected) in relation to fish industry and farms along the Norwegian Barents Sea coast.- Prevalens av forskjellige iktearter i stor strandsnegl (% infiserte snegler) i forhold til fiskeindustri og fiskeoppdrett langs den norske Barentshavkysten.

3.3.2 Groups of trematode species

In this analysis we pooled the prevalence of different trematode species with the same dominant final hosts into two groups: gull trematodes (*M. piriformes*, *M. similis*, *C. lingua*, *Renicola* sp. and *Himastha* sp) and eider trematodes (*M. pygmaeus*, *M. pseudopygmaeus*, *M. triangulatus*, *Parvatrema* sp.).

When pooling all snail species we found a significant difference between sites with different human activities and control sites for gull trematodes ($p= 0.0024$), but not for eider trematodes ($p=0.7$).

In *L. saxatilis* human activities had a significant effect on the distribution of gull trematodes ($p<0.0001$), but not for eider tre-



Figur 18

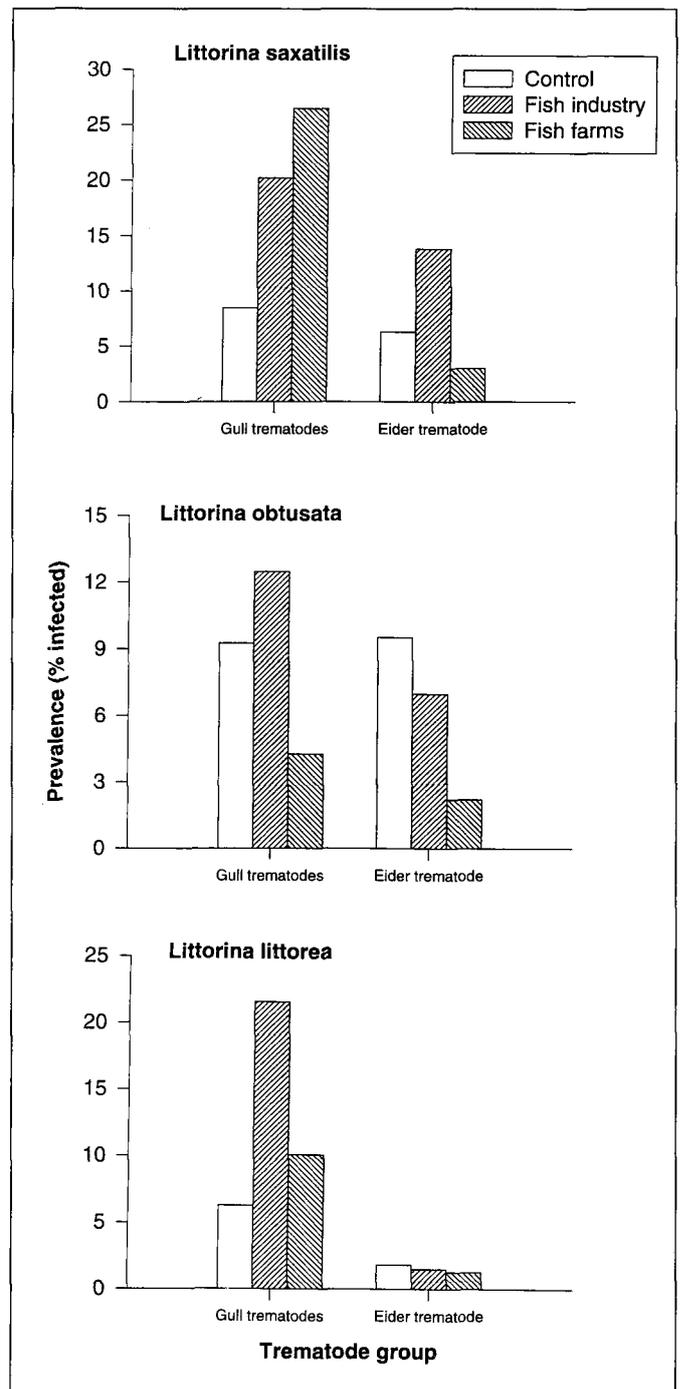
Prevalence of different trematode species in *Nucella lapillus* (% of snails infected) in relation to fish industry and farming along the Norwegian Barents Sea coast.- Prevalens av forskjellige iktearter i purpursnegl (% infiserte snegler) i forhold til fiskeindustri og fiskeoppdrett langs den norske Barentshavkysten.

matodes ($p=0.26$). Gull trematodes were more prevalent close to fish farms (26.4%) and fish industry (20.2%) than at natural sites (8.4%) (table 8, figure 19). There were no significant differences between the sites with different human activities and control sites in *L. obtusata* (table 8, figure 19), *L. littorea* (table 8, figure 19) and *N. lapillus* (table 8, figure 20), when controlling for longitude. This was true for both gull- and eider trematodes, except for eider trematodes in *L. obtusata*.

3.4 Species composition and prevalence of seabird parasite larvae in *Gammarus oceanicus* in northern Norway

We collected crustaceans (*Gammarus oceanicus*) at 38 different stations in northern Norway in September 1994. We found larvae of five parasite species, of which two have seabirds as final hosts. These two were the cestode *Microsomacanthus microsoma* (fam. Hymenolepididae), and the acantocephalan *Polymorphus phippsi* (fam. Polymorphidae), which have the common eider as final host. The other three were the metacercaria of *Podocotyle atomon*, the cestode *Diplocotyle nilandica* (fam. Dilepididae) and the nematode *Ascarophis* sp., which have different fishes as final host (table 9).

In the gammarids, seabird parasites were found only at 10 of 38 different stations. Most were *Polymorphus phippsi* (7 stations), while *Microsomacanthus microsoma* was found at two. These parasites were only found at very low prevalences (table 9). *P. atomon* was found in all stations, except one. There were no differences in prevalence between natural sites and places with human impact.



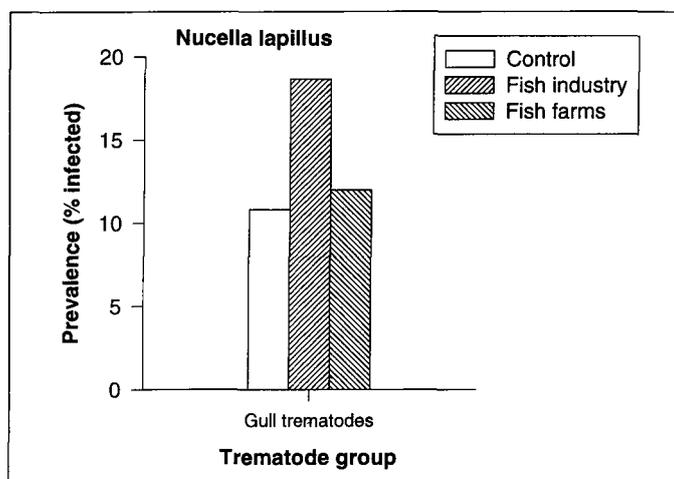
Figur 19

Prevalence of different groups of trematode species in three species of periwinkles (% of snails infected) in sites with fish industry, fish farming and control sites, along the Norwegian Barents Sea coast.- Prevalens av forskjellige iktearter i spiss-, butt- og stor strandsnegl (% infiserte snegler) i forhold til fiskeindustri og fiskeoppdrett og kontroll områder langs den norske Barentshavkysten.

Table 7. Analysis testing the effect of human activities (fish industry and fish farms), controlled for eastern longitude on the prevalence (% of snails infected) of different trematode species in intertidal gastropodes, along the Norwegian Barents Sea coast (PROC GLM, on ranked data PROC RANK, SAS 1990). - Analyse som tester effekten av menneskelige aktiviteter (Fiskeindustri og oppdrettsanlegg,) kontrollert for østlig lengdegrad på prevalensen (% av snegler infisert) av forskjellige iktearter på strandsnegler *Littorina sp.* og purpursnegl *Nucella lapillus*, langs den norske Barentshavkysten (PROC GLM, på rankede data PROC RANK, SAS 1990).

Host species- Vertsart							
Trematode species Iktesarter	Human activities- Menneskelig aktiviteter			Eastern longitude- Østlig lengdegrad			
	DF	F	p	DF	F	p	
<i>L. saxatilis</i>							
<i>Microphallus pygmaeus</i>	1	0.08	ns.	1	17.74	****	
<i>M. piriformes</i>	1	5.92	**	1	0.56	ns.	
<i>M. similis</i>	1	9.85	***	1	0.68	ns.	
<i>Cryptocotyle lingua</i>	1	13.67	***	1	18.45	****	
<i>Renicola sp.</i>	1	0.35	ns.	1	0	ns.	
<i>Himastha sp.</i>	1	0	ns.	1	0	ns.	
<i>Podocotyle atomon</i>	1	0.86	ns.	1	1.45	ns.	
<i>L. obtusata</i>							
<i>Microphallus pygmaeus</i>	1	4.84	**	1	3.98	**	
<i>M. piriformes</i>	1	0.04	ns.	1	0.08	ns.	
<i>M. similis</i>	1	3.17	*	1	0.52	ns.	
<i>Cryptocotyle lingua</i>	1	0.04	ns.	1	8.15	***	
<i>Himastha sp.</i>	1	0.45	ns.	1	0.13	ns.	
<i>Podocotyle atomon</i>	1	0.03	ns.	1	1.25	ns.	
<i>L. littorea</i>							
<i>Cryptocotyle lingua</i>	1	0.69	ns.	1	9.33	***	
<i>N. lapillus</i>							
<i>Renicola sp.</i>	1	0.54	ns.	1	0.57	ns.	

**** : $p < 0.0001$, ***: $p < 0.01$, ** $p < 0.05$, * : $p < 0.1$, ns: $p > 0.1$



Figur 20

Prevalence of different trematode species in *Nucella lapillus* (% of snails infected) in sites with fish industry, fish farming and control sites, along the Norwegian Barents Sea coast. - Prevalens av forskjellige iktearter i purpursnegl (% infiserte snegler) i forhold til fiskeindustri og fiskeoppdrett langs den norske Barentshavkysten.

Table 8. Analysis testing the effect of human activities (fish industry and fish farms), controlled for eastern longitude, on the prevalence (% of snails infected) of two trematode species groups in intertidal gastropodes, along the Norwegian Barents Sea coast (PROC GLM, on ranked data PROC RANK, SAS 1990). - Analyse som tester effekten av menneskelige aktiviteter (Fiskeindustri og oppdrettsanlegg,) kontrollert for østlig lengdegrad på prevalensen (% av snegler infisert) av to grupper av iktearter på strandsnegler og purpursnegl, langs den norske Barentshavkysten (PROC GLM, på rankede data PROC RANK, SAS 1990).

Host species- Vertsart

Trematode species Iktesarter	Human activities- Menneskelig aktiviteter			Eastern longitude- Østlig lengdegrad		
	DF	F	p	DF	F	p
<i>L. saxatilis</i>						
Gull trematodes	1	17.14	****	1	7.97	***
Eider trematodes	1	1.26	ns.	1	14.27	****
<i>L. obtusata</i>						
Gull trematodes	1	0.91	ns.	1	0.84	ns.
Eider trematodes	1	4.25	**	1	3.83	*
<i>L. littorea</i>						
Gull trematodes	1	0.93	ns.	1	8.98	***
Eider trematodes	1	0	ns.	1	2.45	ns.
<i>N. lapillus</i>						
Gull trematodes	1	0.54	ns.	1	0.57	ns.
All host species						
Gull trematodes	1	10.11	***	1	9.53	***
Eider trematodes	1	0.15	ns.	1	3.43	*

**** : p<0.0001, ***: p<0.01, ** p<0.05, *: p<0.1, ns: p>0.1

Table 9. Prevalence (% infected) of different parasites in *Gammarus oceanicus* from 38 stations along the Norwegian Barents Sea coast (Kirkenes to Tromsø), at location close to fishery activities (industry and farms) and control sites. - Prosent av marflo infisert med parasitter langs den Norske Barentshavkysten.

Parasite species Parasittart	Human activities Fiskeindustri/oppdrett		Natural sites Upåvirkede områder	
	\bar{x}	SE	\bar{x}	SE
<i>Polymorphus phippsi</i>	0.3	0.16	1.0	0.5
<i>Microsomacanthus microsoma</i>	0	-	0.25	0.17
<i>Diplocotyle nilandica</i>	0.1	0.10	0	-
<i>P. atomon</i>	41.7	5.9	46.9	6.2
<i>Ascarophis sp</i>	0.8	0.5	0.25	0.25

4 Discussion

4.1 Species composition of the Barents Sea trematode community

The most important final hosts of the 13 seabird trematodes we found in this study, are the common eider and the large gulls (herring gull and great black-backed gull). Common eiders are the main definitive host of *M. pygmaeus*, *M. triangulatus*, *M. pseudopygmaeus*, *Parvatrema* sp. and probably *Notocotylus* sp. Gulls are the most important final hosts of *M. similis*, *C. lingua*, *Himasthla* sp. and *Renicola* sp. Gulls are also the main hosts for *M. piriformes*, but this trematode may also develop in common eider. However in eiders the worms mature more slowly and their individual fecundity is lower (Saville et al. in prep.). Trematodes of waders were rare and only two species, *Parapronocephalum symmetricum* and *Maritrema arenaria* were found. This pattern arises partly because the intertidal zones are important habitats for the final hosts. Intertidal invertebrates are the main component of common eider diet and during the brood rearing period, and periwinkles play a particularly important role (Pertzov & Flint 1963, Belopolskii 1971, Catin et al. 1974, Bianki et al. 1979). Intertidal molluscs and crustaceans are also an important part of the diet of herring gull, great black-backed gull and common gull (Belopolskii 1971, Krasnov et al. 1995). Gulls spend a lot of time feeding and resting in the intertidal zones. Waders such as oystercatcher (*Haematopus ostralegus*), turnstones (*Arenaria interpres*) are rather rare in the eastern part of the Barents Sea and in particular in the White Sea. Other waders visit intertidal zones only during the short periods of the spring and autumn migrations. Although purple sandpipers (*Calidris maritima*) spend the winter in the regions there is very little transmission of trematodes because periwinkles are inactive and *N. lapillus* moves to the subtidal zone in winter.

4.1.1 Number and importance of different trematode species in different regions

We found that the mean number of trematode species per sampling station increased westwards in the periwinkles *L. saxatilis* and *L. littorea*, but not in *L. obtusata*. In *L. saxatilis* the relationship was caused by the low species number in the easternmost region. In the intertidal zone of Novaya Zemlya and Vaygatch, we found all four representatives of the "pygmaeus" group microphallids with autonomic life-cycles in *L. saxatilis*, but only two species with free-living cercariae, *Notocotylus* sp. and *P. atomon*. The trematode species found in *L. saxatilis* and *L. obtusata* in the White Sea and Kola coast (region B and C) were the same as those in western Kola and along the Norwegian Coast (region D and E). The absence of some of the trematode species in *L. obtusata* in region B and C is probably caused by small samples sizes. The total absence of trematodes in *L. littorea* in region C was presumably a result of the low density of individuals in the boundary populations on the eastern Murman coast. This apparently reduces the probability of infection by trematodes to zero.

Our findings on the number of species comply with our result on frequency of different trematodes species. In the eastern regions, the microphallids of the "pygmaeus" group dominated among the infected snails, while in the western regions the percentage of trematodes with complex life-cycles increased drastically. The only exception from this rule was found in *P. atomon*, which does not have seabirds in their life-cycle. The high frequency of this species in region A is probably caused by some specific traits in its life-history (Galaktionov 1993), and by the high concentration of fish (*Boreogadus saida*, *Eleginus navaga*, *Coregonus autumnalis*) near the shore of Vaygatch and the southern part of Novaya Zemlya.

The interregional differences in the number of species and frequency of trematode species can probably be explained by the longitudinal changes in the environmental conditions which are less harsh in the western regions. A better climate facilitates the completion of trematode life-cycles with several hosts and free-living larval stages. The harsh conditions of the arctic littoral zones decrease the probability of the completion of three-host life-cycles, because of small survival chances of free-living larvae (James 1968, Galaktionov 1993, Galaktionov & Bustnes 1995). This is probably one of the reasons why the frequency of trematodes with such life-cycles (Group II and Group III) in both *L. saxatilis* and *L. obtusata* decreased eastwards.

On the whole the three-host life-cycles with one free-living larval stage, cercaria, have a better chance for successful completion than trematodes with autonomic life-cycles such as microphallids of the "pygmaeus" group (Galaktionov 1993). The latter has a significant advantage during extreme environmental conditions only (James 1968; Galaktionov 1993). In more favourable environments, e.g. on the seashores of Germany, France, Britain and Northern Ireland, trematode species with three-host life-cycles predominate in the species composition in periwinkles (Laukner 1980, 1987, Werding 1969, Combescot-Lang 1976, James 1969, Hughes & Answer 1982, Irwin 1983, Matthews et al. 1985). In the Barents Sea, it seems that the trematodes with autonomic life-cycles (Group I) face increased competition with the more complex species in Group II and III in the western regions (D and E) and therefore become less common.

Apart from the environmental conditions, the frequency of different trematodes species larvae in intertidal molluscs is influenced by the availability of suitable final hosts, their density, traits in their biology and behaviour (e.g. James 1968, Werding 1969, Laukner 1980, Galaktionov & Dobrovolskij 1986, Galaktionov & Bustnes 1995). The autonomic life-cycle of microphallids of the "pygmaeus" group is probably relatively independent of the physical conditions, but the frequency of *M. piriformes* in *L. saxatilis* in region A was very low. This is presumably because of the behaviour of gulls which feed mainly on fish and rarely visit the littoral zones at Novaya Zemlya and Vaygatch (Karpovitch & Kohanov 1967). The frequency of *M. piriformes* was higher in region C, but the concentration of common eider broods in the bays of eastern Murman led to the predominance of *M. pygmaeus*. On the outer coast in the western regions (D and E), common eider broods are more dispersed. However, the number of large gulls is higher and they spend much more time in the tidal

zone, mostly close to fishery villages. As a result, we observed a relative increase in the frequency of *M. piriformes* and a parallel decrease in the frequency of *M. pygmaeus* compared to region C. The increase in the frequency index of *M. piriformes* in the White Sea (region B) is probably also caused by the high concentrations of gulls in the sampling area in the Kandalaksha Bay.

The same interregional changes in the frequency of *M. piriformes* and *M. pygmaeus* were found in *L. obtusata*. The relatively lower frequency index for *M. piriformes* compared to *L. saxatilis* is probably caused by the fact that *L. obtusata* inhabit a lower part of the intertidal zone (see material and methods). The low intertidal is more often visited by common eiders than by gulls, which usually concentrate in the upper and middle levels of the littoral where *L. saxatilis* is more common. An increase in gull density westwards may also promote the increase in the frequency of Group II trematodes, primarily *M. similis* and *C. lingua* which are among the most common parasites of gulls in Europe.

4.2 Differences in prevalence (% of infected snails)

The overall percentage of the investigated snails that were infected with trematodes (prevalence) did not show much variation between the regions for *L. saxatilis* (except region A) and for *L. obtusata*, but more so for the less common *L. littorea* and *N. lapillus* (table 4).

Contrary to James (1968), we did not find a significant influence of exposure on the prevalence of most trematode species in periwinkles. The most plausible explanation for this is that the places with the same exposure in the different regions are distinguished by other environmental conditions (temperature regime, absence or presence of ice in winter, etc.), and the availability of the definitive and intermediate hosts. The longitudinal changes among regions are highly significant because of the size of the area studied (40 degrees longitude), and it is therefore not surprising that the regional differences are more important for the prevalence than exposure only. However, we found a significant influence of exposure on *Himastha* sp. which is the trematode species with the most complex life-cycle (two free-living larval stages). This complies with the findings of James (1968).

Environmental conditions (temperature, ice) are the dominant factor influencing trematode distribution in region A. For example, we may compare the Lamchina Bay (Vaygatch Island, region A) and the Yarnshnaya Bay (eastern Murman, region C). They both have a relatively high concentration of common eider broods and are well protected from wave action (same exposure). However, the mean prevalence of *M. pygmaeus* in *L. saxatilis* in the first bay was 10.1%, while in the second it was 42.7%. The regional differences in density of gull and eider populations leads to increased prevalence of gull trematodes (Group II + *M. piriformes*) in periwinkles, and a parallel decrease in prevalence by *M. pygmaeus* (eider trematodes).

The importance of the availability of suitable intermediate hosts is clearly demonstrated by *M. similis* and *C. lingua*. The prevalence of these species in periwinkles was low in region B and C. For *M. similis* this is probably because the second intermediate host, the seashore crab *Carcinus maenas* is absent east of the Varanger Fjord. Metacercariae of this trematode can also develop in the subtidal crab *Hyas araneus* (Uspenskaya 1963, Podlipayev 1979), but the latter is rarely found in the intertidal zone and can therefore not serve as an agent for intensive infection by *M. similis*.

The situation is different for *C. lingua*, because the fishes connected with intertidal zone (second intermediate hosts) are also numerous in eastern regions. However, the low prevalence of this parasite in periwinkles in the eastern regions may be caused by the fact that the main first intermediate host, *L. littorea* is very rare in those areas. The less specific hosts, *L. saxatilis* and *L. obtusata* are not able to support a dense population of *C. lingua* under the relatively harsh environmental conditions of eastern seashores. The same situation is probably the case for *Renicola* sp. in periwinkles, because the main first intermediate host for this species is *Nucella lapillus*.

The reason why exposure had a significant influence on the prevalence of *Himastha* sp. in periwinkles is probably that this species has two free-living stages in its life-cycle. As noted by James (1968) and Galaktionov & Bustnes (1995) the echinostomatids only infect snails in the protected intertidal habitats. Such places are relatively rare on the seashore of the Kola peninsula, resulting in the low total prevalence of *Himastha* sp. in periwinkles. However, the situation in the bays in eastern Murman (low exposure, high concentration of gulls, existence of second intermediate hosts, such as mussels) is favourable for completion of the *Himastha* sp. life-cycle. As a result, a relatively high prevalence of *Himastha* sp. in periwinkles may be found in some places in this region (6.6% in the termination of Yarnishnaya Bay).

It was surprising to find a significant influence of exposure on the prevalence of *M. piriformes*, a species without free-living stages in their life cycle. This is probably caused by the extremely high prevalence of trematodes (60-80%) in periwinkles at some sheltered local seashores. These shores are often visited by gulls and peculiarities of *M. piriformes* life-cycle may promote the transmission.

4.3 Influence of human activities on trematode prevalence

In the eastern regions (A-C), the parasitological situation depends almost exclusively on natural factors (environmental conditions, density of seabird populations, existence of suitable host species, etc.). In the western regions (D and E), however, the anthropogenous factor becomes important. On the Norwegian coast, there are a large number of fishing villages and fish farms. As a result the gulls in Russia are dispersed in a natural environment, while in northern Norway the gulls often gather around the fishing villages and fish farms, and feed on

waste from the activity. This leads to a clumped distribution of the final hosts, which again may lead to increased transmission of parasites between hosts. This conclusion is supported by the results of this study. However, there seemed to be no overall trend toward a higher total prevalence of trematodes in gastropods in the Norwegian regions, especially in *L. saxatilis* (**table 4**), but mainly a change in the frequency and prevalence among the different species.

The prevalence of gull trematodes in the commonest periwinkle *L. saxatilis* was significantly higher in places with human activity than in control sites. The closest connection to human activity was found for *M. piriformes*, *M. similis* and *C. lingua*, although the distribution of the last species also depended on longitude. For other gull trematodes, the occurrence of *Himasthla* sp. was influenced by exposure which plays a more important role for the completion of their life-cycle than concentration of definitive hosts (Galaktionov & Bustnes 1995). The absence of a significant relationship between human activity and prevalence of *Renicola* sp. in periwinkles is probably caused by the fact that periwinkles are not the main first intermediate hosts for this parasite.

An increased prevalence of gull trematodes in places with human activity was also found in the other molluscs studied. However the differences were not significant in most cases. This is possibly a result of incomplete data, because *L. obtusata*, *L. littorea* and *N. lapillus* were collected at fewer places than *L. saxatilis*.

For eider trematodes, the situation was different, and there was no connection between prevalence and human activity. Only one exception was found; a significant increase in the prevalence of *M. pygmaeus* in *L. obtusata* at sites with human activity. The overall result is probably caused by the fact that waste from the fishing industry is not as attractive for eiders as it is for gulls, because the diet of eiders usually consists of benthic invertebrates. However, during the winter large flocks of eiders may feed close to the fishing industry.

Our study also demonstrated that the prevalence of gull trematodes in gastropods is generally higher on the shores near fish industry complexes (fishing villages) than near fish farms. Kristoffersen (1991) found that *C. lingua* infection in *L. littorea* close to charr farms increased with the age of the farms. *C. lingua* infection in periwinkles near the farms established less than 5 years ago was not significantly different from the control sites. In our study we did not include the age of fish farms, a factor which may have influenced our result.

The increased prevalence of trematodes in periwinkles near fishing ports and other regions where gulls flock has been described in several studies (Hoff 1939, Bartoli 1974, James et al. 1977, Lauckner 1984, Matthews et al. 1985). However, except for Kristoffersen (1991), all of these studies have been carried out on the seashores of the western and southern Europe (Germany, France, Great Britain and Northern Ireland). *C. lingua* and *M. similis* are the dominant parasite species there, and microphallids of the "pygmaeus" group were extremely rare. In this study, a representative of this group, *M. piriformes* was a dominant species among the gull trematodes in periwinkles at

places with fishery activity in northern Norway. As mentioned, the autonomic life-cycle of such parasites is well adapted for the relatively harsh environmental conditions of the northern areas (compared to more southern parts of Europe). It seems to compete successfully with the three-host life cycles of *M. similis* and *C. lingua*, particularly in region D. Moreover, the latter two species begin to play a significant role only in the westernmost region (E), and only in this region the combined prevalence of *M. similis* and *C. lingua* in both *L. saxatilis* and *L. obtusata* approached the level of *M. piriformes*.

The high infections of gull trematodes in the regions with human activity may have a double effect. First the infection level of the seabirds probably increases. There are no direct data on the prevalence of trematode infection in gulls in northern Norway, but the high level of infestation of the first intermediate hosts supports that it is rather high. Some indirect data support this. Engström (1989) found that 90% of the kittiwakes at Bleiksøy island, near the fishery port Bleik, were infected with *C. lingua*. The maximal intensity (number of parasites per host) were 660 specimens. For comparison, the values on the Seven Islands archipelago on the Kola Coast was 24.1% of the kittiwakes, and 3 specimens per bird (Galaktionov 1995).

It is difficult to estimate the present influence of helminths on gull populations. However, a survey of the literature shows that pathology has been reported for renicolids and some other intestinal trematodes (Campbell & Sloan 1943, Hill 1952, 1954, Wright 1956, Riley & Wynne Owen 1972). Lauckner (1985) has recorded death of common gulls due to the heavy infection with *C. lingua*. Strong pathology may be caused by microphallids of "pygmaeus" group because of the high number of these worms which may be found in individual birds. This is connected to the high numbers of invasive larvae in the infected periwinkles (up to 7600) (Belopolskaya 1949). One common eider may contain hundred thousands of adult microphallids (Kulachkova, 1979, Galaktionov & Marasaev 1992), which may result in the death of the birds. Young birds are especially vulnerable (Kulachkova 1979, Karpovich 1987). Taking into account the high prevalence of *M. piriformes* in periwinkles near places with human activity, this parasite can probably influence the health of gulls.

The second impact of a high trematode infection is the parasitological pressure on coastal ecosystems (Bartoli 1974, Bartoli & Prevot 1976, James et al. 1977, Lauckner 1984). Trematode larvae parasitizing marine molluscs and impairing their resistance against unfavourable environmental factors can sometimes cause mass elimination of the hosts (Vernberg & Vernberg 1963, Tallmark & Norrgren 1977). Many trematodes (all recorded in present study) can cause parasitic castration of molluscs (Kurtis 1974, Baudoin 1975, Dobson 1988). Castrated individuals are a "population load" as they take no part in reproduction, but still compete intraspecifically for food, refuges and other resources. Under heavy incidences, this results in suppression of the littoral mollusc populations (see Lauckner 1980, 1985 and Galaktionov 1993 for reviews). Our study indicates that the coastal ecosystems in and near fishing villages and fish farms in North Norway may suffer a high pressure because of these parasites.

4.4 Species and prevalence of sea bird parasites in Gammarids

In general, the species composition and prevalence of helminth larvae in *G. oceanicus* in northern Norway (region D and E) are similar to those described from the eastern Murman (Uspenskaya 1963, Marasaeva 1990). Metacercariae of *P. atomon* clearly predominate and all other helminth larvae are very rare (prevalence less than 1%). However, there is one essential difference which is connected with the patterns of common eider behaviour. As mentioned above, the common eider broods concentrate in sheltered bays. In such places the foci of infection of common eider helminths in gammarids are established at a relatively high level. So, in Yarnishnaya Bay (eastern Murman) in summer 1988, the prevalences of *Microsomachanthus microsoma* in *G. oceanicus* was 8% and *Polymorphus phippii* 28.4% (Marasaeva 1990). The reason for the lower level of infection in the western regions is probably a more dispersed distribution of common eider broods.

5 Concluding remarks

This study is the first to present data on the distribution and prevalence of seabird parasites from the whole northern coast of mainland Europe. Our results show clear patterns in which the species composition changes throughout this area. We have investigated several factors, such as longitude (more or less related to climate), exposure and human activity, and found many cases of significant relationships between the parasite distribution and these factors. Some of them may be contrary to what would be expected, while others comply with present theory. However, the area which has been studied covers 40 degrees longitude. It is therefore clear that our 180 sampling stations do not cover this area in detail, and if other types of stations were sampled our result may have been different. For example the fact that we sampled close to fish industrial sites may have given a different result than if we had sampled in more natural sites. There is therefore a great need for further study in these areas to better confirm, or reject our results.

It is also important that the level of parasite infection in the intermediate hosts do not necessarily reflect the situation in the final hosts, but only tell something about the presence and absence of parasite species in the environment of the final hosts.

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