# The structure of parasite component communities in brackish water fishes of the northeastern Baltic Sea

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## SUMMARY

We used nestedness analysis to seek non-random patterns in the structure of component communities of metazoan parasites collected from 31 sympatric fish species from the northeastern Bothnian Bay, the most oligohaline area of the Baltic Sea. Only 8 marine parasite species were found among the 63 species recorded, although some marine fish species reproduce in the bay and others occasionally visit the area. Marine parasite species can utilize both freshwater and marine fish species as intermediate or final hosts, and marine fish can harbour freshwater parasite species. This exchange of parasite species between marine and freshwater fish has probably resulted from ecological factors acting over short time scales rather than from evolutionary processes acting over longer time; the key factor probably being the immediate presence of suitable intermediate and definitive hosts. Marine fish were expected to harbour species-poor parasite communities consisting mainly of generalists acquired from the sympatric freshwater fish species, which would result in a nested pattern among the different component communities. However, an anti-nested pattern was found in the component communities of metazoan parasites of fishes from the Bothnian Bay. A likely explanation for the observed pattern is that there are specialist parasite species, the majority of which are cestodes, in some of the freshwater fish species which otherwise have depauperate parasite communities.

Key words: allogenic species, autogenic species, host specificity, nestedness, richness.

## INTRODUCTION

Component communities of parasites in each of many sympatric host populations represent communities assembled in ecological time from a pool of currently and locally available species. This pool consists of all parasite species exploiting the host populations at one point in time. Separate component communities often share parasite species but only occasionally have identical species composition. They can also be merely stochastic assemblages of available species. Despite the recent focus on the determinants of species richness in parasite communities (Poulin, 1997*a*; Morand, 2000) there is still little information on the patterns of parasite community composition or on the processes responsible for these patterns. A fundamental question at the core of community ecology is what determines the subset of the potential pool of parasites comprising the realized infracommunities and thus the component community (Holmes, 1987, 1990)? Many factors can influence the chances of a host species acquiring parasite species from the locally available pool, including the breadth of its diet, its vagility, its relatedness to other sympatric host species and how long ago it arrived in the area (e.g. Price & Clancy, 1983; Kennedy, Bush & Aho, 1986; Kennedy & Bush, 1994).

Nestedness analysis is one way of testing for patterns in the composition of component communities. In communities of free-living animals, rich assemblages often tend to contain many species specific to them, whereas species-poor assemblages tend to include mainly species shared with other assemblages (Patterson & Atmar, 1986; Wright *et al.* 1998). Such a non-random pattern of species occurrence is referred to as nestedness (Patterson & Atmar, 1986; Worthen, 1996). Parasite communities include both specialist species, that are rather host-specific, and generalist species, that infect a range of host species. If nested patterns occur in the organization of parasite communities as they do in free-living communities, we might expect that host species harbouring few parasite species would harbour mainly generalist parasites, and that specialist parasites would become more common in host species harbouring species-rich parasite communities. In other words, the parasite species forming depauperate communities constitute a proper subset of those in richer communities. This pattern would be consistent with the view that host species differ in their susceptibility to colonization by new parasite species (Poulin, 1997*b*). Other departures from randomness are also possible, such as anti-nestedness

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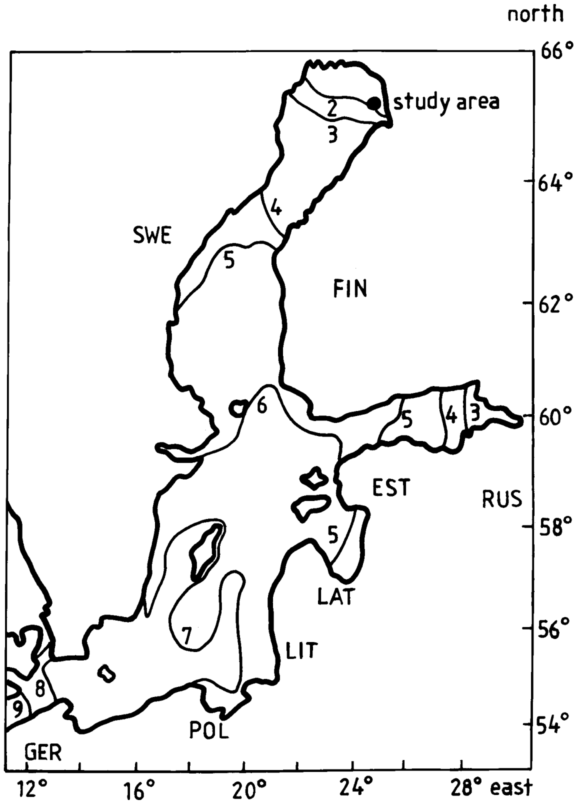

Fig. 1. Surface salinity distribution of the Baltic Sea (‰) in June and location of the study area in the Baltic Sea.

(*sensu* Poulin & Guégan, 2000), in which highly host-specific endoparasite species would be more likely to occur in host species harbouring fewer parasite species than one would expect if parasite species used host species in a random way.

The fish fauna of the Baltic Sea offers an ideal opportunity to elucidate the processes leading to the formation of parasite component communities. The sea shows marked gradients in environmental conditions. At all trophic levels there are components of both the marine and freshwater fauna living side by side, the proportion of marine species decreasing towards the north. Still even in the N.E. Gulf of Bothnia there are populations of several marine fish species reproducing in the area and accidental marine visitors are migrating up to the most northern areas. The idea of an equilibrium of parasite communities resulting from a balance between parasite colonizations and extinctions (Price, 1987) is interesting to study in this area, where several abiotic and biotic filters may prevent the occurrence of parasite species in fishes which do not occur in their usual habitats. On the other hand these fish species may be the source of new parasite colonizers into the area. The few marine fish species that have established reproducing populations in the Bothnian Bay live at the limit of their northern distribution range. In such conditions they can lose their specific parasite species (Dogiel, 1961). Our prediction was that the parasite faunas of marine fish species in the Bothnian Bay are depauperate and composed of generalist species from the component communities of the freshwater fish species in the area (see Polyanski, 1961). This is why a nestedness pattern was expected to occur in the component communities of fishes of the Bothnian Bay.

If found, such a departure from a random association of parasite species would indicate the existence of evolutionary or ecological forces structuring parasite communities. Nestedness in parasite communities has been well studied at the infracommunity level, i.e. in comparisons of parasite species composition among individuals in a host population (e.g. Guégan & Hugueny, 1994; Poulin, 1996; Worthen & Rohde, 1996; Rohde *et al.* 1998). However, only 2 studies have looked for nested patterns in the composition of parasite communities across host species (Guégan & Kennedy, 1996; Poulin, 1997*a*). Both studies, however, used published lists of parasite species known from all freshwater fish species occurring over a large geographical area. These parasite species do not truly represent a species pool available for colonization of the fish species in a given location. The present study is therefore the first test of nestedness among sympatric component communities of parasites.

## STUDY AREA

The Baltic Sea is unique in the world as a northern brackish water basin. After glaciation 10000 years ago, at times it has been connected to the ocean, whereas at other times it has been a lake, a past reflected in the sea's nature today. With decreasing salinity from the Danish straits to the Baltic proper and towards the Gulfs of Bothnia and Finland (Fig. 1) the number of marine species decreases, while the proportion of the freshwater species increases. The study area in the northeastern Bothnian Bay is the least saline (0·5–3·5‰), the most oligotrophic, and the coldest part of the Baltic Sea (Alasaarela, 1979) (Fig. 1). The area is ice-covered for 6 months of each year from mid-November to mid-May. The biota consists of relatively few species, as compared with the proper Baltic Sea, that have adapted to the conditions prevailing in the area. Relicts from the ancient freshwater epochs, such as the amphipod *Monoporeia affinis*, isopod *Saduria entomon* and the four-horn sculpin *Myoxocephalus quadricornis* form an essential part of the fauna of the Bothnian Bay. The soft bottom fauna consists almost exclusively of *Monoporeia affinis*: 1 square meter contains upto 500 amphipods, compared to 5000–10000 in the southern Gulf of Bothnia (Andersin *et al.* 1978). *M. affinis* is the intermediate host of several acanthocephalan species and the nematode *Cystidicola farionis* (Valtonen & Valtonen, 1978; Valtonen & Crompton, 1990). The fish fauna of the Bothnian Bay includes

Table 1. Species and numbers of fish studied for metazoan parasites in the N.E. Bothnian Bay (Baltic Sea) between 1977 and 1979 and the number of parasite species and mean number of parasite individuals per host individual found in each host species

| Species | | No. of fish studied | Occurrence* | No. of parasite species | No. of parasite individuals per host individual |
|---|---|---|---|---|---|
| Freshwater | | | | | |
| *Lampetra fluviatilis* (L.) | Lamprey | 50 | ccc | 6 | 0·4 |
| *Esox lucius* L. | pike | 95 | cc | 18 | 47·7 |
| *Coregonus albula* L. | vendace | 342 | ccc | 14 | 17·7 |
| *Coregonus lavaretus widegreni* (Malmgren) | sea-spawning whitefish | 1164 | ccc | 18 | 47·3 |
| *Coregonus lavaretus lavaretus* (L.) | river-spawning whitefish | 147 | cc | 14 | 48·5 |
| *Salmo trutta* L. | trout | 55 | cc | 15 | 48·1 |
| *Osmerus eperlanus* (L.) | smelt | 772 | ccc | 17 | 26·0 |
| *Abramis brama* (L.) | bream | 2 | a | 1 | 1·5 |
| *Alburnus alburnus* (L.) | bleak | 42 | c | 6 | 2·6 |
| *Carassius carassius* (L.) | Crucian carp | 8 | a | 4 | 4·0 |
| *Leuciscus idus* (L.) | ide | 28 | cc | 5 | 29·6 |
| *Leuciscus leuciscus* L. | dace | 67 | ccc | 10 | 46·7 |
| *Phoxinus phoxinus* (L.) | minnow | 171 | ccc | 2 | 4·4 |
| *Rutilus rutilus* (L.) | roach | 323 | ccc | 10 | 43·5 |
| *Lota lota* (L.) | burbot | 106 | cc | 26 | 64·0 |
| *Gasterosteus aculeatus* L. | 3-spined stickleback | 1141 | ccc | 21 | 17·4 |
| *Pungitius pungitius* (L.) | ten-spined stickleback | 328 | ccc | 13 | 9·3 |
| *Myoxocephalus quadricornis* L. | fourhorn sculpin | 812 | ccc | 16 | 16·3 |
| *Gymnocephalus cernuus* (L.) | ruffe | 713 | ccc | 18 | 19·0 |
| *Perca fluviatilis* (L.) | perch | 311 | ccc | 17 | 19·3 |
| Marine | | | | | |
| *Acipenser sturio* L. | sturgeon | 2 | a | 1 | — |
| *Clupea harengus* L. | Baltic herring | 1212 | ccc | 12 | 2·7 |
| *Anguilla anguilla* (L.) | European eel | 2 | a | 3 | 1·5 |
| *Salmo salar* L. | Atlantic salmon | 21 | cc | 12 | 116·0 |
| *Gadus morhua* L. | cod | 15 | a | 9 | 70·4 |
| *Zoarches viviparus* L. | eelpout | 65 | cc | 11 | 10·7 |
| *Myoxocephalus scorpius* (L.) | bull-rout | 30 | cc | 9 | 33·9 |
| *Liparis liparis* (L.) | common sea snail | 2 | a | 3 | 3·0 |
| *Ammodytes tobianus* L. | sandeel | 172 | ccc | 0 | 0 |
| *Pomatoschistus minutus* (Pallas) | sand gopy | 28 | ccc | 7 | 25·7 |
| *Platichthys flesus* L. | European flounder | 3 | a | 6 | 40·0 |

* ccc, Common species reproducing in the area. cc, Rather common species reproducing in the area. c, Locally rather common, reproducing species. a, Accidentally in the NE Bothnian Bay.

52 recorded species of which about 30 spawn in the region (Andreasson & Petersson, 1982). Most species are of freshwater origin, but some marine species, such as *Zoarches viviparus*, *Clupea harengus*, *Myoxocephalus scorpius*, *Ammodytes tobianus* and *Pomatoschistus minutus* are able to complete their life-cycles in the Bay. The Baltic Sea is also unique in having 2 marine seal species, the ringed seal *Phoca hispida*, a relict from a previous marine period, and the grey seal *Halichoerus crypus*. The present distribution of the grey seal covers almost the whole of the Baltic Sea; it lives in almost total isolation from the oceanic N.E. Atlantic stock. The distribution of the relict population of ringed seal is even more isolated and northern; it occurs and reproduces mainly in the Gulf of Bothnia and Gulf of Finland.

## MATERIALS AND METHODS

In 1977–1979 a total of 8229 fish belonging to 31 different fish species occurring in the Bothnian Bay were studied for metazoan parasites. The fish studied included common species that were sampled monthly or bimonthly from the catches of commercial fishermen, 20 to 30 specimens per species per sample (Table 1). In addition, less regular samples were taken from some common fish species, which are rare in commercial catches or which need to be caught with special traps. Only adult fish were collected. The numbers of fish of each species collected reflect very roughly the relative population sizes of these fish species in the Bothnian Bay. All possible visitors migrating to the study area were

Table 2. Metazoan parasites (excluding monogeneans) in the fish of the N.E. Bothnian Bay (Baltic Sea), with the maximum prevalence for each species and the fish host in which it occurred

(If both larval and adult stages of the same species occur in the studied fish, the data are given separately for both stages.)

| Taxon | Au/Al[†]/m[‡] | Host range | Maximum prevalence (%) | Host with max. prevalence[‖] |
|---|---|---|---|---|
| Digenea | | | | |
| *Diplostomum spathaceum*, l[*] | Al, bird | 25 | 100·0 | *L. leuciscus* |
| *Ichthyocotylurus erraticus*, l | Al, bird | 4 | 57·0 | *C. l. widegreni* |
| *Ichthyocotylurus variegatus*, l | Al, bird | 2 | 43·3 | *G. cernuus* |
| *Tylodelphys clavata*, l | Al, bird | 11 | 79·3 | *P. fluviatilis* |
| *Allocreadium isosporum*, al | Au | 2 | 25·0 | *C. carassius* |
| *Azygia lucii*, a | Au | 4 | 69·0 | *E. lucius* |
| *Brachyphallus crenatus*, a | Au, m | 1 | 14·3 | *S. salar* |
| *Bunodera luciopercae*, a | Au | 8 | 19·9 | *P. fluviatilis* |
| *Phyllodistomum homoion*, a | Au | 1 | 5·1 | *R. rutilus* |
| *Phyllodistomum umblae*, a | Au | 2 | 1·7 | *C. l. widegreni* |
| *Sphaerostoma globiporum*, a | Au | 6 | 20·3 | *L. leuciscus* |
| Cestoda | | | | |
| *Diphyllobothrium dendriticum*, l | Al, bird | 9 | 76·2 | *S. salar* |
| *Diphyllobothrium ditremum*, l | Al, bird | 6 | 18·6 | *C. albula* |
| *Diphyllobothrium latum*, l | Al, mammal[§] | 4 | 38·7 | *L. lota* |
| *Schistocephalus pungitii*, l | Al, bird | 1 | 3·0 | *P. pungitius* |
| *Schistocephalus solidus*, l | Al, bird | 1 | 45·6 | *G. aculeatus* |
| *Triaenophorus crassus*, a | Au | 1 | 29·8 | *E. lucius* |
| *Triaenophorus crassus*, l | Au | 4 | 22·2 | *C. l. lavaretus* |
| *Triaenophorus nodulosus*, a | Au | 1 | 92·9 | *E. lucius* |
| *Triaenophorus nodulosus*, l | Au | 7 | 50·0 | *L. lota* |
| *Caryophyllaeides fennica*, a | Au | 3 | 6·7 | *L. leuciscus* |
| *Eubothrium crassum*, a | Au,m | 2 | 95·0 | *S. salar* |
| *Eubothrium rugosum*, a | Au | 1 | 75·5 | *L. lota* |
| *Khawia rossitensis*, a | Au | 1 | 25·0 | *C. carassius* |
| *Proteocephalus ambiguus*, a | Au | 1 | 7·8 | *P. pungitius* |
| *Proteocephalus cernuae*, a | Au | 1 | 40·1 | *G. cernuus* |
| *Proteocephalus exiguus*, a | Au | 3 | 82·0 | *C. albula* |
| *Proteocephalus filicollis*, a | Au | 1 | 6·8 | *G. aculeatus* |
| *Proteocephalus gobiorum*, a | Au | 3 | 89·3 | *P. minutus* |
| *Proteocephalus longicollis*, a | Au | 1 | 29·2 | *O. eperlanus* |
| *Proteocephalus percae*, a | Au | 1 | 59·7 | *P. fluviatilis* |
| *Proteocephalus torulosus*, a | Au | 1 | 1·7 | *L. leuciscus* |
| Nematoda | | | | |
| *Contracaecum osculatum*, l | Au,m | 9 | 23·1 | *G. morhua* |
| *Desmidocercella* sp., l | Al, bird | 2 | 1·0 | *L. lota* |
| *Eustrongylides mergorum*, l | Al, bird | 9 | 32·1 | *L. lota* |
| *Hysterothylacium aduncum*, a | Au,m | 9 | 30·8 | *G. morhua* |
| *Raphidascaris acus*, a | Au | 2 | 57·5 | *L. lota* |
| *Raphidascaris acus*, l | Au | 15 | 14·9 | *L. leuciscus* |
| *Truttaedacnitis truttae*, l | Au | 1 | 4·0 | *L. fluviatilis* |
| *Camallanus lacustris*, a | Au | 9 | 67·5 | *P. fluviatilis* |
| *Cystidicola farionis*, a | Au | 4 | 79·9 | *O. eperlanus* |
| *Haplonema hamulatum*, a | Au | 1 | 62·7 | *L. lota* |
| *Pseudocapillaria* sp., a | Au | 3 | 6·7 | *M. scorpius* |
| *Pseudocapillaria salvelini*, a | Au | 4 | 8·4 | *L. lota* |
| Acanthocephala | | | | |
| *Corynosoma magdaleni*, l | Au, seal, m | 2 | 7·8 | *G. cernuus* |
| *Corynosoma semerme*, l | Au, seal, m | 10 | 96·7 | *M. scorpius* |
| *Corynosoma strumosum*, l | Au, seal, m | 12 | 90·0 | *M. scorpius* |
| *Acanthocephalus anguillae*, a | Au | 4 | 50·0 | *L. idus* |
| *Acanthocephalus lucii*, a | Au | 4 | 2·8 | *L. lota* |
| *Echinorhynchus borealis*, a | Au | 8 | 4·8 | *S. salar* |
| *Echinorhynchus bothniensis*, a | Au | 13 | 48·2 | *O. eperlanus* |
| *Echinorhynchus gadi*, a | Au, m | 3 | 80·0 | *G. morhua* |
| *Echinorhynchus salmonis*, a | Au | 17 | 80·0 | *G. morhua* |
| *Neoechinorhynchus rutili*, a | Au | 18 | 23·8 | *S. salar* |

Table 2. (Contd.)

| Taxon | Au/Al†/m‡ | Host range | Maximum prevalence (%) | Host with max. prevalence‖ |
|---|---|---|---|---|
| Crustacea | | | | |
| *Achtheres percarum*, a | Au | 1 | 28·1 | *P. fluviatilis* |
| *Argulus foliaceus*, a | Au | 2 | 1·8 | *P. pungitius* |
| *Ergasilus sieboldi*, a | Au | 3 | 8·3 | *E. lucius* |
| *Lernaea cyprinacea*, a | Au | 2 | 71·4 | *L. idus* |
| *Salmincola coregonorum*, a | Au | 2 | 4·1 | *C. l. lavaretus* |
| *Salmincola extensus*, a | Au | 2 | 9·5 | *C. l. widegreni* |
| *Thersitina gasterostei*, a | Au | 2 | 64·4 | *G. aculeatus* |
| Hirudinea | | | | |
| *Cystobranchus mammilatus*, a | Au | 1 | 53·1 | *L. lota* |
| *Piscicola geometra*, a | Au | 11 | 24·5 | *E. lucius* |
| Mollusca | | | | |
| *Anodonta piscinalis*, l | Au | 2 | 8·5 | *L. lota* |

* l = larva, a = adult.

† Au = autogenic species and its definitive host if not a fish, Al = allogenic species and its definitive host.

‡ Marine origin.

§ Other than seals.

‖ Fish with $n < 8$ excluded.

monitored with special care in order to sort out possible carriers of new parasite species to resident fish populations.

Newly caught fish were studied for metazoan parasites (excluding monogeneans) using standard parasitological methods. In addition to *Diplostomum spathaceum*, the diplostomid metacercariae from the lens include 2 other species in some of the fish species (Valtonen & Gibson, 1997), which cannot be separated easily in the metacercarial stage. All 3 species were included in the total count of the species occurring in the Bothnian Bay, but only 1 species (*Diplostomum spathaceum*) was included in the count of the number of parasite species per individual host species. The preliminary investigations indicated, however, that in all cases, where 1 or both of the 2 other diplostomid species were found, the host species harboured *D. spathaceum* as well (Gibson & Valtonen, unpublished observations). Thus the records of the occurrence of *D. spathaceum* are likely to be exact, but in some cases the calculations of the numbers of specimens may include all 3 species. However, in this paper we do not handle the abundances according to fish species. In some fish species only juvenile cestode stages of the genera *Eubothrium*, *Proteocephalus* or very small *Diphyllobothrium* were found and they were regarded as *Eubothrium* sp., *Proteocephalus* sp. or *Diphyllobothrium* sp. and included in the count of the parasite species in that fish species.

For the nestedness analysis, fish species for which fewer than 8 individuals were examined for parasites were excluded from the analyses (5 species, Table 1), as were parasite taxa that could not be identified to the species (when only juvenile stages of *Eubothrium*, *Proteocephalus* and *Diphyllobothrium* or accidental *Ichthyocotylurus* and *Pseudocapillaria* were found in a fish species) and that may have consisted of more than 1 species. Ectoparasites (crustaceans, leeches, and larval bivalves) and endoparasites (larval and adult digeneans, cestodes, nematodes and acanthocephalans) occupy distinct microhabitats on the fish host and represent different guilds. In addition, larval and adult endoparasitic helminths use hosts differently. Larval helminths use fish as intermediate hosts, i.e. as vehicles to their definitive hosts. Their transmission is always dependent on the predation of the fish host. Adult helminths, on the other hand, use their fish host as a source of nutrients for the production of eggs. Larval and adult helminths should be considered as distinct guilds in terms of their use of fish hosts. Nestedness analyses were therefore performed separately for larval endohelminths, adult endohelminths, and ectoparasites.

The existence of a nested pattern of host use was tested by computing the index of nestedness, $N$, proposed by Patterson & Atmar (1986), for each of the 3 parasite groups. Each of these 3 observed values was compared with the expected value under the null hypothesis that parasite species are distributed randomly among host species, with respect to the number of host species used by each parasite species. The index is the sum, for all parasite species, of the instances where a parasite species is absent from a richer host fauna than the most species-poor one in which it occurs. In a perfectly nested pattern, $N$ equals zero, and $N$ increases as nestedness decreases. The observed value of the index, however, must be compared to what one would expect if the parasite species were distributed at random among host species, to determine whether a nested pattern exists. The computer algorithm RANDOM1 of

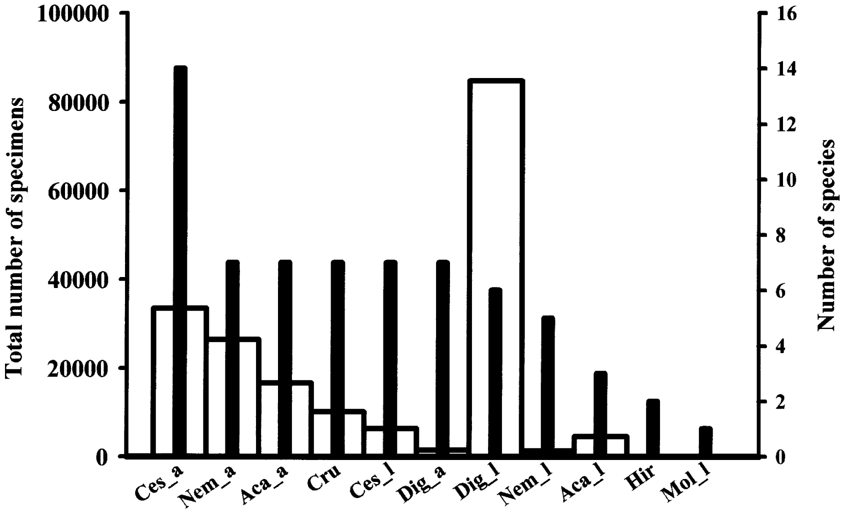

Fig. 2. Number of parasite taxa (■) and total number of specimens (□) in taxonomic groups (l = larvae, a = adult) in all examined fish in the Bothnian Bay. Larval and adult stages of the same species are considered as separate taxa in this figure and the count of larval digeneans includes all 3 *Diplostomum* species found in the area (see Materials and Methods section).

Patterson & Atmar (1986) was used to generate 1000 random host faunas of parasite species and to compute their *N* index scores. In the simulations, the probability of each parasite species being included in a host fauna was set equal to the proportion of the fish species that it infects in nature. The probability that the observed *N* value could have been selected from the normally distributed simulation scores was assessed by determining the number of standard deviates (*z*-scores) between the observed *N* and the mean of the simulated *N*, compared against a *t*-distribution.

Parasites were classified as either autogenic or allogenic (Esch *et al.* 1988). Autogenic parasites mature in fish and seals and have thus a limited ability to colonize new localities. Allogenic parasites use fish as intermediate hosts and mature in either birds or terrestrial mammals; they have therefore a greater chance of being dispersed to new areas. Some basic data on acanthocephalans, cestodes, digeneans and nematodes have been published previously (see e.g. Valtonen, Brummer-Korvenkontio & Rahkonen, 1988*a*; Valtonen, Fagerholm & Helle, 1988*b*; Valtonen, Rintamaki & Lappalainen, 1989; Valtonen & Crompton, 1990; Andersen & Valtonen, 1990, 1992; Chubb *et al.* 1995; Valtonen & Julkunen, 1995; Valtonen & Gibson, 1997). This is the first time that analyses of parasite component communities of all fish species studied in the Bothnian Bay are performed and published in one paper.

## RESULTS

Altogether 63 parasite species were found in the 31 fish species studied from the Bothnian Bay (Tables 1 and 2). The number of parasite species found in single host species varied from 0 to a maximum of 26 (Table 1). The highest average number of parasite individuals per host individual (116) was found in *Salmo salar* (Table 1). Autogenic parasite species dominated in the material (52 species), of which adult cestodes were the largest group. Only 11 allogenic species were found, mainly larval cestodes and digeneans (Table 2). When counting the number of parasite specimens in different taxonomic groups, however, the proportion of digenean larvae was the largest (45·5 % of all parasite specimens) (Fig. 2). The digenean larvae consisted mostly of *Diplostomum* spp., 92 % of which were found in freshwater fish.

A total of 26 fish species, representing 21 genera, were included in the nestedness analysis. These harboured a total of 19 species of larval endohelminths, 34 species of adult endohelminths, and 10 species of ectoparasites. The pattern of host use by ectoparasite species did not differ from that expected from a random assembly of species, i.e. the observed *N* score for ectoparasites did not differ from the expected *N* score (Table 3). However, both larval and adult endoparasites were significantly less nested than expected from chance, i.e. their observed *N* scores were significantly greater than the expected mean *N* scores (Table 3). This anti-nestedness could mean that highly host-specific endoparasite species are more likely to occur in fish species harbouring few parasite species than one would expect if parasite species used host species in a random way.

Parasite species richness increased with increasing numbers of fish studied in the case of larval endoparasites, but not for adult endoparasites or for ectoparasites (Fig. 3). Even if the number of specimens studied is not high for marine fishes, the number of parasite species found was similar as in freshwater fishes, and most of the species-poor communities were found in freshwater fishes. When the host range of each parasite species was plotted

Table 3. Observed index of nestedness, $N$, and the predicted value expected from random associations (derived from 1000 computer simulations) for larval endoparasites, adult endoparasites, and ectoparasites of fish in the Bothnian Bay

| Parasite group | No. of fish species | No. of parasite species | Predicted $N$ (mean ± S.D.) | Observed $N$ |
|---|---|---|---|---|
| Larval endoparasites | 26 | 19 | 66·1 ± 12·5 | 121* |
| Adult endoparasites | 25 | 34 | 123·8 ± 15·3 | 280* |
| Ectoparasites | 13 | 10 | 21·5 ± 5·7 | 22 |

* P < 0·001.

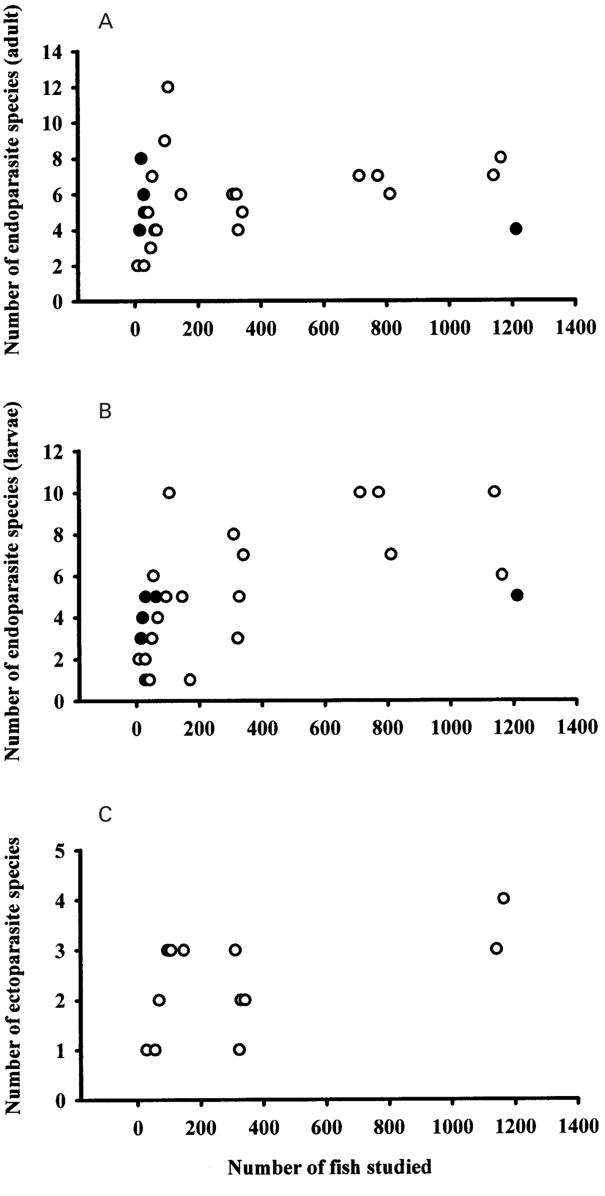

Fig. 3. The relationship between host sample size and the parasite species richness of (A) adult endoparasites, (B) larval endoparasites and (C) ectoparasites in component communities of fish in the Bothnian Bay. Each point represents 1 host species and marine species are marked with black points.

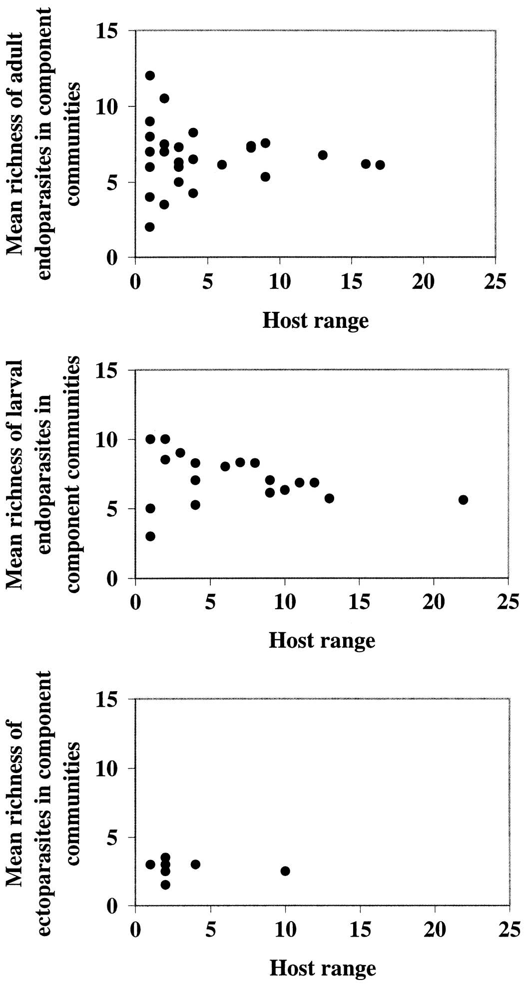

Fig. 4. The relationship between host range of an individual parasite species and mean richness in all the component communities in which the parasite species occurs for adult endoparasites, larval endoparasites and ectoparasites of fish in the Bothnian Bay.

against the mean richness in those component communities where the parasite occurred, the host specific (1–4 hosts) adult endoparasite species were found to occur both in poor and rich component communities (Fig. 4). This pattern was not so clear for larval endoparasites and was not found in ectoparasites. The points in the lower-left hand corner of the graphs in Fig. 4A and B produce a pattern less nested than predicted by the simulated random assemblages (Table 3): there are more points in this region of the graph than one would expect if parasite species were randomly distributed among host species. In the case of endoparasites these points represent 4 species of cestodes (*Khawia rossitensis*, *Proteocephalus torulosus*, *P. ambiguus*, *Caryophyllaeides fennica*), 1 acanthocephalan (*Acanthocephalus anguillae*) and 1 digenean (*Allocreadium isosporum*), and in the case of larval endoparasites, 2 cestodes (*Schistocephalus pungitius* and *Triaenophorus crassus*) and 1 nematode (*Truttaedacnitis truttae*), all of which occurred in freshwater fishes only.

Altogether 24 parasite species, of which 8 were of marine origin, were recorded from the marine fish species. Among marine species occurring in the Bothnian Bay were the cestode *Eubothrium crassum*, 2 nematode species and 4 acanthocephalan species while the only marine digenean *Brachyphallus crenatus* occured accidentally in salmon migrating to spawn (Table 2).

Four of the 8 marine parasite species found in the Bothnian Bay occurred both in freshwater and marine fish. *Echinorhynchus gadi* and *B. crenatus* were the only marine parasite species which did not occur in the freshwater fish or in marine fish with resident populations in the area, but only in accidental visitors and the migratory *S. salar*, respectively. *E. crassum* occurred only in *Salmo salar* and *S. trutta*. The marine nematodes and *Corynosoma* species had a considerable or the largest part of their populations in the freshwater hosts, and *C. magdaleni* occurred only in freshwater fishes.

At the fish species level, the number of host–parasite records of any of the marine parasite species was 23 in 8 marine fish species and 25 in 13 freshwater fish species. In marine fish species the marine parasites constituted 32 % of all host–parasite records and in freshwater fish 10 %, when host species which did not harbour marine parasites were also included. The number of marine parasite individuals per host individual in those hosts where they occurred was higher in marine hosts (2·30) than in freshwater hosts (0·97), because in freshwater fish the marine parasites were divided in a larger number of host species and individuals. For freshwater parasites the numbers were 25·6 parasite individuals per host individual for freshwater fish and 4·4 for marine fish. The maximum prevalences of all the marine parasites (except for *C. magdaleni*) and 6 freshwater parasites occurred in marine fish species. The maximum prevalences attained by the marine parasites were as high as those of freshwater parasites (Table 2).

## DISCUSSION

The decrease in salinity from the Danish straits towards northern areas of the Baltic Sea is reflected in the decrease of the number of marine species at all trophic levels (Voipio, 1981). This decrease is also seen in the richness of parasite communities. In the checklist of metazoan fish parasites from German coastal waters, the data on 62 fish species yielded 160 metazoan parasite species when only the same groups of parasites were included as in the present study (Palm, Klimpel & Bucher, 1999). In German coastal waters 43 % of all parasite species were digeneans, but in the Bothnian Bay their proportion was only 17 %. On the other hand the proportion of cestodes of mainly freshwater origin was 33 % in the Bothnian Bay and only 18 % on the German coast (see also Zander, Reimer & Barz, 1999). Thus a striking difference between the Bothnian Bay and the southern Baltic sea is the lack of marine digeneans and the greater occurrence of freshwater cestodes in the north.

The low number of digenean parasite species in the northern Bothnian Bay is a reflection of the depauperate marine molluscan fauna (first intermediate hosts of digeneans) in the area. The lack of many marine intermediate hosts serves as an efficient filter preventing the establishment of populations of many marine parasites, although some parasite species migrate with migrating fish species into the area, such as the *Brachyphallys crenatus* which is common in the southern Baltic sea (Reimer, 1970). In this study, this species was found in only few salmon which returned to spawn from the southern Baltic (Ojaveer *et al*. 1981). In addition to the lack of marine molluscs, only one marine copepod species, *Acartia bifilosa* (Kankaala, 1987) occurs in the Bothnian Bay and this explains the lack of most marine cestodes in the area. *Eubothrium crassum*, which is usually found in salmonids living in the sea, was the only common marine cestode in the Bothnian Bay, where it was found in the salmon as well as in the trout. The lack of marine plankton species explains the lack of parasites in a pelagic marine fish, the plankton feeding *Ammodytes tobianus*, which is found only in the deeper areas of the Bothnian Bay and is not exposed to eyeflukes penetrating the host skin either. *A. tobianus* has been found to harbour several parasite species in the Wadden Sea (Groenewold, Berghahn & Zander, 1996).

The high proportion of freshwater cestodes in the Bothnian Bay fish communities is explained by the high abundance of fresh and brackish water copepods (first intermediate hosts of cestodes) in the coastal waters of the Bay compared with the Baltic proper with its characteristically low diversity of plankton. In brackish water of a salinity less than 0·6 % the number of freshwater species in all animal groups increases (Wulff *et al*. 1977). The high numbers of freshwater invertebrates are reflected in the great diversity of freshwater parasite species found even in marine fishes in the Bothnian Bay. However, some freshwater acanthocephalans common in Finnish lakes have been unable to establish populations in the Bothnian Bay, including *Acanthocephalus lucii* and *Echinorhynchus borealis*. The reason for this is the same as for most marine parasites, namely the lack of intermediate hosts; *Asellus aquaticus* is not common in deeper areas of the Bothnian Bay and *Pallasea quadrispinosa* is very rare (Valtonen *et al*. 1988*a*; Valtonen & Crompton, 1990).

When looking at individual marine fish species in the Baltic, the component communities of parasites on the German Baltic coast (Palm *et al*. 1999) are much richer than in the Bothnian Bay. For example, the numbers for cod in the two areas are 26 and 9 metazoan species, respectively; for eelpout they are 24 and 11 species, respectively, with digeneans accounting for most of the difference. On the other hand, the component communities of freshwater fishes were richer in the Bothnian Bay in many cases; for instance, burbot has 26 parasite species in the Bothnian Bay versus 11 on the German coast, ruffe has 18 versus 6. The most prominent feature in the Bothnian Bay parasite communities as compared with the Baltic proper is the extremely high dominance of eyefluke larvae in the eyes of fishes from the Bay. *Diplostomum spathaceum*, in particular, is the dominant species when looking at both the host range and numbers of worms found. This phenomenon is specific to the Bay area and reflects the abundant populations of the freshwater snails of *Lymnea* spp. serving as intermediate hosts.

Among the 8 marine parasite species found in the Bothnian Bay only 6 have been able to establish a population in the area: *Eubothrium crassum*, 3 *Corynosoma* and 2 nematode species. *Contracaecum osculatum* and *Hysterothylacium aduncum* nematodes use a broad range of invertebrates as first intermediate and/or paratenic hosts (Fagerholm, 1982). They can utilize both freshwater and marine fish species as intermediate or final hosts: both occur in 9 fish species although they achieve maximum abundance in a marine fish (cod). The isolation of marine seals to the Baltic after the ice age makes possible the completion of 4 marine parasite life-cycles in the area: the final host of *C. osculatum* is the grey seal and all 3 *Corynosoma* spp. mature in ringed and grey seals (Valtonen *et al*. 1988*b*; Nickol, Valtonen & Helle, unpublished observations). The success of *Corynosoma* species is also due to their adaptation to use the freshwater relict amphipod *Monoporeia affinis* as their intermediate host (Valtonen & Crompton, 1990). However, *Echinorhynchus gadi* has not successfully established itself in the Bothnian Bay, since its intermediate hosts (*Gammarus oceanicus* and *Monoporeia femorata*) do not occur there (Valtonen & Crompton, 1990).

The anti-nestedness patterns observed for larval and adult endoparasites suggest that host use by these helminth species departs significantly from randomness. It should be pointed out that almost all larval endohelminths are allogenic species and that all adult endohelminths are autogenic, so that we treated them separately in the nestedness analysis, i.e. they did not cause the observed pattern. For larval endoparasites the pattern found may be caused by the positive correlation between the host sample size and parasite species richness, but in adult endoparasites the pattern is likely to reflect the true structure of the parasite communities. Some adult endoparasites that exploit only one or very few host species tend to exploit host species harbouring few or no other parasite species. Conversely, parasite species found in a wide range of host species tend to exploit host species with relatively rich parasite communities. This will result in species-rich communities of mainly generalist parasites, and species-poor communities of specialist parasites.

Unexpectedly, the anti-nestedness pattern found in the Bothnian Bay is not caused by species-poor parasite communities in marine fishes composed of generalists from the sympatric freshwater fish species. A more likely explanation for the observed pattern is that there are specialist parasite species, the majority of which are cestodes, in some of the freshwater fish species which otherwise have depauperate parasite communities. The pattern found in the Bothnian Bay is the opposite of that found for parasites of four large families of Canadian freshwater fishes (Poulin, 1997*a*). The study of Poulin (1997*a*), however, was performed at the parasite genus level and focused on parasite faunas across the geographical range of their hosts, rather than on true component communities. If the present analysis had been made at the parasite genus level, the observed pattern of anti-nestedness might have remained unnoticed, because some of the parasite species (especially *Proteocephalus* species) responsible for the pattern occur also in hosts which have rich component communities (5–10 species).

A key feature of the Bothnian Bay is the extensive sympatry of its marine and freshwater fish faunas. One of our aims was to determine if exchanges of parasite species between marine and freshwater fish played an important role in the formation of their parasite component communities. Our results indicate that many parasites occurring in the Bothnian Bay have the potential to colonize new atypical hosts. However, this phenomenon has probably resulted from ecological factors acting over short time-scales rather than from evolutionary processes acting over longer time. Given the relatively recent origins of the Baltic Sea and Bothnian Bay, the establishment of marine parasites in the Bay has probably depended on the immediate presence of suitable intermediate and definitive hosts. For instance, the marine acanthocephalans *Corynosoma* spp. found the freshwater amphipod *Monoporeia affinis* to be a suitable intermediate host, which happens to be an important component in the diet of freshwater fish species in the area (Valtonen E. T., unpublished). Thus the transfer of marine parasites to freshwater fish may have been mediated mainly by the proximal availability of suitable freshwater intermediate hosts.

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