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PARASITE COMMUNITIES OF THE EUROPEAN COD "COMUNIDADES PARÁSITAS DE BACALAO EN AGUAS DE EUROPA"

DIANA PERDIGUERO ALONSO

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Tesis doctoral

Valencia, febrero 2008

Directores Juan Antonio Balbuena Díaz-Pinés //Francisco E. Montero Royo

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TESIS DOCTORAL

Por

Diana Perdiguero Alonso

Directores

Juan Antonio Balbuena Díaz-Pinés

Francisco E. Montero Royo

Paterna, febrero 2008

JUAN ANTONIO BALBUENA DÍAZ-PINÉS, Profesor Titular del Departamento de Zoología de la Facultad de Ciencias Biológicas de la Universitat de València, y

FRANCISCO E. MONTERO ROYO, Investigador del programa "Juan de la Cierva" en el Departamento de Biologia Animal, Biologia Vegetal y Ecologia de la Facultad de Vetarinària de la Universitat Autónoma de Barcelona

CERTIFICAN: que Diana Perdiguero Alonso ha realizado bajo nuestra dirección y con el mayor aprovechamiento el trabajo de investigación recogido en esta memoria, y que lleva por título: "Comunidades parásitas del bacalao en aguas de Europa", para optar al grado de Doctora en Ciencias Biológicas.

Y para que así conste, en cumplimiento de la legislación vigente, expedimos el presente certificado en Paterna, a 27 de febrero de 2008

Juan Antonio Balbuena Díaz Pinés Francisco E. Montero Royo

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Summary

This PhD thesis examines the composition and structure of the metazoan parasite faunas and communities in Atlantic cod, *Gadus morhua* L., from six NE Atlantic regions [Baltic, Celtic, Irish and North seas, Icelandic waters and Trondheimsfjord (Norway) and two fish farms located in Iceland and Scotland] and applies the new data to both comparative assessment of patterns at several scales of community organisation and assessment of the usefulness of cod parasites as biological markers to spatial discrimination of cod populations.

Profiting from the design of the project CODTRACE aiming at collection of a variety of biological samples from individual fish to test a range of traceability techniques for determining location of spawning and harvest of the Atlantic cod, 1,254 fish were collected. Of these 816 were sampled in the NE Atlantic during 2002-2003; 60 were sampled from Trondheimsfjord in spring 2003; and 378 represented farmed fish. Parasitological examination followed a standardised protocol and the taxonomic consistency of the identification was ensured thorough the study. All metazoan parasites were identified and counted.

Intraspecific comparisons of abundance distributions were carried out only for species with prevalence > 30%. Analysis of community structure was carried out at both component and infracommunity level. Component community descriptors used were the total species richness; Berger-Parker dominance index; and Shannon-Wiener's diversity index. Infracommunity descriptors were species richness, abundance, Berger-Parker index and Brillouin's diversity index. Diversity indices were calculated using natural logarithms ($\log_e$). Comparative analyses of community composition were carried out at both infra- and component community level using Bray-Curtis index following ln (x+1) transformation of abundance data. Non-parametric tests were performed on raw data due to their aggregated distributions and when parametric analyses were required ln (x+1) transformation of the data was performed (*i.e.* Cluster analysis, Analysis of Principal Components, Multidimensional Scaling, Analysis of Similarities, Linear Discriminant Analysis). Classifications with Random Forests and Artificial Neural Networks were performed on raw data.

Altogether 57 parasite taxa were found. The predominant groups in regional parasite faunas were the trematodes (19 species) and the nematodes (13 species). Nine parasite species were found for the first time in cod (*Diclidophora merlangi*, *Rhipidocotyle* sp., *Fellodistomum* sp., *Steringotrema* sp., *Schistocephalus gasterostei*, *Cucullanus* sp.,

Spinitectus sp., *Acanthochondria soleae* and *Chondracanthus ornatus*). The first seven represent new host records whereas *S. gasterostei* and *A. soleae* are considered part of the food content. *Contracaecum osculatum, Hysterothylacium aduncum* and *Echinorhynchus gadi* were the only parasite species found to infect farmed fish.

Regional parasite faunas in cod showed lower richness with respect to the total list (*c.* 65%) with a notable decrease in the Baltic Sea and Trondheimsfjord (21 and 32%, respectively). Eleven species were present in all regions: *Lepidapedon elongatum, Anisakis simplex, C. osculatum, H. aduncum, H. rigidum, Pseudoterranova decipiens, Ascarophis crassicollis, Capillaria gracilis, Corynosoma semerme, C. strumosum* and *E. gadi*. The species representation was very similar in all regions except for the Baltic Sea and Trondheimsfjord which had the poorest fauna. Although nematodes were the richest taxon in the Baltic Sea collection, the high numerical dominance of acanthocephalans was the most distinctive trait of the fauna of this region. Trondheimsfjord fauna was distinct in the exceptionally high relative abundance of trematodes.

Generalist parasites comprised the best represented group of cod parasite faunas in all regions except for that of Trondheimsfjord which exhibited the highest representation of gadoid specialist parasites. The relative abundance of the species with Arctic-Boreal distribution was the highest in all regions, and noticeably higher in the Baltic Sea, Trondheimsfjord and Icelandic faunas.

Despite of the small size of the monogenean *D. merlangi* recovered in the present study, the Analysis of Principal Components showed that morphologically they are more similar to *D. merlangi* from whiting (*Merlangius merlangus*, type-host), than to other congeneric species from the North Atlantic, thus supporting their assignment to *D. merlangi*. The morphological and morphometrical analyses of *D. merlangi*, reported here for the first time on cod, suggested a flexible response in attachment to a non-specific host. Quantitative data documented the potential reproductive consequences of *D. merlangi* occurring on cod. The testes and germaria of the specimens on cod were noticeably smaller than those of *D. merlangi* on whiting, but the number of testes was similar and spermatozoa were observed in the sperm duct. By contrast, the aspect and smaller size of the oöcytes suggested that *D. merlangi* on cod could not produce viable ova, although a specimen exhibited an egg with normally sized and shaped shell. The observations also suggested that the uterus also participates in the assembly of the egg capsule and the egg shape and size is genetically fixed.

Parasite infra- and component communities in cod from the six NE Atlantic regions were described in detail. The composition of parasite communities and the infection parameters of each parasite species in each component community were determined; parasite abundance distributions and prevalences of the most prevalent species were compared between samples. Parasite community predictability was estimated both for component communities within a region and for infracommunities within samples. Comparative analyses at the infracommunity level were also carried out on larval and gastrointestinal helminth assemblages and ectoparasite assemblages. The species that contribute most to the similarity patterns at both levels were identified.

The results of the comparative community analyses agreed well with the predictions based on the higher-level taxonomic structure of the regional parasite faunas. The most species rich and abundant parasite communities were observed in cod from the open water regions (Celtic, North and Irish seas and Icelandic waters) whereas communities from the low-salinity regions (Baltic Sea and Trondheimsfjord) were characterised by the lowest richness, abundance and diversity and exhibited higher heterogeneity of infracommunity composition and structure. Overall, parasite infracommunities exhibited lower predictability than component communities, due to the fact that only a restricted set of the species contributing to the similarity between component communities exhibited high abundance and dominated infracommunities. Three species with a wide geographical distribution, *H. aduncum*, *A. simplex* and *D. varicus*, were found to dominate consistently at both the component and infracommunity level.

The results of the three multivariate techniques applied to examine similarity patterns of component communities across regions exhibited good agreement and detected distinct compositional segregation of those in cod from the two low-salinity regions (Baltic Sea and Trondheimsfjord). The highest homogeneity with respect to the composition and structure of parasite communities was observed in cod from Celtic, Irish and North seas. The similarity patterns observed in total communities did not generalise to the component community clades since no significant regional differences were found in the composition of ectoparasite assemblages; larval helminth assemblages showed lower regional differentiation; and gastrointestinal helminth assemblages in cod from the open water regions exhibited overlapping composition.

Non-random macroecological patterns were detected in the analyses based on data for component communities and regional faunas. Decay of similarity with geographical distance was observed in component communities but not in regional parasite faunas, the

higher homogenisation of the latter being related to the migratory behaviour of cod and the domination of generalist parasites with wide geographical distribution. The spatial compositional autocorrelation exhibited by component communities and the substantially higher rates of similarity decay compared to other marine fish systems indicate that communities in cod are more strongly constrained by the spatial configuration of locations and the dispersal abilities of cod parasites. The relationship between regional and local richness observed at the two scales of analysis provided evidence to reject the null hypothesis of a proportional sampling. Nested subset analyses revealed non-random patterns of faunal/community composition with poor faunas and communities from low-salinity regions (Baltic Sea and Trondheimsfjord) nested in the richer faunas/communities from the high-salinity open water regions. The temporal autocorrelation of parasite communities observed which might be related to a temperature anomaly (high water temperature in the summer of 2002) indicates that large-scale processes can affect the composition of parasite communities in cod.

The comparison of the learning behaviour of the three classification approaches, Random Forests (RF), Linear Discriminant Analysis and Artificial Neural Networks, using the same version of the parasite community data derived from cod populations in five regions in the NE Atlantic, revealed that RF appears as the best classifier. Anisakid nematodes, *C. cirratus*, *D. varicus*, *H. communis*, *E. gadi*, and *C. adunca* were selected as important for RF model development. The high accuracy of the predictive models developed for the Baltic and Icelandic samples indicate that the populations of these stocks can be confidently differentiated from the other stocks studied in the NE Atlantic. The lower discrimination between the Celtic and Irish stocks might be related to the geographical proximity and migration of cod stocks between Irish and Celtic seas whereas the highest misclassification rates of the North Sea sample might be due to the heterogeneity in the sampling design. The comparative analyses and the validation experiment with the 'blind' sample confirmed that RF models generalise better with a large and diverse training set and a large number of variables. These results suggest that parasite community data can be used successfully to discriminate cod populations (putative stocks) of the NE Atlantic cod using RF. The fact that good discrimination results were obtained for a migratory fish species with largely overlapping parasite communities reflects the high potential of RF for developing predictive models using data that are both complex and noisy and indicates that it is a promising tool for parasite tagging studies.

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1. Introduction

1.1. Atlantic cod *Gadus morhua* L. (Teleostei: Gadidae): economic importance for humans

The Atlantic cod, *Gadus morhua* L., 1758, is one of the dominant commercial species of the North Atlantic, accounting in 2005 for nearly 1.2% of the world's total marine groundfish catch (FAO website). Evidence indicates that this benthopelagic fish was already fished in the Neolithic and has been exploited commercially since the Middle Ages (Flick *et al.*, 1990; Kurlansky, 1998). Cod has been so important to the economy of countries on both sides of the Atlantic, that an enormous amount of knowledge of cod biology and its fisheries has been accumulated over the years (see Kurlansky, 1998 for review).

In the early 1960s, cod landings in the whole North Atlantic fluctuated around 2.5 to 3 million tonnes per year, with a peak in 1969 of 4 million tonnes. Landings went down to 1.8 million tonnes in 1975 and declined to 0.8 million tonnes in 1992 (FAO). In the early 1990s, many cod populations collapsed in areas where commercial fishing was intense. The collapse was attributed to overfishing, and specifically to the commercial fishing of older/larger cod which resulted in a smaller population of fertile females and the harvesting of young fish before they have had a chance to mature and reproduce (ICES, 2005a). The over-exploitation of Atlantic cod triggered off that the species was listed as a Vulnerable Species in 1996. Some efforts have been made to help some cod populations to recover. However, by 2005 landings were approximately 0.84 million tonnes; of these 0.04 million tonnes in North America and 0.80 million tonnes in Europe (FAO). Moratoria and fishing regulations were placed in some regions but have so far been unsuccessful in increasing or even maintaining population sizes, because overfished populations recover slowly (Hutchings, 2000).

Stock division serves as a very useful management unit for administration of the cod resources. The cod stocks are managed separately because the effect of past fisheries and changing environmental conditions on many of them was more severe, as in the eastern coast of Canada (Hutchings & Myers, 1994, O'Driscoll *et al.*, 2000; Bundy, 2001), the Baltic Sea (Jonzen *et al.*, 2002; Hutchinson *et al.*, 2003), and the North Sea (Cook *et al.*, 1997), than in others. Stocks are defined as recognizable units displaying characteristics unique to each of them with very little mixing between adjacent stocks. However, cod stocks are occasionally shared by different fisheries because of the regular movements in

accordance with the growth and development of the cod (Gulland, 1980; Robichaud & Rose, 2004). At present, 14 cod stocks are defined in the NE Atlantic (regulated by ICES) and around 10 cod stocks in the NW Atlantic (regulated by NAFO) (ICES, 2005a). Some of these stocks are large in terms of numbers or biomass, such as those from the Arctic-Boreal fishing grounds off Norway, Iceland, Newfoundland and West Greenland, and the Barents Sea. Others are small, such as the Rockall cod stock west of Ireland (ICES, 2005a).

The main deterrent in properly managing cod stocks relates to the geographic range of cod (Fahay *et al.*, 1999; Robichaud & Rose, 2004; ICES, 2005a). Cod occur throughout the North Atlantic and, since most of its range is in international waters, it makes it difficult for any one region to impose universal regulations. The European Commission (EC) has recognized the significance of firm management action to restore European cod stocks. In the New Common Fishery Policy for the EU, an important part is devoted to provide a framework for the conservation, control and enforcement of fish stocks (February commission 2001 (CE) Nº259/2001), moreover cod has an specific legislation [26th February 2004 COUNCIL REGULATION (EC) Nº 423/2004].

1. 2. Cod biology

1.2.1. Physical description

Atlantic cod attains a mean size between 32 and 41 cm and a maximum length of 150-200 cm (the minimum landing size according to ICES is 35 cm in the North Sea and 30 cm in the Skagerrak/Kattegat). Cod weight averages 2.3-3.6 kg and the greatest recorded weight was 96 kg (see COSEWIC, 2003 and references therein). The colour of Atlantic cod varies with respect to the environment in which the fish lives and possibly with the type of prey consumed. Those feeding on crustaceans tend to appear more brownish, whereas a blue-green pigmentation may result from a diet consisting primarily of fish (COSEWIC, 2003; Riede, 2004). The Atlantic cod has 1 chin barbel, 3 dorsal fins, and 2 anal fins. It also has a pronounced lateral line from the gills to the tail. The colouring of cod is often shaded from top to bottom. The dorsal area of the fish may be a rich brown to green and fade to silver towards the ventral side. Some fish may have brown/red spots on the sides and back (Cohen *et al.*, 1990) (see Figure 1.1).

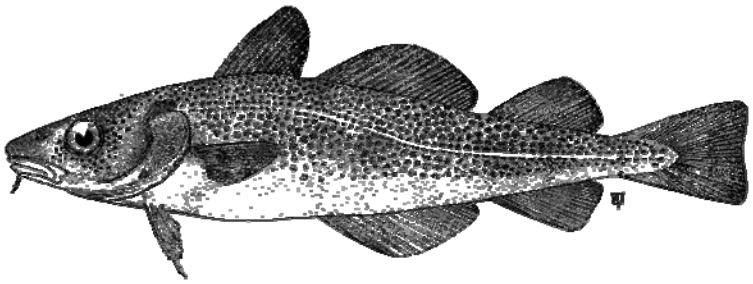

Figure 1.1. Atlantic cod, *G. morhua*. Picture by Canadian Museum of Nature (Otawa, Canada) in Froese & Pauly (2007).

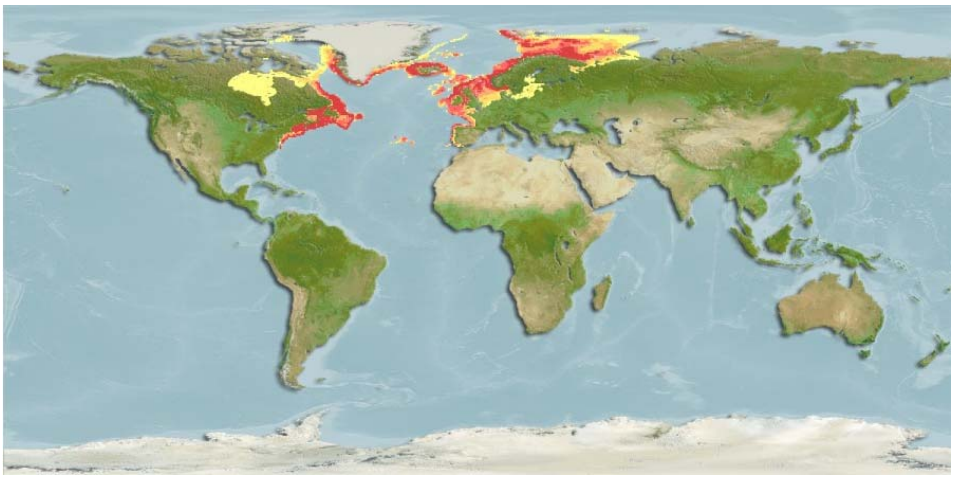

Figure 1.2. Distribution map of *G. morhua.* From Kathleen K. Reyes, AquaMaps in Froese & Pauly (2007).

1.2.2. Habitats and distribution

Atlantic cod occur along the eastern and northern coasts of North America, along the coasts of Greenland, and from the Bay of Biscay to the Arctic Ocean, including the Atlantic waters around Iceland, the North Sea, Baltic and the Barents Sea (Cohen *et al.*, 1990, Froese & Pauly, 2007) (see Figure 1.2). Cod are oceanodromous, benthopelagic euryhaline fish, tolerating from nearly fresh to full oceanic water. Cod occur in a wide range of habitats, from inshore shallow waters (*c*. 5 m deep) to the edge of the continental shelf in water as deep as 600 m, but are mostly found within the continental shelf (50-200 m). The species is distributed in cold and temperate waters (temperature range 0-20 ºC). However, for unknown reasons, in most areas larger fish occur in colder waters (0-5°C). The presence of cod usually depends on prey distribution. Regarding their social behaviour, they are gregarious during the day, forming compact schools that swim between 30-80 m above the bottom, and they scatter at night. To the south of its range, cod is found in shallow waters

only during the winter, and there, as elsewhere, only the younger (smaller) fish live close inshore (Fahay *et al.*, 1999; ICES, 2005; Froese & Pauly, 2007).

Robichaud & Rose (2004) categorized cod into four types according to site and homing fidelity: sedentary, accurate homers, inaccurate homers and dispersers. Sedentary residents exhibit strong site fidelity within a relatively small geographical range. The inaccurate homers perform seasonal movements and return to a broader homing area than the accurate homers whereas dispersers move and spawn in a haphazard pattern within large geographical areas. These authors also observed that coastal groups did not differ significantly from offshore groups in the relative frequency of these migratory behaviours. However, the NE Atlantic cod were found to exhibit more sedentary and accurate homing groups than their NW Atlantic counterparts, which have shown more dispersing groups. Seasonal migrations of Atlantic cod are attributed to water temperature, food supply, and spawning grounds. Atlantic cod move as a group and tend to follow warmer water currents during migration. Although they prefer habitats within the water temperature range from 2º to 11ºC, some populations were found in waters as cold as -1.5 ºC (Fahay *et al.*, 1999; ICES, 2005). Some local inshore populations migrate only short distances. They remain mainly in the inshore area but move a short distance offshore into deeper waters during winter and return inshore during summer. Other cod stocks may migrate up to 800 km from their winter spawning grounds to the inshore feeding area in summer. This homing behaviour is by no means as high as for Atlantic salmon, but is nevertheless significant in maintaining uniqueness to the characteristics of stock components. Very little is known about the movements of young cod in their early years on the nursery grounds. It has been suggested that they undertake a seasonal migration to shallow waters during the summer and return to deeper waters in winter; these movements seem to be restricted to feeding, but there is not enough evidence yet in support of this hypothesis (Fahay *et al.*, 1999 and references therein).

1.2.3. Reproduction and development

As indicated above, many cod stocks migrate during their reproductive season. However, cod populations appear to form units reproductively isolated from each other which are, presumably, spatially distinct at least during the spawning season (ICES, 2005a). Typically, a cod population moves into warmer waters during winter and early spring to begin spawning. Although spawning can occur year round, peak spawning levels occur in the winter and spring, during a three-month period. As the population moves inshore it may

disperse temporarily to feed if large amounts of prey are present. Cod spawning occurs over a wide area of the continental shelf and over a wide range of bottom depths in temperatures between 5-7ºC. There is some evidence that cod leave the bottom to spawn pelagically when bottom temperatures are unsuitable. The distribution of spawning stocks widely depends on the oxygen content of the bottom water (Fahay *et al.*, 1999; ICES, 2005a and references therein).

Many spawning areas of cod have been identified. The most productive spawning ground in the NW Atlantic is the eastern half of Georges Bank and the area south of the Grand Banks (Newfoundland) (Fahay *et al.*, 1999; COSEWIC, 2003). The southern North Sea is the main spawning area in the NE Atlantic in which spawning occurs generally at depths of less than 50 m and never beyond 200 m, especially in the north-west of the Dogger Bank where egg density appears to be rather high from late April to the end of May (ICES, 2005a). Cod spawn in dense concentrations of more than 1 fish/m^3 and multiple pairs of fish can be observed spawning in the same water column. Their complex mating systems allow segregation on spawning areas associated to the preferences for depth, temperature and songs (Rowe & Hutchings, 2004; Joensen *et al.*, 2005).

Age and size at maturity often vary amongst different populations. A recent finding suggests that cod are moving towards a reduction in age and size for sexually mature fish. The earliest reported maturity ages for Atlantic cod are 2 years in its eastern and 4 years in its western distribution. The males generally mature at a slightly younger age and smaller size than the females. Although cod is mostly dioicous, hermaphrodites have been reported. The sex ratio is nearly 1:1, with a slight bias towards females (Fahay *et al.*, 1999; COSEWIC, 2003; Rowe & Hutchings, 2004; ICES, 2005a).

There is no indication that any parental involvement exists on behalf of either females or males after the eggs are released. Cod is one of the most fecund fishes of the world. Its average egg production is about 1 million per female, with a maximum recorded at 9 millions eggs by a 34 kg female (COSEWIC, 2003). However, the mortality rate of cod is very high, since it is reckoned that only one egg per million succeeds in completing the cycle to become a mature cod.

Growth rates of Atlantic cod are different in different areas, and annual differences in growth rate in the same area depending on the population sizes, temperature, and food availability, also occur. The growth rate is fairly high, females growing slightly faster than males. Atlantic cod can live for over 20 years. However, typical life spans have changed drastically in the last century, as a result of commercial cod fisheries. Most recently,

fisheries have begun harvesting younger fish and fish older than 15 years are rare nowadays (COSEWIC, 2003; ICES, 2005a).

1.2.4. Food habits

Atlantic cod is a voracious omnivorous species (trophic level 4.4, see Froese & Pauly, 2007). It is best described as an opportunistic feeder because cod feed on anything that they are capable of capturing. In fact, cod can eat a wide variety of things, including stones, so that it can digest sea anemones, hydroids, and other organisms. Larvae and postlarvae consume smaller organisms, such as plankton, whereas juveniles feed mainly on invertebrates, and older fish on invertebrates and fish, including young cod (Daan, 1989; COSEWIC, 2003; ICES, 2005a; Froese & Pauly, 2007).

Small crustaceans are of great importance (90%) in the food of juveniles (up to 25 cm in length). These preys are progressively replaced by decapods of medium and large size as the cod grows, and fish become more important than crustaceans in the diet of adult individuals. Other taxa play a smaller role as forage organisms: polychaetes (less than 10%); echinoderms and other benthic organisms (minor quantities); and occasionally seaweeds and others. The proportion of benthic organisms shows hardly any change throughout the year, but fish consumption varies more seasonally. Feeding occurs at dawn and dusk, but small fish (<20 cm) feed continuously (Daan, 1989; COSEWIC, 2003; ICES, 2005a; Froese & Pauly, 2007).

1.2.5. Ecosystem roles

Atlantic cod populations respond differently to predators depending on what region of the Atlantic Ocean they occupy. Atlantic cod are susceptible to being consumed by marine mammals and sharks. In some parts of the Atlantic Ocean with large harp seal populations, the number of Atlantic cod has been greatly reduced due to consumption by seals (COSEWIC, 2003). Cod yolk sac larvae (0.33-0.57 cm) are vulnerable to smaller predators such as zooplankton (Bailey, 1984). Juveniles (2-7 cm) are preyed upon by species such as spiny dogfish (*Squalus acanthias*), winter skate (*Leucoraja ocellata*), silver hake (*Merluccius bilinearis*), squid (*Thunnus thynnus*) and halibut (*Hippoglossus stenolepis* and *H. hippoglossus*). Cannibalistic behaviour becomes apparent as adult Atlantic cod readily consume juveniles. On the other hand, in many areas of the Atlantic the majority of the large predatory fish have been removed and cod (and similar species) act as dominant predators in this region feeding on a variety of organisms such as small fishes and

invertebrates (COSEWIC, 2003; ICES, 2005a). The interplay between predators and prey is the key way in which cod influence their ecosystem. Moreover the rich parasite fauna has also an important role in the specific relationships such as mutualism and parasitism.

Marcogliese & Cone (1997) highlighted the importance of integration of parasites as components of food webs; omission of parasites may lead to inaccurate web patterns and predictions of trophic structure. Cod serve as an intermediate, paratenic or definitive host for a large number of parasite species. In this regard, the long list of cod parasites illustrates the omnivorous nature of its diet, and illustrates the complexity of the life-cycle and the involvement at different trophic levels of the parasites (Marcogliese & Price, 1997).

1.3. Biological tags of cod populations

The idea of stocks, or populations, is central to fisheries management. If stocks are to large degree independent biological entities, management can assign exploitation rates and patterns to them, with the underlying assumption that there is a stock-specific sustainable yield (Hammer & Zimmermann, 2005). Further, identification of stocks may help the recognition and protection of nursery and spawning areas and the optimisation of monitoring and conservation strategies (Begg, 2005). This is why stock separation and population discrimination techniques, that display different characteristics for individuals from different areas or stocks, have developed rapidly in fisheries research (Nielsen *et al.*, 2001; Thorrold *et al.*, 2001). The principle of discrimination is that individuals from different areas (*i.e.* populations or stocks) display different characteristics for a given biological trait. Useful biological tags for stock discrimination that have been applied to Atlantic cod are genetic markers (Bentzen *et al.*, 1996, Jónsdóttir *et al.*, 1999; Ruzzante *et al.*, 1999; Hutchinson *et al.*, 2001, Nielsen *et al.*, 2003), elemental composition of otoliths (Campana *et al.*, 1994; Campana *et al.*, 1999), otolith shape (Campana & Casselman, 1993), parasite assemblages (Hemmingsen *et al.*, 1991; Larsen *et al.*, 1997), and morphometric characters (Pepin & Carr, 1993, Swain *et al.*, 2001).

While genetic markers are useful alternatives for the long-term distribution patterns in cod (Ruzzante *et al.*, 1999; Nielsen *et al.*, 2001), otolith chemistry and parasites reflect conditions to which the individual fish has been exposed, reflecting events that occurred during the lifetime of the individual (Williams *et al.*, 1992; Larsen *et al.*, 1997; Campana *et al.*, 1999). Although the usefulness of the comparative approach in stock identification in order to detect the relative sensitivities of stock analysis techniques and to use combined multisource evidence has been emphasized (*e.g.* Waldman, 1999; Cadrin *et al.*; 2005),

multidisciplinary studies have rarely been conducted for fish population discrimination [*e.g.* Larsen *et al.*, 1997 who used otolith structure and parasites as tags for cod discrimination and the holistic approach of HOMSIR project using parasite genetic markers as biological tags for stock identification of horse mackerel, *Trachurus trachurus* (Abaunza *et al.*, 2008; Mattiucci *et al.*, 2008)].

1.4. Studies on parasites of cod. Cod parasites as biological tags

Numerous studies on cod parasites and/or host-parasite interactions have been conducted on both sides of the North Atlantic (reviewed by Hemmingsen & MacKenzie, 2001). A sizeable part of these studies focuses on various aspects of the populational variability (geographical, seasonal, genetic) of cod anisakid nematodes (Des Clers, 1989; 1991; Brattey & Bishop, 1992; Jensen & Idas, 1992; Rokicki *et al.*, 1993; McClelland & Marcogliese, 1994; Myjak *et al.*, 1994; Boily & Marcogliese, 1995; Hemmingsen *et al.*, 1995; Petter & Cabaret, 1995; Brattey & Davidson, 1996; Jensen, 1997; Balbuena *et al.*, 1998; Stromnes & Andersen, 1998; 2000; 2003).

Anisakids have drawn wide attention because cod hosts species of considerable economic and medical importance (*e.g. Anisakis simplex* and *Pseudoterranova decipiens*). Anisakid larvae can occur in the flesh of fish, which makes the product unappealing to consumers, and can be transmitted to humans after consumption of raw or poorly cooked fish.

Other parasitic groups studied due to their pathological effects on cod include: copepods (Khan & Lee, 1989; Khan *et al.*, 1993), monogeneans (Kulachkova & Timofeeva, 1987; Appleby, 1996), Myxozoa (MacKenzie *et al.*, 2005) and Protozoa (Karlsbakk *et al.*, 2005). Recently studies on veterinary aspects related to infection problems in mariculture have also been carried out (Karlsbakk *et al.*, 2001; Bricknell *et al.*, 2006). Another group of studies is associated with taxonomy/faunistic aspects of some cod parasites: digeneans (Køie, 1985; Bray & Gibson, 1991; MacKenzie, 1991; Bray & Des Clers, 1992; Bray & Gibson, 1995; Gaevskaya, 1996; Lysne *et al.*, 1994; 1997); monogeneans (Kulachkova & Timofeeva, 1987; Perdiguero-Alonso *et al.*, 2006); and acanthocephalans (Valtonen & Crompton, 1990; Buchmann, 1986; 1988; 1995; Wayland *et al.*, 2005). Reimer (1995), Zander (1998) and Zander & Reimer (2002) commented on long-term alterations in parasite faunas in relation to eutrophication in the Baltic Sea. Among the parasites considered by these authors were some occurring in cod. Khan & Chandra (2006) observed an overall decline of parasites in cod from areas in NW Atlantic

in 2000-2003 compared with levels before the collapse of commercial fishery in 1990 and suggested that climatic changes perhaps associated with the decline of the major food source and the low population density of the cod population were responsible.

Overall, the literarature data on cod parasites reveal both, differential study effort and an uneven geographical coverage (see Appendix). On the other hand, comparative faunistic and/or ecological analyses on cod parasites are virtually lacking in the NE Atlantic. A notable exception represents a series of studies by Hemmingsen and colleagues carried out off Northern Norway. Hemmingsen *et al.* (1992) revealed impoverished and to a large extent boreal parasite fauna in cod from Balsfjord compared with that of cod from the Barents Sea which the authors related to the age, size and isolation of Balsfjord. Hemmingsen *et al.* (1995) examined seasonal variations in the macroparasite fauna of cod in Balsfjord and found no statistically significant effect of season on infection parameters of all 13 parasite species. Hemmingsen *et al.* (2000) studied the occurrence of the metazoan parasites of *G. morhua* in Balsfjord in relation to fish age and sex and suggested that differences may exist in feeding behaviour between male and female cod in this fjord.

Another aspect of ecological studies on cod parasites, both in the NE and NW Atlantic regions, is their use as biological markers (tags). Typically, a selected number of cod parasites has been used as tags according to the criteria suggested by Kabata (1963) and updated by MacKenzie & Abaunza (1998).

In NW Atlantic the regional variation in the occurrence of anisakid nematodes and the copepod *Lernaeocera branchialis* has inspired most of the studies using cod parasites as population tags. A pioneer study used prevalences of *L. branchialis* to identify four general groups from the 13 sub-areas off the coast of New-England (Sherman & Wise, 1961). A similar study carried out by Templeman & Fleming (1963) around Newfoundland confirmed the interrelationship between stocks previously suggested by meristic and tagging studies. Moreover, Templeman *et al.* (1976) proved the usefulness of different occurrence rates of *L. branchialis* to detect inshore-offshore migrations of cod in the Newfoundland area. Bishop *et al.* (1988) combined the parasitological data of two anisakid nematodes (*A. simplex* and *P. decipiens*) with studies on meristic characters of the host to conclude that inter-mixing of stocks in the Gulf of Saint Lawrence area occurs. Using multivariate analyses, McClelland & Marcogliese (1994) studied the infection levels of 3 anisakid larvae (*A. simplex, Contracaecum osculatum* and *P. decipiens*) in cod to distinguish between migrant and resident populations in the Breton Shelf (southern Gulf of Saint Lawrence area). Another tag parasite species employed in the NW Atlantic is

Trypanosoma murmanensis. Khan *et al.* (1980) suggested the existence of six stocks in the Gulf of Saint Lawrence-Newfoundland area on the basis of the different rates of infection of this parasitic protozoan. In a subsequent study Khan & Tuck (1995) used more parasite species as tags (*P. decipiens*, *L. branchialis*, *Echinorhynchus gadi*, gastrointestinal nematodes and the protozoan *Loma branchialis*) and provided evidence for the existence of at least 6 cod stocks, with some degree of mixing in the cited area.

Only two studies using parasites as biological tags have been carried on cod around Greenland and Iceland. Platt (1976) distinguished between the two areas because *P. decipiens* was almost absent in Greenland cod populations and relatively frequent in fish in the spawning areas of western Iceland. Boje (1987) found that from the pool of 14 parasite species recorded only two species (*Hemiurus levinseni* and *Hysterothylacium aduncum*) had significantly different infection rates between inshore locations in the west part of Greenland and the offshore locations of the east of Greenland. Despite the results of Boje (1987) suggesting a good stock discrimination of these areas, the small sample size of the study (86 cod examined) do not provide enough confidence about the discrimination.

A larger variety of parasite species have been employed in tag studies in the NE Atlantic. Reimer (1970) and Buchman (1986) discriminated between a resident stock and a migratory population that mix in the spawning area of Borholm basin in the Baltic Sea. These populations were differentiated because the increasing gradient of salinity in the western part of Baltic Sea allows the presence of marine parasite species in cod. These marine species were absent in the areas with lower salinity. Polyansky & Kulemina (1963) used the parasite fauna of cod to discriminate between adult and young cod from different parts of the Barents Sea. They found significant differences only in the rates of infection with parasites of younger cod and suggested that only young cod form local populations with little migration between areas. Hemmingsen *et al.* (1991) focused on the differences of seven parasite species to discriminate between two fjords (Balsfjord and Ullsfjord) and one offshore site in Barents Sea concluding that cod in Balsfjord may represent a separate population. However, in a subsequent multidisciplinary study using otolith structure and four selected parasites, Larsen *et al.* (1997) identified mixed populations in the studied areas (*i.e.* offshore and in both fjords). They found that only coastal cod migrate between offshore and the fjords, whereas the resident populations of Arcto-Norwegian cod were mainly found in the fjords. Karasev (1994) identified species which could be used as tags in cod population studies using the literature on parasites of cod in the Barents Sea. However,

later this author did not find useful biological tags for identifying local stocks in the north Norway and north Russia (Karasev, 1998).

1.5. This study

This study has been carried out within the framework of a multidiscipline project 'Establishing traceability for cod (*Gadus morhua*): determining location of spawning and harvest' (CODTRACE), financed by the 5th Framework Programme 'Quality of Life and Management of Living Resources' (Key Action 5.4.3 Common Fisheries Policy) of the European Commission. The main aim of the project was to combine different traceability techniques (morphological, biochemical, microbiological, genetic and parasitological) to establish spawning and harvest location of cod. It has been developed jointly by six research groups from European universities and research organizations (see codtrace web-page). The Marine Zoology Unit of the Cavanilles Institute of the University of Valencia was responsible for the study of parasite assemblages.

The present study profits from the examination of large samples of cod collected from six regions of the North East Atlantic in 2002-2003 which yielded abundant baseline data on parasite communities in this host. The large taxonomically consistent dataset gained in the course of the study afforded comparative assessment of the structure of the parasite communities in cod at several nested scales of community organisation (*i.e.* infracommunities, component communities and faunas). Furthermore, the dataset enabled a search for non-random patterns of community richness, composition and structure focusing on the larger scales of community organisation that may reveal the action of large-scale biogeographical processes on parasite communities in cod in the North East Atlantic. Finally, the data gathered at the infracommunity level for fish sampled in five areas allowed the potential of a novel approach, Random Forests, to be explored for assignment of cod samples to their putative stocks. The latter enabled an assessment of the usefulness of cod parasites as biological markers to spatial discrimination of fish populations and stock discrimination to be carried out.

The present study therefore, attempts to add to the current knowledge on parasite communities in cod in the North East Atlantic by addressing the following questions regarding the structure of parasite communities in this host:

(i) What constitutes the recent parasite fauna in cod in the North East Atlantic? Is there a common pattern in the composition and structure of the parasite regional faunas?

(ii) Do parasite faunas and component communities in cod exhibit non-random, macroecological patterns in composition and structure?

(iii) What are the characteristics of parasite communities in cod? Are there regional differences in complexity, abundance and predictability of infracommunities and component communities?

(iv) Is it possible to predict cod populations/stocks from parasite community data?

2. Aim and objectives

Aim

This study aims to provide novel data on the present state of the composition and structure of the parasite faunas and communities in *G. morhua* in the NE Atlantic and to apply this knowledge to both comparative assessment of patterns at several scales of community organisation and assessment of the usefulness of cod parasites as biological markers for the spatial discrimination of cod populations.

Objectives

The following objectives were targeted in the investigation:

(i) Description of the composition and structure of the metazoan parasite faunas of *G. morhua* from six NE Atlantic regions: Baltic, Celtic, Irish and North Seas, Icelandic waters and Trondheimsfjord (Norway).

- Identification of the metazoan parasites and quantitative characterisation of the parasite populations in each region.
- Description of the composition and comparative assessment of the structure of parasite faunas with respect to the higher level taxonomic groupings, host specificity and geographical distribution of the parasites.

(ii) Redescription of *Diclidophora merlangi* (Kuhn, in Nordmann, 1832) (Monogenea: Diclidophoridae), a new host record for *G. morhua*.

(iii) Description of the composition and structure of parasite communities in *G. morhua* in the regions of study and assessment of the spatial and temporal variations in the richness, abundance and predictability of infra- and component communities.

(iv) Search for non-random, macroecological patterns in the composition and structure of parasite faunas and component communities in *G. morhua*.

(v) Evaluation of the applicability and predictive power of a novel ensemble classification approach using Random Forests (Breiman, 2001) to fish population discrimination using parasite communities as biological indicators.

- Comparison of the learning behaviour of Random Forests and two other algorithms (Linear Discriminant Analysis and Artificial Neural Networks) previously applied in studies using parasites as biological population tags.
- Evaluation of the importance of annual and seasonal variation in parasite community composition and structure for discrimination between cod populations using parasite community data.

3. General materials and methods

3.1. Fish samples

The present study is based on 1,254 fish. Of these 766 were sampled in five areas of the NE Atlantic (Baltic, Celtic, Irish and North seas and Icelandic waters) during 2002-2003. Two spring samples [corresponding to spawning populations further referred to as FSS (first spring sample) and SSS (second spring sample)] and one autumn sample (2002, corresponding to feeding populations referred to as AS) were collected. Fish sampled from the five areas represent five different stocks, according to the demarcation in management units of the International Council of Exploration of the Sea (ICES, 2005a) (see Figure 3.1 and Table 3.1).

A sample of 60 cod from Trondheimsfjord (Norway) captured in spring 2003 and 50 additional fish obtained as 'blind' samples were also examined. The blind samples were collected in spring 2003 in the five areas mentioned above and were labelled blindly by a third party, who kept a record of the actual origin of each cod. The predictive models to establish harvest location of fish developed in the present study with parasite data from fish of known origin, were applied to this blind sample in order to assess their accuracy.

The remaining 378 cod came from two farms located in the North of Scotland and in South-Eastern Iceland (Figure 3.1). Although no important infections were expected in farmed fish, examination was part of the CODTRACE project design in which these samples were included in order to test traceability techniques for discrimination of wild from farmed cod.

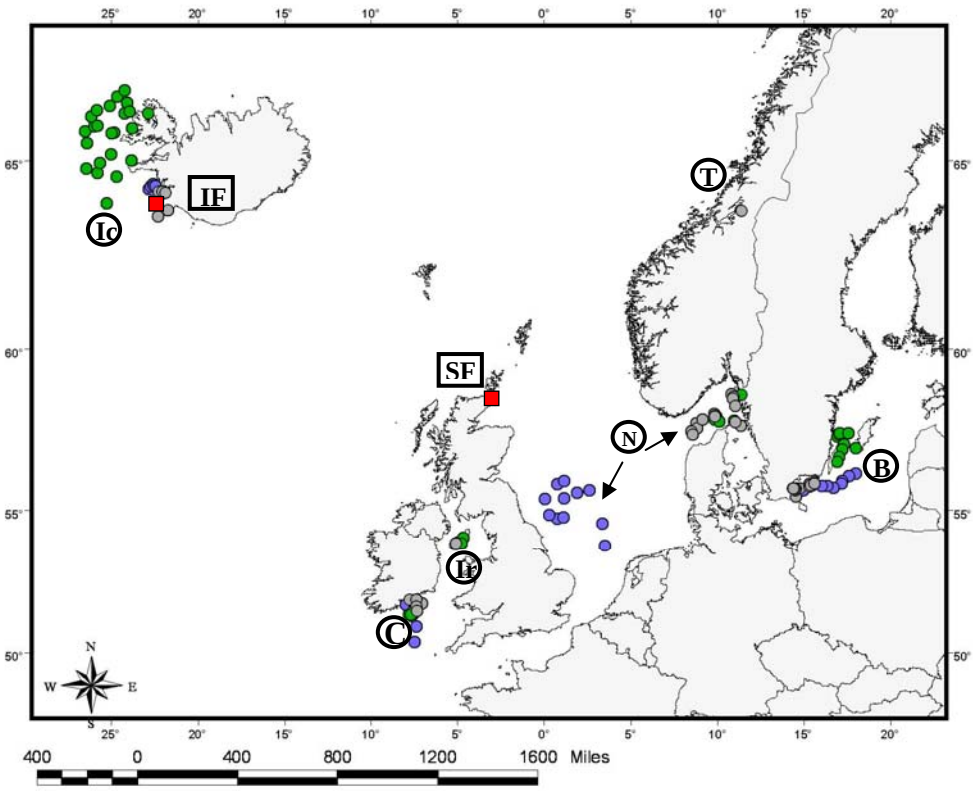

Figure 3.1. Sampling locations in the regions of study. Sample sequence indicated as follows: FSS, blue; AS, green; SSS, grey; fish farms, red. *Abbreviations*: B, Baltic Sea; C, Celtic Sea; Ic, Icelandic waters; Ir, Irish Sea; N, North Sea; T, Trondheimsfjord; IF, Icelandic farm; SF, Scottish farm.

Table 3.1. Number of cod examined by area (currently demarcated by ICES) and season of sampling.

Sampling area	ICES area	Spring 2002	Autumn 2002	Spring 2003	Total
Baltic Sea	Div IIId Subdiv 25 and 27	59[a]	61[b]	60[a]	180
Celtic Sea	Div VIIg	23	56	59	138
Icelandic waters	Div Va	45	62	58	165
Irish Sea	Div VIIa	60	52	24	136
North Sea	Div IVb and IIIa	27[c]	60[d]	60[d]	147
Trondheimsfjord Fish farms	Div IVa/NCC[e]			60	60
Iceland		58	76	62	196
Scotland		61	61	60	182
Total		333	428	443	1204

[a]Subdiv 25; [b]Subdiv 27; [c]Div IVb; [d]Div IIIa; [e]NCC: Norwegian Coastal Cod stock

3.2. Fish collection and processing

Fish were processed at the point of capture either on scientific research vessels during groundfish surveys or at the fish farms. All samples were processed immediately after collection.

Temperature and salinity information, as well as sampling characteristics of each study area for the wild cod samples are summarized in Table 3.2. Table 3.3 summarises the data on migratory behaviour, period of spawning and age-at-maturity of cod in the regions of study.

Table 3.2. Available data for the hydrographic characteristics at the sampling locations where wild cod were collected and fishing depth/gear.

Areas of sampling location	Temperature range (ºC)	Salinity range (‰)	Depth of fishing range (m)	Trawl type
Spring 2002				
Baltic Sea	2.5-8.7	7.0-13.6	44-70	TV3 standard trawl
Celtic Sea			68-105	Portuguese high-headline trawl
Irish Sea			65-76	Bottom trawl
North Sea	7.0-7.4	34.7-34.9	64-93	GOV standard trawl
Icelandic waters			45-73	Gillnet
Autumn 2002				
Baltic Sea	4.3-7.9	7.4-8.1	63-76	TV3 standard trawl
Celtic Sea				Demersal trawl
Irish Sea			30-83	Handline, Bottom trawl
North Sea	7.5-12.6		35-160	GOV standard trawl
Icelandic waters				Bottom trawl
Spring 2003				
Baltic Sea			36-62	
Celtic Sea				Demersal trawl
Irish Sea				Bottom trawl
North Sea	5.1-7.5		39-225	
Icelandic waters	5.2-5.8		29-209	Bottom trawl, Gillnet
Trondheimsfjord			20-25	Shrimp trawl

Table 3.3. Migratory behaviour, date of spawning and age-at-maturity of cod stocks in the regions of study. Data after Robichaud & Rose (2004) and ICES (2005a).

Stocks	Migratory behaviour	Period of spawning	Age-at-maturity*
Baltic Sea	Sedentary/variable**	March - September	
Celtic Sea	Sedentary	February - April	2.3
Irish Sea	Inaccurate homing	January - May	2
North Sea	Inaccurate homing	January - April	2-3
Icelandic	Accurate homing	March - May	6.6♀ 5.8♂
Norwegian coastal	Accurate homing	March – April	

* 50% of individuals are mature; ** Accurate homing/Inaccurate homing/Dispersive

Each fish was measured [total length (TL) and standard length (SL)], weighted and assigned an individual identification code, which ensured that biological samples for each individual were distinctive. Fish ranged from 16.5 to 119.5 cm in length (SL, mean 50 ± 16.5 cm) (see Figure 3.2A) and from 0.045 to 15.3 kg in weight (mean 2.0 ± 2.2 kg). The individuals from each region were processed to obtain data useful for six "traceability techniques": body and otolith morphometrics, microsatellite loci, otolith chemical composition, bacteria and parasite assemblages.

Visible parasites from the external and internal body surfaces were removed and preserved in 70% ethanol and the entire viscera including the gills of each fish were removed and stored frozen (-20ºC). These were shipped to the University of Valencia for parasitological examination. Age was determined from otoliths by the team of the University of Göteborg, Sweden (see Figure 3.2B for cod age distribution in each sample).

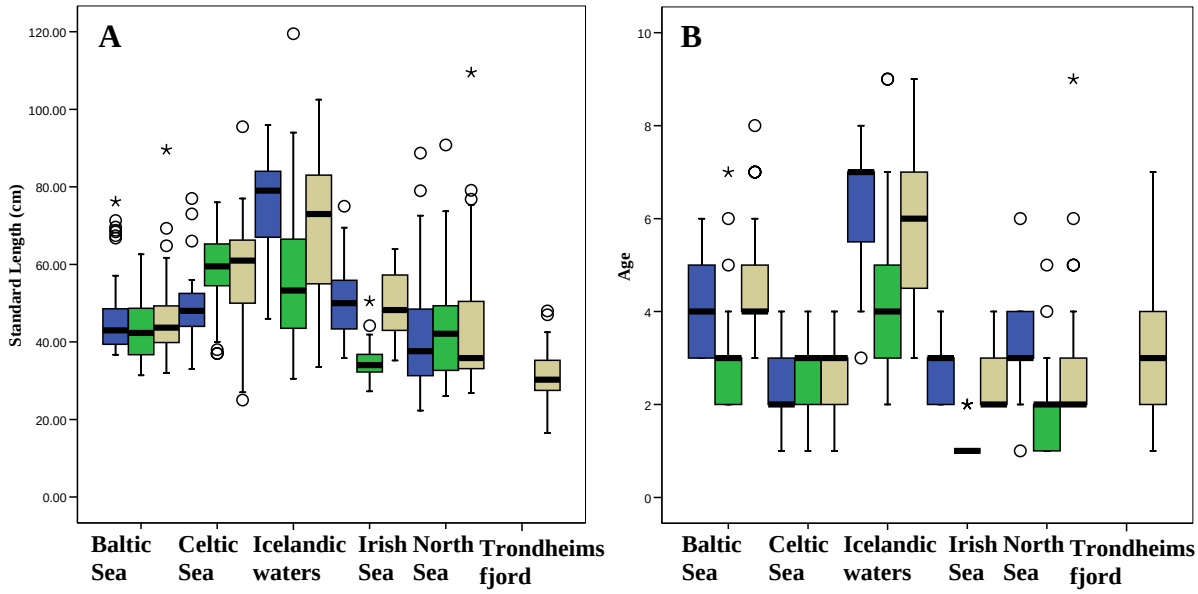

Figure 3.2. Box-plots of standard length (A) and age (B) of *G. morhua* from the three samples in the six NE Atlantic regions studied. FSS, blue; AS, green; SSS, grey. Asterisks represent outliers.

3.3. Parasite collection and processing

The gills and internal organs (oesophagus, stomach, intestine, pyloric caeca, liver, heart, spleen, gall bladder and gonads) were examined separately. Muscles were not available for examination. Gills were rinsed in saline and the gill arches examined individually. After collection of all parasite specimens, all organs were pressed individually between glass plates and further screened for parasites. Examination was carried out with the aid of high magnification stereomicroscope (6–40 X or 8-80 X). All parasites were collected, fixed and preserved in 70% ethanol. Representative sub-samples of 30 specimens (when parasite numbers very high) or all specimens (when few) were prepared for detailed morphological examination and identification in Canada balsam mounts whereas the remaining specimens were identified in wet mounts. Trematodes, monogeneans and cestodes were stained with iron acetocarmine (Georgiev *et al.*, 1986), dehydrated through an alcohol series, cleared in dimethyl phthalate and examined/identified as permanent mounts in Canada Balsam. Nematodes and acanthocephalans were examined as wet mounts in saline solution or temporary mounts in clearing liquids (lactic acid or glycerine).

As a result of the sample processing skin and eyes were not subjected to examination and therefore the metacercariae (*Cryptocotyle lingua* and *Diplostomum spathaceum*) and cutaneous monogeneans of the genus *Gyrodactylus* were not collected. Furthermore, gill monogeneans of the latter genus were not detected probably due to their degradation during freezing. The abundance of the copepod *Holobomolochus confusus* from the nasal cavity of cod, as well as of some other external parasites such as hirudineans, amphipods and isopods may appear underestimated since the samples were collected in the field by non-specialists. Similarly anisakine individuals present in the musculature were not analysed.

Despite these sampling problems, the vast material of cod analysed in the present study was collected using identical sampling procedure in all six regions. Parasitological examination was carried out following a standardised protocol and the taxonomic consistency of the identification was ensured thorough the entire study.

3.4. Study regions. Cod characteristics in the studied regions

This section presents brief introductions to the physical environments and cod populations of the study regions to allow the biological data to be placed in context. For each region (sea) the main characteristics are outlined, followed by the available data on cod biology in the region and the characteristics of the sampling locations.

3.4.1. Baltic Sea

The Baltic Sea is a brackish, semi-enclosed sea characterized by an estuarine circulation and strongly influenced by the continental climate. River runoffs have a strong influence on salinity by directly freshening surface waters. The bottom water of the deep Baltic basins is renewed by inflows of saline and oxygenated water from North Sea *via* the Kattegat and Belt Straits. A permanent halocline limits vertical interchanges between the low-salinity surface layer and the deep saline layer. This results in a distinct difference in zooplankton communities above and below the halocline. The upper layers are dominated by organisms that tolerate low salinity whereas in and below the halocline marine species dominate. These zooplankton species are salinity and temperature dependent and follow seasonal dynamics (Dippner *et al.*, 2000; Möllmann *et al.*, 2000). Zooplankton community is also influenced by the five phytoplankton phases in the annual cycle; the more remarkable being the blue-green algae (Wasmund *et al.*, 1998).

Cod is the only gadoid present in the Baltic, except for occasional visits of haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*). Cod is regarded as the major predator in this ecosystem, since seal populations are small. However, cod eggs and larvae are predated by clupeids (Köster & Möllmann, 2000) and adult cod (Uzars & Plikshs, 2000). Additionally, unfavourable temperature and oxygen conditions, disease caused by dumping (Kosior *et al.*, 1997) and overfishing are degrading the cod population in all phases of its development. The vertical and horizontal distribution of cod is related to its salinity preference. Outside the spawning period, cod are distributed mainly near the bottom at intermediate depths, *i.e.* below the halocline (Neuenfeldt, 2002). However, prior to spawning (March to September, on average June to July) ripe cod migrate to deep basins so that during spawning there is a significant difference in the distribution of mature and inmature cod (Tomkiewicz & Köster, 1999). The spawning cod mainly aggregate in the pelagic zone below the halocline but avoid the low oxygen concentrations which often prevail in the deeper central parts of the basins. Immature and spent cod remain demersal at intermediate depths (Tomkiewicz *et al.*, 1998). However, the homing behaviour is uncertain and fish may use different spawning areas in successive years (Aro, 1989).

Two cod stocks occur in the Baltic Sea: the eastern Baltic stock and the western Baltic stock complex (ICES, 2001; Nielsen *et al.*, 2001; 2003). The eggs from the eastern Baltic cod reach neutral buoyancy at low salinities but eggs from the western stock do not show such trait (Nissling & Vallin, 1996). During the feeding period adult cod spread over

large areas and may move long distances. The homing behaviour is uncertain and the fish may use different spawning areas in successive years (Aro, 1989). Six main spawning areas have been identified in the Baltic Sea: Gotland Basin (Subdivision 26 and 28), Gdansk Deep (Subdivision 26), Borholm Basin (Subdivision 25), Arkona Basin (Subdivision 24), the Sound (Subdivision 23) and the Belt Sea (Subdivision 22) (ICES, 2005a).

Cod sampled in the present study belong to the eastern Baltic stock. This stock has a prolonged spawning period which extends from March to September (ICES, 2005a). Tagging experiments (Aro, 1989; Robichaud & Rose, 2004) have shown that most of these cod make seasonal migrations to spawn south-east of Bornholm Island. The cod that migrate to Bornholm Basin to spawn come mainly from the feeding grounds in Hanö Bight (Netzel, 1974). During the feeding period adult cod spread over large areas and may move long distances. In the eastern Baltic, the feeding migration after spawning occurs in general from deeper waters towards more shallow areas (Aro, 1989; Robichaud & Rose, 2004).

Cod samples from Baltic Sea were collected from two neighbouring areas (Hanö Bight and Öland Island). Hanö Bight is south-eastern of the southern Swedish coast and north of Bornholm Island, whereas Öland Island is off the south-western side of Sweden. The hydrographic conditions of the Hanö Bight and Öland Island are similar. There is permanent stratification into an upper low salinity layer (about 7‰) and a deeper saline layer (12-16‰). Late summer of 2002 was unusually warm, which resulted in higher than normal sea surface temperatures (ICES, 2003).

3.4.2. Celtic Sea

The Celtic Sea represents a transition zone between Atlantic waters, at the margins of the European continental shelf, and the coastal waters of the Bristol Channel and the Irish Sea. The variability in topography and tidal force determines the water column structure which from May to November is dominated by thermal stratification. The deep waters are influenced by warmer waters from the North Atlantic Drift in winter. During summer bottom temperatures are *c.* 5-6º C cooler due to stratification, given that the tidal force is not enough to mix the layers from the water column (Brown *et al.*, 2003).

Cod in the Celtic Sea grow faster than in other areas (Brander, 2000). Spawning in this area has been shown to take place relatively later in the year (February to April, on average March) compared with other stocks around the British Isles. The lateness of spawning is not primarily influenced by temperature and may be due to the later occurrence of the production cycle in the area due to strong tidal mixing (Brander, 1994). The seasonal abundance of

plankton with cod eggs and larvae are closely linked. Transport of eggs is thought to be limited because cod larvae also appear to remain close to the spawning areas (Horstman & Fives, 1994), although there is no evidence of cannibalism (Pinnegar *et al.*, 2003).

Although there is insufficient evidence, the cod in Celtic Sea have been regarded as a single stock unit. However, cod released in the Irish Sea have been recaptured in the Celtic Sea (ICES, 2005a and references therein). Pawson (1995) also reported some Celtic cod from Irish Sea. Thus, the separate stocks status of cod populations from the Celtic and Irish Seas appears unclear. In addition, Pawson (1995) suggested that there is a limited migration between the western English Channel and Celtic Sea.

3.4.3. Icelandic waters

Icelandic waters are mainly influenced by three ocean currents: the warm Gulfstream, and the cold East-Greenland and East-Iceland Currents. Moreover a low-salinity coastal current due to freshwater run-off from several rivers occurs, causing stratification of the water column. For this reason the spring phytoplankton bloom occurs in coastal waters before than in the waters farther offshore. In the south and southwest areas cod spawning seems linked to this bloom and the presence of capelin (*Mallotus villosus*) (ICES, 2005a and references therein). Spawning of cod in these coastal and southern areas generally starts in the middle of March and is completed in the first week of May (Jónsson, 1982; Marteinsdóttir & Björnsson, 1999).

Icelandic cod are genetically different from cod in other areas, such as the Barents Sea, North Sea and Newfoundland (Pogson *et al.*, 1995). The Icelandic stock consists of distinct spawning populations in the Northeast and the Southwest, although there is migration in both directions. In fact, genetic differences were found to be more pronounced between fish from different depths than between locations (Pampoulie *et al.*, 2006). Icelandic cod exhibit spawning site fidelity (Taggart *et al.*, 1995; Robichaud & Rose, 2004) and also display high fidelity to local spawning regions (Thorsteinsson & Marteinsdóttir, 1992; 1993). After the breeding season, individual cod tend to migrate to the main feeding regions located off the western and northern coasts of Iceland (Jónsson, 1996; Jónsdóttir et al, 2006). However, a recent tagging study on the main spawning ground suggests that some individuals remain in relatively shallow, warm waters in the regions off the southern coast (Pálsson & Thorsteinsson, 2003). Furthermore, juvenile cod appear to be stationary during the first 2-3 years of their life so the majority of the dispersal is likely to happen before the juvenile years (see Pampoulie *et al.*, 2006 and references therein). Jónsson

(1996) observed that both mature and immature tagged fish have only been caught in the Icelandic Shelf area in the latest years. Nevertheless, during some years migrations of cod from Greenland to the spawning grounds at Iceland have been recorded, but they were thought to be made up mainly of individuals that originally drifted as larvae to Greenland from the Icelandic spawning grounds (Jamieson & Jónsson, 1971).

3.4.4. Irish Sea

The Irish Sea separates the islands of Ireland and Great Britain, and entirely surrounds the Isle of Man. It is connected to the NE Atlantic by St George's Channel, running between the Republic of Ireland, and Wales and Cornwall to the south, and by the North Channel, situated between Northern Ireland and Scotland to the North-East. Its western part is characterized by a deepwater trough (> 80m) from the North Channel to St George's Channel, whereas the eastern side slopes gently to form a relatively shallow bay (< 50m). The Isle of Man straddles a hydrographic boundary between permanently well-mixed and seasonally stratified waters. The degree of tidal mixing and water depth chiefly determine areas that can become stratified, such as the southwest of the Isle of Man, which shows a seasonal stratification between April and October (Nichols *et al.*, 1993). In the North Channel, the water column remains vertically mixed for most of the year. Both vertical gradients in temperature and salinity contribute to stratification, although salinity contributes more to water column stability in the North Channel. The bathymetry of the Irish Sea is characterised by a deepwater trough running centrally and a shallow bay in the eastern part. Water circulation is relative weak and shows no particular directionality although, there is a south-going residual current. Movements of water masses are driven by differences in density, tides and weather conditions (ICES 2005a, and references therein).

Cod in Irish Sea carry out continual vertical shifts throughout the year. However, recapture studies show that the majority of fish returns to the same spawning grounds each year. This suggests separation between cod in the eastern and the western Irish Sea. In addition, movements in a north-south direction seem common although the component of Irish Sea cod in the Celtic Sea is low (Connolly & Officer, 2001). This fact agrees with the apparent lack of genetic sub-structuring within the Irish Sea, and between the Irish and Celtic Seas (Hutchinson *et al.*, 2001). Irish Sea cod populations are also characterized by the proportion of mature individuals not being a monotonic function of length (ICES, 2005a and references therein; Armstrong *et al.*, 2004).

Spawning in the western part of the Irish Sea is restricted to the coastal region, which is related to the earlier food production in this region. Moreover, spawning occurs before the development of a strong front related to the western Irish Sea gyre. After spawning, cod move southwards into St George's Channel and the Celtic Sea (ICES, 2005a).

The area of the sampling locations of this study is located southwest of the Isle of Man. This is an area of weak tidal currents which is reflected in the distribution of bottom sediments. Dominant winds along the axis connecting the two channels determine water circulation (Young *et al.*, 2000; 2001). These characteristics account for the stratification of the area. The establishment of the stratified area and the associated gyre were suggested as important for the growth and survival of juvenile cod (ICES, 2005a and references therein).

3.4.5. North Sea

The North Sea is a relative shallow basin, although, the Skagerrak has a maximum depth of 700 m that allows large inflows of Atlantic water into the North Sea (ICES, 1983). The daily mean temperature in the southern North Sea is more consistent throughout the year than the cyclical seasonal pattern in the northern part.

Cod in the North Sea generally remain within one region and do not disperse uniformly throughout the North Sea. Cod spawn in early spring (January to April, on average February-March), related to the onset primary production, and the larvae occur in the stratified regions during summer where they feed. Usually cod undertake southward migrations to spawn and migrate northward to feeding grounds post-spawning (ICES, 2005a). The spawning areas are characterised by salinity gradients in the winter and thermal stratification from late spring to summer.

Cod populations in the North Sea appear to form units that are reproductively isolated from each other and which are, presumably, spatially distinct, at least during the spawning season (Hutchinson *et al.*, 2001; ICES, 2005a). According to tagging data, five regional groupings have been suggested: (i) the Norwegian side of Skagerrak; (ii) the Danish side of Skagerrak; (iii) coastal regions from Flamborough to the Scottish east and north coasts; (iv) the central North Sea; and (v) the Southern Bight (ICES, 2005a). Juvenile cod compete strongly with adult cod (Macer, 1983). Moreover, important predators of juvenile cod are cod themselves, whiting (*Merlangius merlangus*) and saithe (*Pollachius virens*) (Daan, 1989).

Both regions of the study are mainly nursery areas of 1 and 2 year-old cod, but adults are also present in both areas (Fox *et al.* 2005; ICES, 2005a; 2007). Although spawning grounds appear to be widespread and not restricted to specific areas, the most important concentration of cod eggs occurs in a limited area to the North-West of Dogger Bank (Fox *et al.* 2005; ICES, 2007). Dogger Bank and Kattegat (southern to Skagerrak) appear to be spawning areas, judging from the distributions of adult cod. Juvenile cod from Skagerrak undertake an offshore migration to deeper water. The main direction is to south and west suggesting migration to spawning areas in the eastern North Sea or in the southern Kattegat (Pihl & Ulmestrand, 1993). The nature of the transition area for cod populationss between the North and the Baltic Seas has been controversial. Recently, it was considered as a hybrid zone exhibiting a closer relationship between Baltic and North Sea cod. Hybrid cod, that have characteristics of the populations from both seas, are thought to be maintained by migration balance (Nielsen *et al.*, 2003).

Cod from the North Sea was sampled at two different locations: Dogger Bank (between the Jutland Peninsula and the NE England coast) and Skagerrak (between the southern tip of Norway and Jutland). The two locations fall within the ICES areas of the North Sea and Skagerrak cod stocks, respectively. The hydrographic conditions of the Dogger Bank and Skagerrak are very dissimilar. Dogger Bank has 50 m of maximum depth, and houses a stable front that generates strong wind and consequently along-frontal circulation. In contrast, Skagerrak has a maximum depth of 700 m. The water masses in this area are mainly influenced by the inflow of the Atlantic current at depth and this results in large salinity variations. In both locations primary production is guaranteed; moreover the year 2002 was unusually warm (ICES 2003; 2005a).

3.4.6. Trondheimsfjord (Norway)

Trondheimsfjord is an inlet of the Norwegian Sea and represents Norway's third longest fjord (130 km long) in the west central part of the country. The ‘typical’ depth of the fjord is 400 m and its maximum depth is 617 m. Waves are usually lower than 0.5 m although occasionally reaching heights of *c.* 4 m. Its drainage area is about 20,000 km^2 causing marked seasonal variations in the freshwater input that result in high salinity (10-33‰) and temperature (2-20°C) fluctuations. The estuarine circulation derives mainly from six large rivers that flow into the fjord. None of these runoffs have a glacial origin and they are rich in humus matter. Most of the fjord edges are hard and rocky, while the deep bottom is mainly covered with sand, clay or mud. Tidal flows dominate the water exchange above the

sill level, as well as the turbulent vertical mixing and diffusion that eventually lead to replacement of the deep water in the basins. Variations in the vertical stratification outside the fjord are found to be important for water exchange. The main part of Trondheimsfjord is ice-free year-round.

Trondheimsfjord has a rich marine life, with more fish species than any other fjord in Norway (Jacobson, 1983; Rikardsen et al, 2004). Cod from the fjord belong to the Norwegian coastal stock (IVa Division of ICES). Although the information on cod populations in Trondheimsfjord is scarce, other studies in northern areas (Sarvas & Fevolden, 2005) have shown little mobility of cod in the fjords. Cod leave the fjords to the outer coastal waters during the feeding season but the majority return back to their nursery fjord for spawning (March to April, see Pedersen, 1984) (Godø, 1986; Jakobsen, 1987). Dahle *et al.* (2006) found genetic differences between Norwegian coastal cod populations. Cod from Trondheimsfjord were sampled inshore, where salinity is low.

3.4.7. Fish farms

Cod in the Icelandic farms were reared in tanks with running sea water at 7-9ºC. They represented a F1-generation resulting from the crossing of 3-4 males and 10 females, all originating from south-western Icelandic waters. Cod from the Scottish farm originate from wild stock off Orkney located close to the farm. All subsequent generations were spawned from these adults. Fish were kept in land-based ponds and were fed on artificial feed.

3.5. Terminology and statistical analysis

Parasitic infection and ecological terms are used according to Bush *et al.* (1997). The measures of parasitic infection referred to in this study are: (i) *prevalence* (the number of fish infected divided by the number of fish examined, expressed as a percentage); (ii) *mean abundance* (the total number of parasites of a particular taxon found divided by the *total* number of fish examined); and (iii) *mean intensity* (the total number of parasites of a particular taxon found divided by the number of *infected* fish). Ecological terminology is described according to the hierarchical nested structure of parasite populations and communities. A parasite *infrapopulation* includes all individuals of a species in an individual host at a particular time. *Infracommunity* is a community of parasite infrapopulations in a single host. A parasite *component population* refers to all of the individuals of a species recovered in a particular host population sample. A *component community* refers to all infracommunities within a given host population sample. Parasite

compound community consists of all the parasite communities within an ecosystem (see Esch *et al.*, 1990).

The general approach in statistical analyses is that non-parametric tests were performed on raw data due to their aggregated distributions [*i.e.* Mann–Whitney U-test (M-W) for paired comparisons, Kruskal-Wallis test (K-W) for multiple comparisons and Spearman rank correlation (r_s)]. When parametric analyses were required $\log_e$–transformation of the data was performed [*i.e.* Cluster analysis, Principal Component Analysis (PCA), Multidimensional Scaling (MDS), Analysis of Similarities (ANOSIM), Linear Discriminant Analysis (LDA)] (see Zar, 1996; Clarke & Gorley, 2006). Classifications with Random Forests (RF) and Artificial Neural Networks (NN) were performed on non-transformed data. Due to the variety of statistical procedures and programs used for specific analyses, these are described in detail the corresponding chapters' Material & Methods sections.

4. The parasite fauna of Atlantic cod, *Gadus morhua*, in the NE Atlantic

This chapter presents an analysis of the parasite fauna of cod from the six NE Atlantic regions and two fish farms examined in the present study. The new data on parasites provided here adds to the most recent checklist of cod parasites (Hemmingsen & MacKenzie, 2001) especially with respect to species composition and geographical distribution. The chapter includes comments on the parasite identification and taxonomy in specific cases, a general description of the composition and structure of the parasite fauna of cod in the six regions studied, and data on the parasites of farmed fish.

4.1. Comments on parasite identification and taxonomy

The 171,821 metazoan parasites collected in 1,204 fish were identified to the lowest taxonomic level possible (most often to species level). The identification of some of the species found in this study is still controversial. Thus, Brinkman (1975) pointed out that *Progonus muelleri* (Levinsen, 1881) has been confused with *Derogenes varicus* (Müller, 1774), the differences being the presence of a cyclocoel and the thicker egg shell in *P. muelleri*. Consequently many studies could have underestimated the presence of the latter species in cod. The material reported here as *D. varicus* agrees well with the morphology and metrical data for this species by Bray (1973). However, although *D. varicus* was the only species found in our study, an overestimation of its presence as in other studies is possible, especially in the cases of high parasite abundance where identification was based on representative sub-samples.

Another case of difficult identification is that of the species of the genus *Stephanostomum* Looss, 1899. Of the three species listed in cod by Hemmingsen & MacKenzie (2001) one, *S. baccatum* (Nicoll, 1907), belongs to group 1 of Bray & Cribb (2003) [*i.e.* vitellarium anterior extent (% of hindbody devoid of follicles) <10%] whereas the two other species, *S. caducum* (Looss, 1901) and *S. pristis* (Deslongchamps, 1824) belong to group 2 (*i.e.* vitellarium anterior extent >10%). Køie (1984) reported *S. pristis* from *G. morhua* in Danish waters. She found that, in hundreds of adult specimens, the number of circumoral spines ranged from 2 × 18 to 2 × 26, with a dominance of specimens with 2 × 23-25 whereas the 2 × 18 arrangement was rarely found. Køie (1984) concluded that *S. caducum* (described with 2 × 25 oral spines) was probably a synonym of *S. pristis* (originally described with 2 × 18 spines). However, Bartoli & Bray (2001) redescribed *S. pristis* on Mediterranean material and detected no variation in circumoral spine number. They concluded that two species were mixed in Køie's study. Similarly, Karlsbakk (1993) found no variation in circumoral spine number in his specimens from *Enchelyopus cimbrius*

and *G. morhua* from off western Norway. This author pointed out that the specimens he considered to be *S. caducum* from *Trisopterus esmarkii* and *Gadiculus argenteus thori* also show minimal variation in spine number, with 2 × 24-25 circum-oral spines. Both *S. pristis* and *S. caducum* were present in the total collection of cod parasites in this study. However, circumoral spines are very fragile and can be lost in frozen material or during the handling process. It was, therefore, impossible to identify at species level the numerous specimens in all samples; these are henceforth referred to as *Stephanostomum* spp.

A third species-identification problem concerns the pseudophyllidean cestode *Parabothrium gadipollachii* (Rudolphi, 1810) which is difficult to differentiate from *Abothrium gadi* van Beneden, 1871 (but see Williams, 1960). Although reported, the former species is infrequent in cod and common in other gadoids. The only adult cestode recovered in the present study was identified as *A. gadi* on the basis of its agreement with the morphological data of Williams (1960). Moreover, cross-sections confirmed the main distinctive feature at the generic level of the present material, *i.e.*, vitelline follicles continuous throughout the length of the proglottis and intermingled with testes in *A. gadi* (*vs* partly cortical and partly medullary vitelline follicles, not intermingled with testes in *P. gadipollachii*, see Bray *et al.*,1994).

Larval stages pose a number of obstacles to parasite identification mostly because of their simple morphology and the fact that many of the species discriminating features are not yet present at the early stages of parasite development. One of the new host records, *Rhipidocotyle* sp., was found at a metacercarial stage and identified to generic level only.

Larval anisakids represent a more complex case with respect to identification due to the limitations in using morphological characters (Olson *et al.*, 1983; Fagerholm 1988; Dick *et al.* 1991) and the overall complicated taxonomy due to the presence of sibling species. Thus, *Anisakis simplex* (Rudolphi, 1809) is a complex of three sibling species with fairly similar morphology (Mattiucci & Nascetti, 2006). *A. simplex* A for which the name *A. pegreffii* was proposed recently, is mainly Mediterranean, whereas *A. simplex* B has a North Atlantic distribution and *A. simplex* C was recently reported from the Pacific by Mattiucci *et al.* (1997) (see also Anderson, 2000; and references therein). Although it is possible that the third-stage larvae (L3) and adult *Anisakis* collected in the present study belong to *A. simplex* B, a more conservative identification was adopted, designating the specimens to *A. simplex sensu lato*.

Pseudoterranova decipiens (Krabbe, 1878), another anisakid species, also represents a species complex. Electrophoretic analyses of gene enzyme systems identified

three sibling species: A, in grey seals (*Halichoerus grypus*) in the northeast Atlantic; B, in harbour seals (*Phoca vitulina*); C, in bearded seals (*Erignathus barbatus*) (Mattiucci & Paggi, 1989; Paggi *et al.*, 1991). Similarly, Nascetti *et al.* (1993), in a multilocus electrophoretic study, recognised three species within *Contracaecum osculatum* (Rudolphi, 1802) species complex: A, occurring mainly in bearded seals in the eastern and western North Atlantic; B, found mainly in harp seals (*Phoca groenlandica*) in the eastern and western North Atlantic; C, found mainly in grey seals in the eastern North Atlantic. Orecchia *et al.* (1994) added two other species, named D and E, found as adults in Weddell seals (*Leptonychotes weddellii*) in the Antarctic. Unfortunately, the above distinctions cannot be applied to the abundant larval collection in the present study due to the lack of reliable morphological features to discriminate the sibling species within *P. decipiens* and *C. osculatum.* Therefore, these forms were designated as *P. decipiens sensu lato* and *C. osculatum sensu lato*.

The larval specimens *Hysterothylacium* (Ward & Magath, 1917) in the present collection were assigned to two species. Most third-stage (L3), and all fourth-stage larvae (L4) and adults, were identified as *H. aduncum* (Rudolphi, 1802) (following Berland, 1991; Anderson, 2000), whereas the L3 forms found spirally encysted in the submucosa of the digestive tract were identified as *H. rigidum* (Rudolphi, 1809) (see Køie, 1993a). Morphological observations in the course of this study lead to the suggestion that the larval nematodes reported as *Spiruroideorum* "larvae" of Janiszewska (1938) by Palm *et al.* (1999) actually represent L3 larva of *H. rigidum*.

All cuculanid nematodes were identified as *Cucullanus cirratus* Müller, 1777 except for one individual found in the stomach. The specimen was somewhat damaged which precluded its identification to the species level. However, its small oral capsule indicated that it represents a form different from both *C. cirratus* and *Cucullanus heterochrous* Rudolphi, 1802. *Cucullanus* sp. was, therefore, considered a new host record. The three additional new host records, namely *Spinitectus* sp., *Fellodistomum* sp. and S*teringotrema* sp. were only identified to the generic level due to the scarcity of the material and the problematic taxonomy of the respective groups. However, our study represents the first record of representatives of the above genera in cod (see Hemmingsen & MacKenzie, 2001).

The most commonly reported adult acanthocephalan in cod, *Echinorhynchus gadi* Zoega in Müller, 1776 which has also been reported in a large number of other teleost species (Hemmingsen & MacKenzie, 2001), was found to actually represent a species

complex comprising three distinct, partially sympatric species in the NE Atlantic, all occurring in cod (Väinölä *et al.*, 1994). Since the distinction of these species was inferred from molecular evidence, we were not able to discriminate *E. gadi* which is further referred to as *E. gadi sensu lato*.

The monogenean *Udonella caligorum* Johnston, 1835 was found on the copepods *Caligus curtus* Müller, 1785 and *C. elongatus* Nordmann, 1832 collected in the cod sample. According to Carvajal *et al.* (2001) *U. caligorum* is a copepod commensal. This species was not included in the analysis of the parasite fauna because its presence depends on the presence of the copepods on fish. *U. caligorum* appeared to be more associated with *C. elongatus* in all regions since the prevalence was higher than that in *C. curtus* (see Table 4.1). Moreover, the mean intensity of *U. caligorum* on *C. elongatus* was higher than those of *U. caligorum* on *C. curtus* (Table 4.1) as was the maximum intensity (Celtic Sea: 24 *vs* 0; Icelandic waters: 5 *vs* 2;); Irish Sea: 40 *vs* 1; North Sea: 26 *vs* 14).

Table 4.1. Prevalence (P) and mean intensity (MI) of *Udonella caligorum* Johnston, 1835 on *Caligus curtus* and *Caligus elongatus* parasitising cod in Celtic, Irish and North seas and Icelandic waters.

	Celtic Sea	Icelandic waters	Irish Sea	North Sea
C. curtus				
Sample size	2	10	88	40
P (%)	0	40	2.3	45
MI	0	1	1	4.2
C. elongatus				
Sample size	281	99	59	247
P (%)	51.6	53.5	37.3	79.8
MI	3.9	1.1	5.8	3.2

4.2. Composition and structure of the parasite fauna of cod

4. 2. 1. General description

All fish from the six open water locations (n=826) were infected, except for three fish from the Baltic Sea. Species composition, prevalence and mean abundance of each parasite species in each region are summarized in Table 4.2 which also includes data on parasite specificity and distribution. The classification of the species with respect to the latter characteristics were based on the divisions and data of Hemmingsen & MacKenzie (2001) to which data compiled from the literature and the Host-Parasite Database of the Natural History Museum, London (http://www.nhm.ac.uk/research-curation/projects/host-parasites/database/) were added. Specificity and distribution categories were only assigned to parasites identified to species level.

Altogether 57 different parasite forms were found. Of these, 41 were identified to species level (including two species which were not considered true parasites of cod, see below), 12 were identified to generic level whereas five larval forms (one digenean, four cestodes and the copepod larvae which certainly represented juvenile stages of the copepod species recovered) were identified to family/order (Table 4.2).

Nine species were found for the first time in cod in the present study: the monogenean *Diclidophora merlangi* (Kuhn, in Nordmann, 1832) (redescribed in detail in Chapter 5); the trematodes *Rhipidocotyle* sp., *Fellodistomum* sp. and *Steringotrema* sp.; the larval cestode *Schistocephalus gasterostei* Fabricius, 1780; the adult nematodes *Cucullanus* sp. and *Spinitectus* sp. and the copepods *Acanthochondria soleae* (Krøyer, 1838) and *Chondracanthus ornatus* Scott, 1900. Two of these cannot be considered true parasites of cod but rather part of the fish food content, namely the copepod *A. soleae* which was recovered from the stomach of one fish in a rather decomposed state (digested) and *S. gasterostei* was found in the body cavity of a three-spined stickleback *Gasterosteus aculeatus* from the stomach content of one cod. The two species (labelled 'D' in Table 4.2) were, therefore, excluded from all analyses. *G. morhua* is therefore a new host record for seven species recovered in the present study.

The predominant groups of cod parasites were digeneans (19 species) and nematodes (13 species). The other higher taxonomic groups had low representation: 8 cestodes, 7 copepods, 3 acanthocephalans, 2 hirudineans, 1 monogenean, 1 isopod and 1 amphipod. Overall, 60% of the species were represented by adult parasites. However, more than half of the parasite individuals were larval forms (58.8%). The majority of the larvae were anisakid nematodes which comprised 58.2% of the total number of individuals.

Data in Table 4.2 reveal an overall high variation in the prevalence and abundance of the 55 parasite forms between the six study regions. Eleven species were present in all regions (the trematode *L. elongatum*; the nematodes *A. simplex, C. osculatum, H. aduncum, H. rigidum, P. decipiens, A. crassicollis* and *C. gracilis*; and the acanthocephalans *C. semerme, C. strumosum* and *E. gadi*). Three species (*Hysterothylacium aduncum, Derogenes varicus* and A*nisakis simplex)* showed high prevalence and abundance in the overall sample (prevalence 83.9%, 65.6% and 53.4%, respectively; mean abundance 31.58, 21.80 and 85.27, respectively). In contrast, ten species infected only one fish each.

Table 4.2. Host specificity, distribution, prevalence (P), mean abundance (MA ± SD), median abundance (M, shown if >0 only) and site of recovery of parasites in *G. morhua*, from the Baltic, Celtic, Irish and North seas, Icelandic waters and Trondheimsfjord (Norway). New host records are marked with an asterisk. *Abbreviations for host specificity categories*: D: food content; G, generalist; GS, gadoid specialist. *Abbreviations for distribution categories*: A-B, Arctic-Boreal; B, Boreal; W, worldwide; NA, Not applicable. *Abbreviations for site of infection*: C, caeca; DC, digestive content; GI, gills; IN, intestine; L, liver; SK, skin; ST, stomach; VC, visceral cavity.

Region (sample size) Parasite species	Host specificity	Distribution	Baltic Sea (n = 180) P (%) MA ± SD (M)	Celtic Sea (n = 138) P (%) MA ± SD (M)	Icelandic waters (n = 165) P (%) MA ± SD (M)	Irish Sea (n = 136) P (%) MA ± SD (M)	North Sea (n = 147) P (%) MA ± SD (M)	Trondheimsfjord (n = 60) P (%) MA ± SD (M)	Site of recovery
MONOGENEA									
Diclidophora merlangi	GS	[a] A-B		0.7 0.01 ± 0.09			0.7 0.01 ± 0.08		GI
TREMATODA (metacercariae)									
Bucephalinae gen. sp.	G	NA		8.7 0.12 ± 0.52	1.2 0.01 ± 0.11	12.5 0.93 ± 5.53	2.0 0.08 ± 0.70		C-GI-IN-ST
Cryptocotyle lingua	G	A-B					1.4 0.01 ± 0.12		SKIN
Otodistomum sp.	G	NA			1.8 0.02 ± 0.13		2.7 0.34 ± 2.46		C-GI-IN-ST
Prosorynchoides gracilescens	GS	B		2.9 0.09 ± 0.71	0.6 0.01 ± 0.16	0.7 0.01 ± 0.17			GI-ST
Prosorhynchus crucibulum	G	NA		5.8 0.09 ± 0.39		2.9 0.03 ± 0.17		1.7 0.02 ± 0.13	GI-ST
**Rhipidocotyle* sp.	G	NA				0.7 0.01 ± 0.09			ST

Region (sample size)			Baltic Sea (n = 180)	Celtic Sea (n = 138)	Icelandic waters (n = 165)	Irish Sea (n = 136)	North Sea (n = 147)	Trondheimsfjord (n = 60)	Site of recovery
TREMATODA (adult forms)									
Derogenes varicus	G	W		85.5 15.05 ± 23.34 (6)	86.1 54.85 ± 155.91 (10)	100,0 34.92 ± 43.29 (20.50)	87.1 14.83± 38.23 (4)	30,0 0.48 ± 0.93	C-GI-IN-ST
**Fellodistomum* sp.	G	NA			0.6 0.01 ± 0.08				GI
Gonocerca phycidis	G	W		10.1 0.14 ± 0.44		23.5 1.07 ± 4.08	0.7 0.01 ± 0.08		GI-ST-IN-C
Hemiurus communis	G	B	0.6 0.01 ± 0.07	49.3 3.20 ± 10.29		75.0 8.40 ± 26.00 (2)	48.3 4.73 ± 20.29	50,0 1.90 ± 3.12 (0.50)	C-GI-IN-ST
Hemiurus levinseni	G	A-B			7.9 0.34 ± 1.67				GI-ST
Hemiurus luehei	A	B [a]				5.2 0.10 ± 0.44	10.9 0.78 ± 4.04		ST
Lecithaster sp. ?*gibbosus*	G	A-B				0.7 0.03 ± 0.34	0.7 0.02 ± 0.25		ST
Lepidapedon elongatun	GS	A-B	2.2 0.18 ± 1.7	0.7 0.01 ± 0.09	9.7 1.72 ± 11.21	5.9 0.17 ± 0.84	2.0 0.21 ± 1.88	60.0 177.47 ± 585.76 (2)	C-GI-IN-ST
Lepidapedon rachion	GS	B		2.2 0.06 ± 0.43	1.8 0.05 ± 0.42	2.2 0.05 ± 0.39		45.0 49.42 ± 191.24	C-GI-IN-ST
Opechona bacillaris	G	B			0.6 0.01 ± 0.08	0.7 0.01 ±0.09			C

Table 4.2. Continued (i)

Region (sample size) Parasite species	Host specificity	Distribution	Baltic Sea (n = 180) P (%) MA ± SD (M)	Celtic Sea (n = 138) P (%) MA ± SD (M)	Icelandic waters (n = 165) P (%) MA ± SD (M)	Irish Sea (n = 136) P (%) MA ± SD (M)	North Sea (n = 147) P (%) MA ± SD (M)	Trondheimsfjord (n = 60) P (%) MA ± SD (M)	Site of recovery
Podocotyle reflexa	G	A-B			6.1 0.08± 0.38				C-ST
Stephanostomum spp.	GS	B [a]		21.0 1.41± 5.53	3.6 0.07 ± 0.40	29.4 1.85 ± 7.39	40.1 4.69 ± 14.68		C-GI-IN-ST
**Steringotrema* sp.	G	NA					0.7 0.01 ± 0.08		GI
CESTODA (larval forms) *Grillotia* sp.	G	NA					0.7 0.03± 0.33		VC
Hepatoxylon sp.	G	NA		1.5 0.03 ± 0.27					VC
Lacistorhynchus sp.	G	NA		2.9 0.11± 0.79		5.2 0.06 ± 0.27	2.0 0.02 ± 0.14		VC
Scolex pleuronectis [b]	G	W			0.6 0.01 ± 0.08	2.2 0.02 ± 0.15			IN-ST
Pseudophyllidea fam. gen. sp.	G	NA		2.2 0.04 ± 0.25	0.6 0.01 ± 0.08				IN-ST
**Schistocephalus gasterostei*	D		0.6 0.02 ± 0.30						DC

Region (sample size)			Baltic Sea (n = 180)	Celtic Sea (n = 138)	Icelandic waters (n = 165)	Irish Sea (n = 136)	North Sea (n = 147)	Trondheimsfjord (n = 60)	Site of recovery
Trypanorhyncha fam. gen. sp.	G	NA		4.4 0.06 ± 0.31	1.2 0.01 ± 0.11	5.2 0.07 ± 0.30	3.4 0.14 ± 1.06		VC
Unidentified plerocercoids	G	NA			0.6 0.01 ± 0.08		1.4 0.02± 0.18		VC
CESTODA (adult forms)									
Abothrium gadi	GS	B		16.7 0.21 ± 0.50	3.6 0.04 ± 0.19	22.1 0.31 ± 0.66	5.4 0.05 ± 0.23		C- IN-ST
NEMATODA (larval forms)									
Anisakis simplex s.l. (L3)[c]	G	A-B [a]	15 2.37 ± 13.25	92.0 74.89 ± 134.59 (19.50)	99.4 327.29±433.06 (121)	36.0 4.65 ± 42.41	50.3 34.33 ± 127.02 (1)	5.0 0.05 ± 0.22	C-IN-L-ST-VC
Contracaecum osculatum s.l. (L3)	G	A-B	53.9 6.84 ± 16.07 (1)	72.5 8.19 ± 15.50 (2)	94.6 56.62 ± 62.85 (34)	62.5 10.94 ± 23.40 (2)	15.7 1.29 ± 5.73	8.3 0.23± 0.96	C-IN-L-ST-VC
Hysterothylacium aduncum (L3)	G	A-B	41.7 1.83 ±5.49	68.8 11.28 ± 20.80 (3.5)	97.6 37.9 ± 35.71 (28)	72.8 11.85 ± 20.67 (3.5)	78.2 11.95 ± 39.37 (4)	65,0 1.20 ± 1.47 (1)	C-IN-L-ST-VC
Hysterothylacium rigidum (L3)	G	B	40.6 6.34 ± 51.17	52.2 14.57 ± 36.15 (1)	6.7 0.37 ± 2.47	8.1 0.20 ± 0.95	23.1 1.33 ± 7.19	8.3 0.12 ± 0.42	C-IN-L-ST-VC
Pseudoterranova decipiens s.l. (L3)	G	A-B	3.9 0.07 ±0.39 (7)	51.5 2.23± 4.22 (1)	52.7 3.51 ± 12.47 (1)	22.1 0.86 ± 3.00	12.9 1.38 ± 9.77	1.7 0.02 ± 0.13	C-IN-L-ST-VC
Rhapidascaris sp. (L3)	G	NA					0.7 0.01±0.08		IN

Table 4.2. Continued (ii)

Region (sample size) Parasite species	Host specificity	Distribution	Baltic Sea (n = 180) P (%) MA ± SD (M)	Celtic Sea (n = 138) P (%) MA ± SD (M)	Icelandic waters (n = 165) P (%) MA ± SD (M)	Irish Sea (n = 136) P (%) MA ± SD (M)	North Sea (n = 147) P (%) MA ± SD (M)	Trondheimsfjord (n = 60) P (%) MA ± SD (M)	Site of recovery
Ascarophis morrhuae	GS	A-B		20.3 1.11 ± 4.83	52.1 11.96± 32.49 (1)	66.9 7.96 ± 20.64 (2)	20.4 1.01 ± 3.78	1.7 0.02± 0.13	C-IN-ST
Ascarophis crassicollis	GS	A-B	1.1 0.01±0.11	26.8 2.20 ± 11.49	1.8 0.03 ± 0.23	45.6 3.38 ± 8.08	31.3 11.39 ± 37.92		C-IN-GI-ST
Ascarophis filiformis	GS	A-B		0.7 0.01 ± 0.09	7.9 0.18 ± 1.01	2.9 0.03 ± 0.17			IN-ST
Capillaria gracilis	G	A-B	3.9 0.13± 0.76	7.3 0.10 ± 0.41	32.7 1.14 ± 4.15	1.5 0.01 ± 0.12	4.8 0.09 ± 0.44	88.3 18.25 ± 38.34 (8)	C-IN-ST
Cucullanus cirratus	GS	A-B		71.0 4.80 ± 9.29 (2)	79.4 6.74 ± 9.21 (3)	53.7 3.38 ± 10.29 (1)	55.1 3.24 ± 7.21 (1)	93.3 14.32 ± 19.43 (8)	C-IN-ST
**Cucullanus* sp.	G	NA		0.7 0.01±0.09					ST
Hysterothylacium aduncum	G	A-B	13.9 0.36 ± 1.28	94.2 31.67 ± 40.02 (19)	87.3 25.78 ±33.40 (14)	79.4 25.69 ± 38.41 (13.5)	85.7 16.33 ± 35.28 (6)	5,0 0.12 ± 0.58	C-IN-ST
**Spinitectus* sp.	G	NA		5.1 0.13 ± 0.90	1.2 0.01 ± 0.11	1.5 0.02 ± 0.19			C-GI-IN-ST
ACANTHOCEPHALA (post-cystacant)									
Corynosoma semerme	G	A-B	10.6 0.36 ± 1.28	3.6 0.04± 0.24	0.6 0.01 ± 0.16	0.7 0.01 ± 0.09	0.7 0.01 ± 0.08	1.7 0.02 ± 0.13	C-IN-VC
Corynosoma strumosum	G	B	6.1 0.14 ± 0.73	18.8 0.36 ± 1.02	7.3 0.09 ± 0.35	14,0 0.26 ± 1.26	14.3 1.24 ± 6.33		C-IN-VC

Region (sample size)			Baltic Sea (n = 180)	Celtic Sea (n = 138)	Icelandic waters (n = 165)	Irish Sea (n = 136)	North Sea (n = 147)	Trondheimsfjord (n = 60)	Site of recovery
ACANTHOCEPHALA (adult forms)s									
Echinorhynchus gadi s.l.	G	A-B	88.3 32.24 ± 44.79 (16)	5.1 0.16 ± 1.30	53.9 4.55 ± 9.87 (1)	12.5 0.29 ± 1.42	28.6 2.35 ± 9.02	30,0 0.48 ± 1.02	C-GI-IN-ST
HIRUDINEA									
Calliobdella nodulifera	G	A-B				0.7 0.01 ± 0.09	2.0 0.02 ± 0.14		SKIN
Johanssonia arctica	G	A-B [a]			0.6 0.01 ± 0.08				SKIN
COPEPODA (larval forms)									
Caligus sp. copepodite	G	NA				0.7 0.01 ± 0.09			GI
Copepoda fam. gen. sp. copepodite	G	NA		0.7 0.01 ± 0.09					
COPEPODA (adult forms)									
**Acanthochondria soleae*	D					0.7 0.01 ± 0.09			DC
Caligus curtus	G	A-B		1.5 0.01 ± 0.12	3.6 0.06 ± 0.38	16.2 0.65 ± 2.97	9.5 0.27 ± 1.56		GI-SK
Caligus diaphanus	A	B		0.7 0.01 ± 0.09					GI
Caligus elongatus	G	A-B		24.6 2.04 ± 5.35	13.3 0.60 ± 3.84	16.9 0.43 ± 1.69	20.4 1.68 ± 6.44		GI-SK

Table 4.2. Continued (iii)

Region (sample size) Parasite species	Host specificity	Distribution	Baltic Sea (n = 180) P (%) MA ± SD (M)	Celtic Sea (n = 138) P (%) MA ± SD (M)	Icelandic waters (n = 165) P (%) MA ± SD (M)	Irish Sea (n = 136) P (%) MA ± SD (M)	North Sea (n = 147) P (%) MA ± SD (M)	Trondheimsfjord (n = 60) P (%) MA ± SD (M)	Site of recovery
**Chondracanthus ornatus*	A	W [a]		0.7 0.01 ± 0.09					GI
Clavella adunca	GS	W		72.5 2.96 ± 3.88 (2)	56.4 2.06 ± 3.45 (1)	67.7 2.74 ± 5.22 (2)	71.4 2.36 ± 3.95 (1)	43.3 0.92± 1.41	GI-SK
Holobomolochus confusus	GS	B						1.7 0.02 0.13	GI
Lernaeocera branchialis	G	A-B		6.5 0.09 ± 0.37	19.4 0.30 ± 0.68	4.4 0.04 ± 0.21	17.0 0.30 ± 0.96	21.7 0.33± 0.73	GI-SK
AMPHIPODA *Lafystius sturionis*	G	A-B					0.7 1.27 ± 15.42		SK
ISOPODA *Gnathia elongata* (praniza larva)	G	A-B [a]		0.7 0.01 ± 0.09	1.8 0.02 ± 0.19				SK

[a] Distribution according to other authors, see text; [b] According to (Appy & Burt, 1982); [c] According to Mattiucci *et al*. (1997), see text.

4. 2. 2. Taxonomic structure of parasite fauna

Concerning species richness, the maximum number of species (37 species) was found in the collection from the Celtic Sea, followed by those from Icelandic waters and the Irish and North Seas (36 species each). Species richness of the parasite faunas of cod was substantially lower in Trondheimsfjord and the Baltic Sea (18 and 12 species, respectively). The higher-level taxonomic structure of the parasite faunas in cod from the 6 regions is graphically represented in Figure 4.1. The figure shows the relative representation in terms of both number of species and individuals of the major parasite taxonomic groupings in cod, namely, Trematoda, Cestoda, Nematoda, Acanthocephala and Copepoda. The four remaining higher-level taxonomic groups, *i.e.* Monogenea, Hirudinea, Amphipoda and Isopoda, were poorly represented, both in terms of species and individuals, and were omitted for clarity.

The species representation was very similar in all regions except for the Baltic Sea and Trondheimsfjord where nematodes represented a distinctly higher proportion of all species and cestodes were absent (Figure 4.1A, B). The four other regional faunas (*i.e.* in cod from Celtic, Irish and North seas and Icelandic waters) exhibited similar richnesses of the higher taxa groupings.

The above two distinct faunas also showed marked differences with respect to the relative abundance of the higher taxonomic groups. Although nematodes were the richest taxon in the Baltic Sea collection, the high numerical dominance of acanthocephalans was the most distinctive trait of the fauna of this region. Three species [*Echinorhynchus gadi* Zoega in Müller, 1776, *Corynosoma semerme* (Forssell, 1904) and *Corynosoma strumosum* (Rudolphi, 1802)] represented nearly 64% of all parasite individuals in the Baltic Sea collection (Figure 4.1G). On the other hand, Trondheimsfjord fauna was distinct in the exceptionally high relative abundance of trematodes (86.4%, see Figure 4.1H) which was mainly due to two species with similar high prevalence and abundance, *Lepidapedon elongatum* (Lebour, 1908) and *Lepidapedon rachion* (Cobbold, 1858), which accounted for 67% and 19% of all individuals, respectively. Another characteristic feature of the Trondheimsfjord fauna was the low representation of larval nematodes and the numerical dominance of adult nematodes. Thus, two species, *Capillaria gracilis* (Bellingham, 1840) and *Cucullanus cirratus* Müller, 1777 (accounting for 7% and 5%, of the total parasite number, respectively) represented 53.2% and 41.8%, of all nematodes in this collection, respectively.

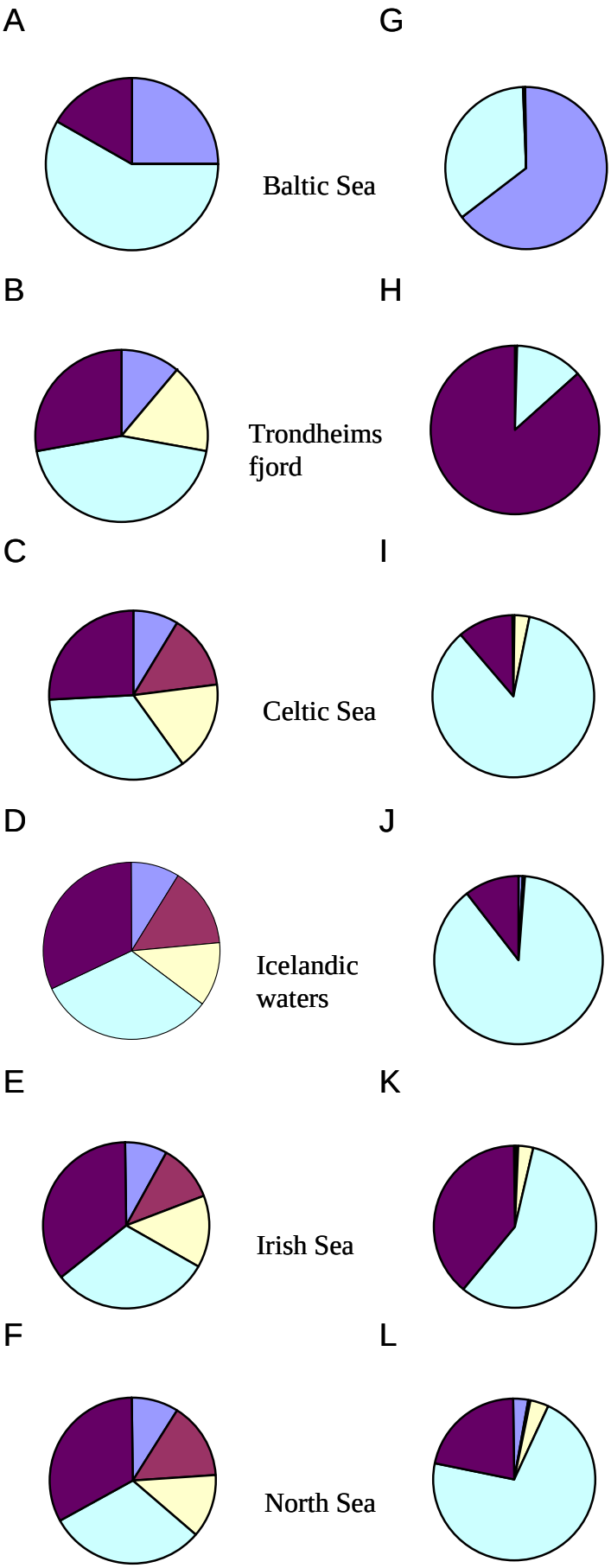

Figure 4.1. Taxonomic structure of the parasite faunas of cod in the six NE Atlantic regions with respect to species richness (A-F) and relative abundance (G-L) of the higher parasite taxa: Acanthocephala, Cestoda, Copepoda, Nematoda and Trematoda.

Overall, the taxonomic structure of the fauna based on the relative abundance of the higher taxa (Figure 4.1G-L) differed substantially from that based on species richness (Figure 4.1 A-F). Thus, a much higher representation of nematodes was revealed in the four regions which exhibited similarity with respect to the species richness structure of the faunas (*i.e.* Celtic, Irish and North Seas and Icelandic waters). These could be grouped in pairs with respect to the relative abundance of the numerically dominant taxa: (i) Celtic Sea and Icelandic waters faunas exhibited substantially elevated numbers of nematode individuals (Figure 4.1 I, J); and (ii) Irish and North seas faunas had higher proportions of trematode individuals (Figure 4.1 K, L).

Nematodes represented over 85% of individual parasites in the Celtic Sea collection. The most representative species were *A. simplex, H. aduncum* and *C. osculatum* which comprised 42%, 24% and 5% of the total nematode abundance. Trematodes were less abundant as compared to the faunas of the second group (11% of all parasites). *D. varicus, H. communis* and *Stephanostomum* spp. accounted for 8%, 2% and 1% of all parasite individuals, respectively and represented 74.7%, 15.9% and 7% of all trematodes. The fauna of cod in Icelandic waters was very similar to that of the Celtic Sea in terms of proportions of nematodes and trematodes (88 and 11% of all individuals, respectively). The most abundant nematodes were (as in the Celtic Sea collection) *A. simplex*, *H. aduncum* and *C. osculatum* which comprised 61%, 12% and 10%, respectively, of all individuals. The most abundant trematode species in the Icelandic waters fauna was *D. varicus* which represened 10% of all individuals.

The cod parasite fauna of the Irish Sea was characterised by the higher numerical representation of trematodes (39%) and a comparatively low relative abundance of nematodes which represented 57% of all parasites (Figure 4.1 J). The digeneans *D. varicus, H. communis* and *Stephanostomum* spp. comprised 29%, 7% and 2% of all parasites, respectively. Although the most widespread and abundant nematode species were roughly the same as in the Celtic and Icelandic faunas, their proportions of the total abundance differed. *H. aduncum, C. osculatum, Ascarophis morrhuae* Van Beneden, 1871 and *A. simplex* accounted for 31%, 9%, 7% and 4% of all parasites, respectively.

The parasite fauna of the North Sea cod could be considered as intermediate between the Irish Sea and the other two (*i.e.* Celtic Sea and Icelandic regional faunas) with respect to the relative trematode abundance which accounted for nearly 22% of parasite individuals. *D. varicus*, *H. communis* and *Stephanostomum* spp. accounted for 13%, 4%

and 4% of all forms in the North Sea collection whereas nematodes comprised 70% of all parasite forms. Again, the most common and abundant species were almost the same as in the Irish Sea fauna, but their relative proportions differed. The nematodes *A. simplex, H. aduncum, A. crassicollis* and *C. osculatum* represented 29%, 24%, 9% and 1% of all parasites, respectively.

The above distinctions of the faunas with respect to the higher taxonomic level structure translated into a similar but more refined picture at the species level, as revealed by a cluster analysis using the similarity matrix (Bray-Curtis similarity) based on species prevalence (Figure 4.2 A) and abundance (Figure 4.2 B). The major differences between regions observed at the higher taxonomic level appeared valid in the species similarity analysis in that the Baltic Sea and Trondheimsfjord faunas were most dissimilar whereas the four other regions formed a cluster at high similarity levels (72.2% and 58.5% for matrices based on prevalence and mean abundance, respectively) (Figure 4.2). However, the grouping within the latter differed from that described above on the basis of the higher-level parasite representation. The faunas of North, Celtic and Irish Seas formed a group at high similarity levels (79.7% and 72.2% for matrices based on prevalence and mean abundance, respectively) whereas the fauna of cod in Icelandic waters was somewhat distinct and occupied an intermediate position between this group and the Trondheimsfjord/Baltic Sea faunas (Figure 4.2). The latter two joined at low similarity levels (prevalence data 53.6% and 41.6%; abundance data 29.6% and 21.9%, respectively).

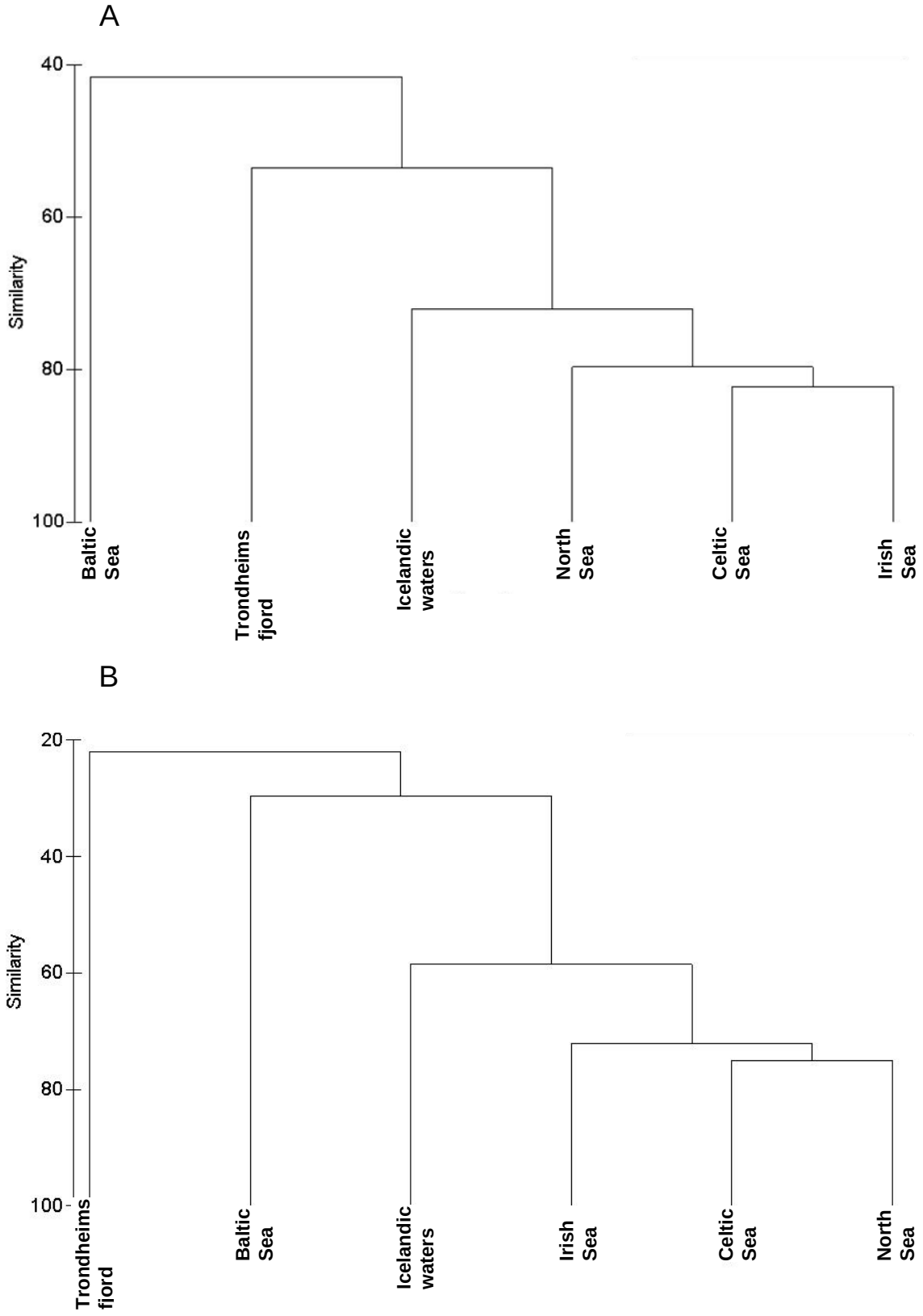

Figure 4.2. Cluster analysis dendogram (group-average linkage) of the parasite faunas of *G. morhua* in the six NE Atlantic regions, using Bray-Curtis similarity matrices based on species prevalence (A) and mean abundance (B).

4. 2. 3. Host specificity of cod parasites

The classification of Hemmingsen & MacKenzie (2001) was generally followed with respect to host specificity of cod parasites. No specific parasites of cod were found in this study. In fact, very few specific parasites are recognized in this fish (Hemmingsen & MacKenzie, 2001). Therefore two main groups are recognised here: (i) parasite species reported from cod and other gadoid fish species (gadoid specialists, labelled 'GS' in Table 4.2); and (ii) parasite species reported from a wider range of host species (generalists, labelled 'G' in 4.2). Hemmingsen & MacKenzie (2001) considered an additional 'accidental species' category (labelled 'A' in Table 4.2) but stressed that this is an arbitrary decision and that 'accidental species' can also be placed in the 'generalist species' category due to their low specificity behaviour. This suggestion was followed in the present study for the species not listed by the latter authors.

Generalist parasites comprised the majority of the cod parasite fauna (40 species which accounted for 85% of all individuals) whereas gadoid specialist were poorly represented (12 species, 15% of all parasite individuals). The three species considered as accidental made up a minute proportion of the species and individuals.

The structure in terms of parasite specificity of the parasite faunas of cod in the six regions is illustrated in Figure 4.3. Generalist species dominated over gadoid specialists with respect to both relative richness and abundance. This dominance was most expressed in the fauna of the Baltic Sea where only two gadoid specialist species (16.7% of the species) were present (the digenean *L. elongatum* and the nematode *Ascarophis crassicollis* Dollfus & Campana-Rouget, 1956). These also had very low abundance (0.4% of all individuals).

The fauna of cod from the other low salinity region, Trondheimsfjord, exhibited an opposite pattern, *i.e.* the highest, especially with respect to abundance, representation of the gadoid specialists category. Six species of this category, the trematodes *L. elongatum* and *L. rachion*; the nematodes *A. morrhuae* and *C. cirratus*; and the copepods *Clavella adunca* (Strøm, 1762) and *Holobomolochus confusus* (Stock, 1953), represented 33.3% of the species and 91.3% of the individuals found in this collection (Figure 4.3).

The other four regions showed similar proportions and shared the same gadoid specialist species. Seven gadoid specialists were common for the four regions: *L. elongatum*, *Stephanostomum* spp., *A. gadi*, *A. morrhuae*, *A. crassicollis*, *C. cirratus* and *C. adunca*. Three species, *Prosorynchoides gracilescens* (Rudolphi, 1819), *L. rachion* and *Ascarophis filiformis* Polyansky, 1952 were present in the Celtic and Irish seas and

Icelandic waters faunas but absent in the North Sea fauna. However, gadoid specialists were numerically better represented in the Irish and North Sea faunas as compared to the Celtic Sea and Icelandic waters faunas (16.4 and 19.5% of individuals *vs* 7.2 and 4.3%, respectively, see Figure 4.3B).

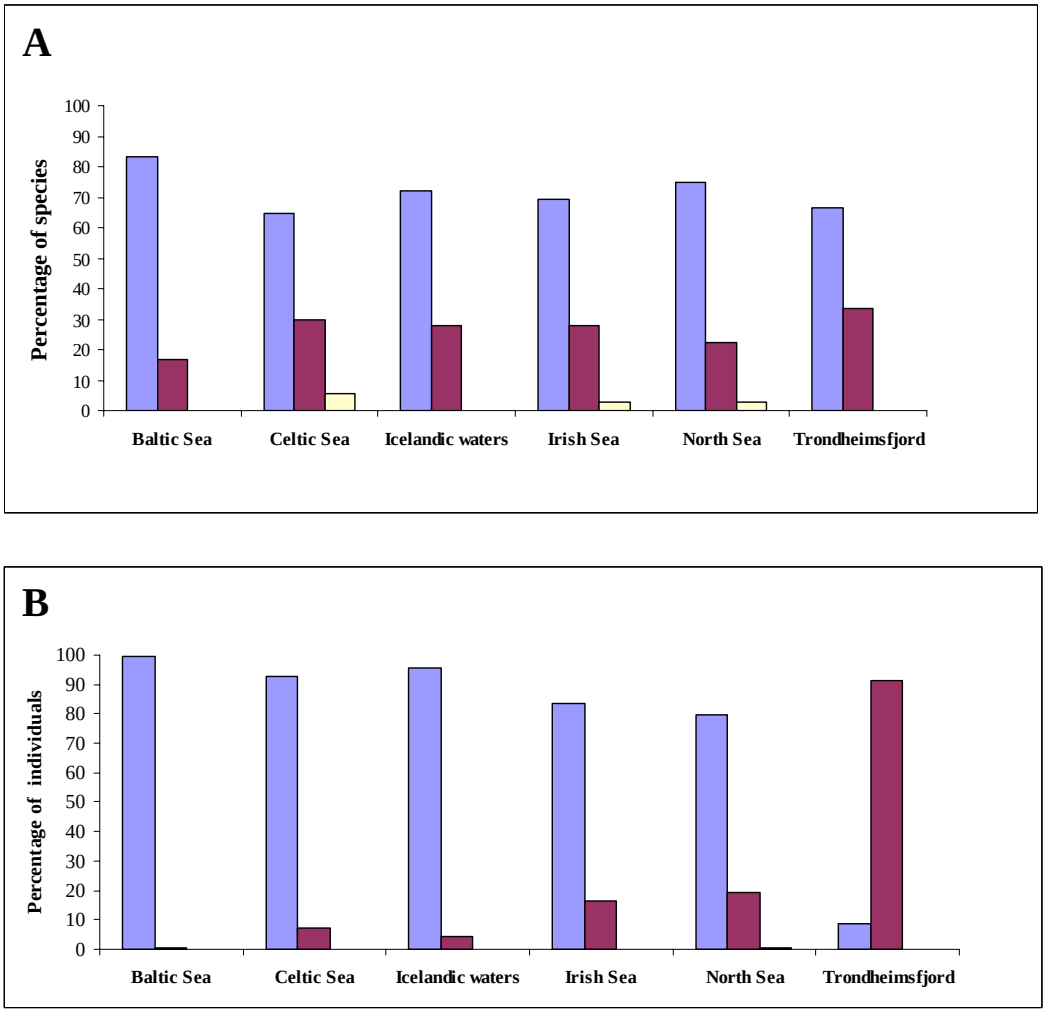

Figure 4.3. Relative richness (A) and abundance (B) structure of the parasite fauna of cod in the six NE Atlantic regions with respect to host specificity of the parasites: Generalists, Gadoid specialists, Accidental species.

4. 2. 4. Geographical distribution of cod parasites

Although the criteria for the geographical distribution of Hemmingsen & MacKenzie (2001) are rather general and related to the geographical distribution of cod only, their classification was followed to ensure the consistency of the comparisons. Parasite species were split into three categories with respect to their geographical distribution: (i) Arctic-Boreal species (labelled 'A-B' in Table 4.2) which 'infect cod in the northern part of its distribution but not in southern warmer waters'; (ii) Boreal species (labelled 'B' in Table

4.2) whose distributions 'overlap that of cod and extend beyond it to more temperate southern waters'; and (iii) species of worldwide distribution (labelled 'W' in Table 4.2) which have been reported from many different parts of the world. The category 'not applicable' (labelled 'NA' in Table 4.2) refers to materials not identified to species level.

The present study added new data on the distribution of most species infecting cod in the NE Atlantic (Table 4.2). Among these is the new host record, the monogenean *D. merlangi* found in the Celtic and North seas. This species was also recorded in the Arctic (samples examined by us from the Natural History Museum, London; see also Rubec & Dronen 1994), which leads us to consider its distribution as Arctic-Boreal following the definitions of Hemmingsen & MacKenzie (2001). The hemiurid *Hemiurus luehei* Odhner, 1905 [not mentioned by Hemmingsen & MacKenzie (2001)] actually belongs to the Boreal group (found in Irish and North Seas in our study, see also Gibson & Bray, 1986). Hemmingsen & MacKenzie (2001) considered that *A. simplex sensu stricto*, which has only been reported from cod (Mattiucci *et al.*, 1997), has a northern hemisphere distribution (within the worldwide category) in both the Atlantic and Pacific Oceans. However, recent data suggesting that of the three sibling species only *A. simplex* B has a North Atlantic distribution (Mattiucci & Nascetti, 2006) and the present data (see Table 4.2) suggest that the anisakid larvae in cod in the NE exhibit an Arctic-Boreal distribution.

The hirudinean *Johanssonia arctica* (Johansson, 1899) was considered a low Arctic species. Although we found this species in cod from Icelandic waters only, data by Appy & Dadswell (1981) suggest that it has an Arctic-Boreal distribution. The copepod species recovered in cod for the first time in our study, *C. ornatus*, appears to have a worldwide distribution (see Kabata, 1979) whereas the isopode *Gnathia elongata* (Krøyer, 1847) should be considered an Arctic-Boreal species (see also Lawrence & Keast, 1990). On the other hand, the present study confirmed the classification of six species as Boreal by Hemmingsen & MacKenzie (2001): *Prosorhynchoides gracilescens* (Rudolphi, 1819), *Lepidapedon rachion* (Cobbold, 1858), *Opechona bacillaris* (Molin, 1859), *A. gadi*, *H. rigidum* and *C. strumosum* (Rudolphi, 1802); these were also found in Icelandic waters in the course of the study.

In all regions, the best-represented group in terms of parasite species was the Arctic-Boreal (Table 4.2, Figure 4.4A-F). Roughly 20% of the species were Boreal, and the reminder had worldwide distribution except for the Baltic Sea fauna which lacked species of the latter category. The relative abundance of the species with Arctic-Boreal distribution was distinctly higher (Figure 4.4G-H). The latter group dominated in the Baltic Sea,

Trondheimsfjord and Icelandic waters faunas representing 87%, 80% and 89% of all individuals, respectively).

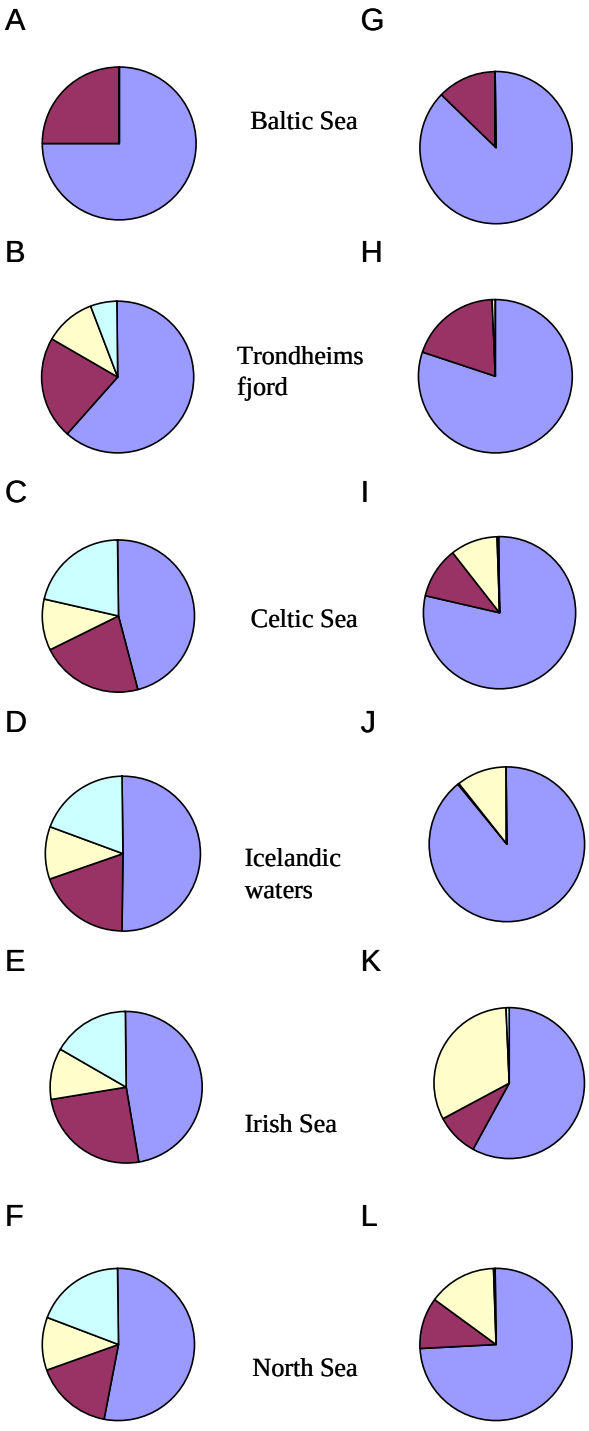

Figure 4.4. Relative richness (A-F) and abundance (G-L) structure of parasite faunas of *G. morhua* from the six NE Atlantic regions with respect to the geographical distribution of parasites. Arctic-Boreal; Boreal; Worldwide; NA, not aplicable.

Of the 11 parasite species present in all regions studied, nine had an Arctic-Boreal distribution (*L. elongatum, A. simplex, C. osculatum, H. aduncum, P. decipiens, C. gracilis, C. semerme* and *E. gadi*) and two species (*H. rigidum* and *C. strumosum*) had Boreal distributions. The relative abundance of the Boreal species was higher in the Trondheimfsjord fauna (19% of all individuals) than in the other regions (range 9-13% of all individuals) except for the parasite fauna of cod in Icelandic waters which showed a negligible proportion of this distribution category (0.1% of all individuals). The relative abundance of species with worldwide distribution was highest in the Irish Sea fauna (32% of all individuals). In contrast, Trondheimsfjord fauna had very few individuals with worldwide distribution (0.5% of all individuals) due to the presence of only two species of this group, *D. varicus* and *Clavella adunca* (Strøm, 1762).

4. 2. 5. Parasite fauna of farmed cod

Only 32 out of the 378 farmed cod harboured parasites (40 individuals). The fish studied belonged to the F1-generation of enclosed parental fish and their development was in captivity. Prevalence and mean abundance of the three helminth species recovered in the fish farms are summarized in Table 4.3. *H. aduncum, C. osculatum* and *E. gadi* were the only parasite species that have survived farm conditions, such as anthelmintic treatments. The mode of transmission of these parasites is *via* food ingestion since planktonic crustaceans (copepods, amphipods and mysids) act as intermediate hosts. Rosenthal (1967) and Karlsbakk *et al.* (2001) found that parasitic copepods (*Caligus* spp., *Clavella adunca, Holobomolochus confusus* and unidentified lernaeocerid) and some helminths (*Contracaecum* sp., *Scolex pleuronectis, Hemiurus* spp., *Derogenes varicus, Lecithaster* sp., H. *aduncum* and unidentified pseudophyllideans) are introduced to the farm tanks through the water circulation, the latter *via* their first or second intermediate hosts (copepods). Although the three species could be considered as more resistant and with high transmission levels, the frequency of infections and parasite abundance were very low (Table 4.3).

Table 4.3. Prevalence (P%) and mean abundance (MA ± SD) of parasites of *Gadus morhua* from two fish farms in Scotland and Iceland.

Locality (sample size) Parasite	Scotland land-based ponds (n = 182)		Iceland tanks (n = 196)	
	P (%)	MA ± SD	P (%)	MA ± SD
Contracaecum osculatum	0.5	0.01 ± 0.07	5.6	0.06 ± 0.26
Hysterothylacium aduncum	0.5	0.01 ± 0.07	3.1	0.05 ± 0.32
Echinorhynchus gadi	6.6	0.08 ± 0.35	0.5	0.01 ± 0.07

4.3. Discussion

The list of 57 species reported in the present study (Table 4.2) comprises nearly 56% of the parasites found in *G. morhua* throughout its distributional range (a total of 97 species, resulting from compilation of data gathered as early as 1932 from both NW and NE Atlantic, see Hemmingsen & MacKenzie, 2001) indicates a high regional richness of the metazoan parasites of cod in the NE Atlantic. This is supported by the seven new host records. Of these, only the gadoid specialist *D. merlangi*, which mainly parasitises whiting, *Merlangius merlangus* (L.) (Rubec & Dronen, 1994) belongs to the Arctic-Boreal distribution category. The newly recorded helminth species mainly belong to generalist genera with a wide geographical distribution. The copepod *Chondracanthus ornatus* is typical of calionomid perciforms (Kabata, 1979). The geographical distribution of the Callionymidae overlap with cod, thus its recovery indicates some interaction with calionomids. Furthermore, this study provides more detailed data on the distribution in the NE Atlantic of the majority of cod parasites. The results conform with the diverse and non-selective diet of cod, its wide depth distribution and migratory behaviour. It is also possible that increased sampling effort has contributed to the high diversity of the parasite list reported here.

However, the regional parasite faunas of cod exhibited a generally lower richness (63-65% of the total list) with a notable decrease in the Baltic Sea and Trondheimsfjord (21 and 32%, respectively). Parasites from all multicellular metazoan taxa were recorded in the present study, with eleven species present in all regions (the trematode *L. elongatum*; the nematodes *A. simplex*, *C. osculatum*, *H. aduncum*, *H. rigidum*, *P. decipiens*, *A. crassicollis* and *C. gracilis*; and the acanthocephalans *C. semerme*, *C. strumosum* and *E. gadi*). The predominant groups in the regional faunas in terms of number of species were trematodes and nematodes. However, the taxonomic structure of the fauna based on the relative abundance of the higher taxa revealed that nematodes (mostly anisakid larvae) represent the

majority of all parasite individuals. This fact can be related to cod being a voracious predator, and with a long life-span, which facilitates larval accumulation (due to the long life-span of anisakids as well).

The regional faunas exhibited differences with respect to both higher-level taxonomic structure and species-level comparisons. Generally, the fauna of the brackish-water regions [Baltic Sea (7-13.6‰) and Trondheimsfjord (10-33‰)] differed substantially from those in the open water regions (Celtic, Irish and North seas and Icelandic waters, range 34.2-35.4‰). The much lower species richness observed in the former two regions agrees with the lower salinity conditions that restrict the distribution and richness of the invertebrate fauna and consequently limiting the diversity of successful parasite life-cycles (Zander, 1998; Zander & Reimer, 2002). Remarkably, none of the species characteristic of low salinity and freshwater distributions reported previously in cod [*i.e. Podocotyle angulata*, *Raphidascaris acus*, *Acanthocephalus lucii*, *Echinorhynchus salmonis*, *Neoechinorhynchus rutiei* and *Pomporhynchus laevis* (Zander, 1998; Hemmingsen & MacKenzie, 2001; Pilecka-Rapacz & Sobecka, 2004)] was recorded in Baltic Sea and Trondheimsfjord.

On the other hand, although both regional faunas consisted of marine parasite species, their structure differed from that of the fauna in the open water regions in: (i) the poorer numerical representation of nematodes; (ii) the absence of cestodes; (iii) the absence or low abundance of species with worldwide distribution; and (iv) the composition with respect to host specificity categories [*i.e.* the strong numerical domination of generalists (Baltic Sea fauna) or gadoid specialist species (Trondheimsfjord fauna)]. These differences, therefore, indicate notably different transmission conditions in the two low-salinity regions. This suggestion is further reinforced by the notably different structure of the faunas in the latter regions characterised by the numerical dominance of generalist acanthocephalans (mostly *E. gadi*, Baltic Sea) or gadoid specialist trematodes (*Lepidapedon* spp., Trondheimsfjord).

The overall prevalence of 88.3% of *E. gadi* observed in the present study agrees well with the high levels of infection in cod recorded in previous studies: 71.4% in the southern Baltic Sea (Reimer & Walter, 1993) and 99.4% in the Bornholm Basin of Baltic Sea (Buchmann, 1995). The mean intensities recorded here are similar (32.2 worms/host) to those in the latter study: 54.7 in smaller cod (21 to 30 cm body length) and 33.3 in larger cod (52 to 60 cm body length). Gammarid (*Gammarus oceanicus*) and caprellid (*Monoporeia femorata*) amphipods serve as intermediate hosts of *E. gadi* in the Baltic Sea

(Valtonen *et al.*, 2001). Whereas the high infection levels in small cod may indicate that amphipods are an important component their diet, the heavy infection of large cod (> 61 cm; normally not feeding on amphipods) was explained by a transfer of parasites from prey fish to the large cod (Buchmann, 1995). It is possible that both processes contribute to the infection of cod in the Baltic Sea collection since the size ranged from 31.4 to 89.6 cm (SL).

The dominance of trematodes in the Trondheimsfjord fauna reflects the highest infection levels of two *Lepidapedon* species (see comparative data in Table 4.2). Both belong to the subfamily Lepocreadiinae of the Lepocreadiidae, which are found either in deep-sea fishes or in fishes from cold, shallow waters, most usually in Gadiformes (Bray & Gibson, 1995). Whereas the present data on the overall prevalence of *L. elongatum* (60%) agree with previous observations in cod [up to 94.3% at various stations in Danish and adjacent waters (Køie, 1984); up to 62% in juvenile (0+) cod (Polyansky & Shulman, 1956; Polyansky & Kulemina, 1963; Karasev, 1983; 1984)], *L. rachion* has so far been recovered at much lower prevalences in various locations in the NE Atlantic (range 3.3-20% *vs* 45%, see Køie, 1984). Bray & Gibson (1995) listed a wider range of final hosts (mostly gadoids) in the NE Atlantic for the latter species (*Gadus morhua, Melanogrammus aeglefinus, Merlangius merlangus, Pollachius pollachius, P. virens, Gymnacanthus tricuspis, Aspitrigla cuculus*). The Trondheimsfjord has a rich fish fauna (16 gadiform species including 10 species of gadoids: *Gadiculus argenteus thori*, *G. morhua*, *M. aeglefinus*, *M. merlangus*, *Micromesistius poutassou*, *P. pollachius*, *P. virens*, *Trisopterus esmarki*, *T. minutus*, *Raniceps raninus*; the latter uncommom, J.A. Sneli pers. comm.) and this may explain the higher infection levels of *L. rachion* in this region. It is also possible that the dominance of the two *Lepidapedon* species in the Trondheimsfjord cod parasite fauna is related to appropriate conditions for completing their life-cycles. The life-cycle of *L. elongatum* was elucidated by Køie (1985a). The rediae and cercariae develop in the gastropod *Onoba aculeus* and the metacercariae encyst in a variety of annelids; some may encyst in molluscs and echinoderms, but infections in these hosts are rare and probably short-lived (Køie, 1985a). The first intermediate host of *L. rachion* is believed to be *Nassarius reticulatus* and the metacercariae are said to occur in planktonic cnidarians, ctenophores, chaetognaths and polychaetes (Køie, 1985b). Sneli & Gulliksen, (2006) reported both intermediate hosts, *O. aculeus* and *N. reticulatus*, in Trondheimsfjord. However, the life-cycle of *L. rachion* has not apparently been completed experimentally. Bray & Gibson (1995) found the data on the second intermediate puzzling, since the main

final host of *L. rachion*, the haddock, *Melanogrammus aeglefinus* (L.), feeds as an adult almost entirely on benthic organisms. Nevertheless, cod studied at Trondheimsfjord were generally small-sized (SL range 16.5-48.0 cm) and it may be plausible to suggest that the proportion of small invertebrates in the diet of fish has contributed to the high representation of *Lepidapedon* spp.

Higher gadoid richness may also be associated with higher transmission rates which resulted in the dominance in the Trondheimsfjord fauna of the adult stages of two gadoid specialist nematodes, *C. cirratus* and *C. gracilis*. Final hosts of *C. cirratus* are Gadidae and Merluccidae, exceptionally salmon, *Salmo salar* (Moravec, 1994). Although Anderson (2000) suggests a direct infection of final host (by direct ingestion of free-living second-stage larvae, L2), calanoid (*Acartia* sp., *Centropages* sp., *Temora* sp.) and cyclopoid (*Oitona similis*) copepods and sand gobies, *Pomatoschistus minutus*, were found to serve as experimental intermediate hosts of *C. cirratus* (Køie; 2000; Marcogliese, 1994). Third-stage (L3) larva of *C. gracilis* hatch from the egg in the intestinal tract of either the intermediate fish host (sand goby, *P. minutus*; experimental data) or an invertebrate transport (paratenic) host (Køie, 2001a). Køie's (2000) data, based on examination of 350 naturally infected cod (8-78 cm long), support this suggestion. She found that group 1 and older cod contained L3-stage larvae, intermediate stages and adult worms of *C. cirratus*, indicating that they could become infected throughout the year; however the pattern of infection suggested that cod over 20 cm long became infected mainly in summer by eating infected fish (including smaller cod). It is possible that the high infection levels with *C. cirratus* and *C. gracilis* in cod from Trondheimsfjord are also due to ingestion of sand gobies which are common in the region.

One of the main results of the present study was the overall higher structural similarity of the parasite faunas in cod from Celtic, Irish and North seas and Icelandic waters, perhaps due to the similar oceanographic characteristics of these four regions. The domination of the generalist Arctic-Boreal anisakid nematodes (*A. simplex*, *C. osculatum* and *H. aduncum*) represented a characteristic feature of the four faunas.

A. simplex and *C. osculatum* utilise marine mammal predators of cod (Hemmingsen & MacKenzie, 2001) as final hosts and follow a similar life history pattern. Adult *A. simplex* has been reported in a large number of cetaceans (belonging to 18 genera) and pinnipeds (belonging to 10 genera) (Davey, 1971). Eggs passed by marine mammals embryonate to the L2-stage larvae in sea water. When ingested by marine crustaceans (e.g. euphasiids, copepods) they develop to the L3 stage. Teleosts become infected by ingesting

the first intermediate hosts (Anderson, 2000 and references therein). Klimpel *et al.* (2004), who studied the life-cycle of *A. simplex* in the northern North Sea, found that one copepod and four euphasiid species served as obligatory intermediate hosts. These authors revealed an obligatory second intermediate host, *Maurolicus muelleri* (Sternoptychidae), and stated that piscivorous (*Pollacius virens, Melanogrammus aeglefinus, Etmopterus spinax*) and planktivorous and juvenile fishes (*Clupea harengus, Trisopterus esmarki, Melanogrammus aeglefinus*) serve as paratenic hosts of *A. simplex*. *C. osculatum* is a parasite of seals. Although the data on the life-cycle of this species are somewhat wanting (see Anderson, 2000) copepods appear important as hosts that carry L2-stage to fish intermediate hosts where the development of the L3-stage occurs (Køie & Fagerholm, 1993; Anderson, 2000).

Klimpel *et al.* (2004) and Klöser *et al.* (1992) suggested that *A. simplex* and *C. osculatum*, respectively, are able to utilise fish host species that are available in a given locality. This versatile behaviour coupled with the vagility of the final hosts, may explain the wide distribution and abundance of these species. *H. aduncum* possesses an even more resourceful life-cycle. Final hosts of this species are numerous predaceous teleosteans (clupeids, gadids, salmonids and others, see Moravec, 1994). Third stage larvae develop in *Acartia tonsa* and other harpaticoid copepods, various amphipods, isopods and mysids (Køie, 1993b). The latter can also serve as second intermediate hosts (Klimpel *et al.*, 2003). Furthermore, ctenophores, chaetognaths, polychaetes and ophiuroids which become infected by ingesting infected crustaceans, may act as obligatory intermediate hosts or paratenic (transport) hosts (Margolis, 1971; Køie, 1993b).

Despite their overall structural similarity, the four faunas could be grouped in two pairs, those from Celtic Sea and Icelandic waters *vs* those from the Irish and North Seas. It appears that the grouping with respect to the higher trematode representation in cod parasite faunas in Irish and North Seas (*vs* Celtic Sea and Icelandic fauna) is related to the sampling locations. Thus, the fauna from deeper and ocean influenced locations in the Celtic Sea and Icelandic waters were dominated by nematodes whereas the more coastal and shallower locations (in the Irish and North Seas) exhibited higher proportions of trematode individuals.

Overall, generalist parasites with Arctic-Boreal or worldwide distribution comprised the best represented group of the cod parasite fauna with respect to both richness and numerical dominance (due to the presence of anisakid nematodes). This finding supports the conclusion of Hemmingsen & MacKenzie (2001) that cod acts as a distribution agent of generalist parasites in the North Atlantic because of its omnivorous diet, migratory

behaviour and the mixture of stocks (see also Nielsen *et al.*, 2003; Robichaud & Rose, 2004; ICES, 2005a).

To summarise, the higher-level faunal comparisons suggest that differences may exist in the feeding behaviour between cod sampled in the six regions. On the other hand, the composition of the local faunas may be determined largely by variations in the abundance of the intermediate hosts. These suggestions are supported by the high regional variation in the prevalence and abundance of the parasite species (Table 4.2) which translated into somewhat different clustering pattern based on similarity at the species level. Based on the above comparisons, the following predictions can be made:

(i) Parasite communities in cod from the Baltic Sea and Trondheimsfjord would show much lower richness, abundance, diversity and would exhibit higher variation in composition and structure.

(ii) Parasite communities in cod from the open water regions (Irish, Celtic and North seas and Icelandic waters) would have the highest richness, abundance, diversity and similarity and would be dominated by larval nematodes.

(iii) With 11 species (nearly a fifth of the total number) shared between the six regions there would be a substantial homogenisation in the composition of both the component and infracommunities. *A. simplex*, *H. aduncum* and *D. varicus* would contribute substantially to the structural homogeneity between communities.

5. Redescription of *Diclidophora merlangi* (Kuhn, in Nordmann, 1832) (Monogenea: Diclidophoridae), a new host record for *Gadus morhua*

5. 1. Introduction

During a comprehensive survey for parasites of over 1,250 Atlantic cod, *Gadus morhua* L., from the northeast Atlantic (see Chapter 3), only two monogeneans were collected. The specimens were ascribed to *Diclidophora merlangi* (Kuhn, in Nordmann, 1832) because of their clamp morphology and general body appearance. However, the body size of these worms was considerably smaller than that reported for *D. merlangi* (Rubec & Dronen, 1994).

All members of *Diclidophora* Krøyer, 1838 show very strict host specificity, and *D. merlangi* is specific to the whiting *Merlangius merlangus* (L.) (Sproston, 1946; Llewellyn, 1958). The morphological or reproductive changes of alternative hosts on monogeneans so far have been little considered, despite the possibility that their study might provide insights into mechanisms accounting for the maintenance of host specificity. The working hypothesis of the present study is that the small body size of *D. merlangi* on cod actually resulted from colonizing an unusual host. The aim of the present study is to characterize morphologically the two monogeneans from cod, provide evidence to validate or refute the working hypothesis by morphological comparison with *D. merlangi* occurring on whiting, and present quantitative data to document some potential reproductive consequences of the specimens found on cod.

5.2. Materials and methods

The gills of 1,254 Atlantic cod caught in eight Northeast Atlantic localities (North, Irish, Celtic, Norwegian and Baltic Seas, Icelandic waters and two farms from Scotland and Iceland) were surveyed for parasites. The two specimens of *Diclidophora* occurred on two cod from the North Sea and Celtic Sea caught in spring 2001 and 2002, respectively. They were collected from gills preserved frozen, and were fixed in 70 % ethanol, stained with iron acetocarmine (Georgiev *et al*., 1986) and mounted in Canada balsam. Morphological observations were carried out using a light microscope equipped with a drawing tube (Figures 5.1, 5.2). Linear measurements and areas were taken from digitized drawings using Image Tool 3.00 (developed at the University of Texas Health Science Center at San Antonio and available at http://ddsdx.uthscsa.edu/dig/itdesc.html). The anatomical terminology follows Llewellyn (1958), and Rubec & Dronen (1994).

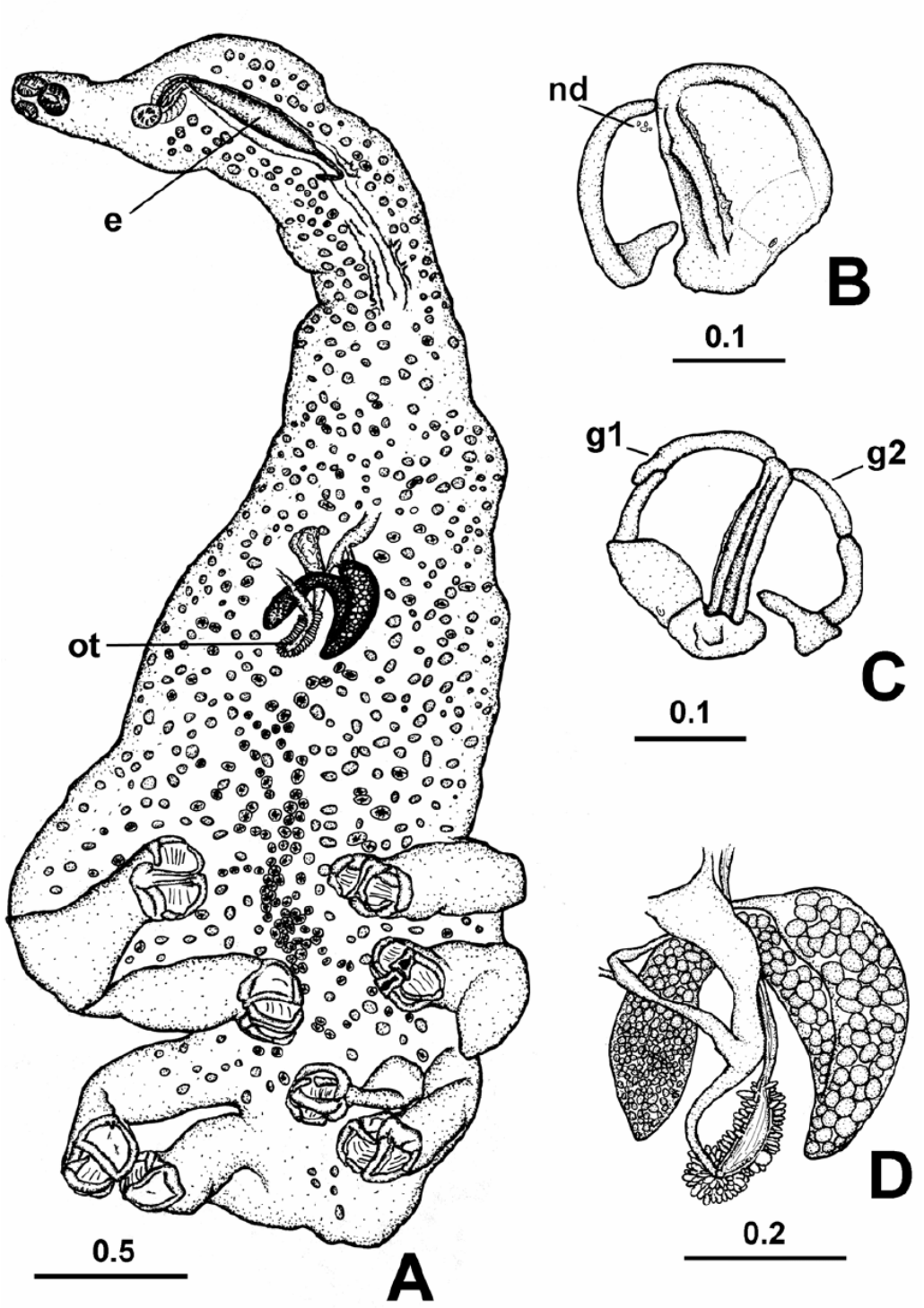

Figure 5.1. *Diclidophora merlangi* on cod, *Gadus morhua*. (A) Specimen *in toto*, ventral view. (B) Clamp, isolated anterior jaw, ventral view. (C) Clamp, isolated posterior jaw, dorsal view. (D) Region of germarium. Bars in millimeters. *Abbreviations*: Reproductive system: e. egg; ot. oötype. Clamp sclerites: anterior jaw: nd. nodules; posterior jaw: g1, g2.

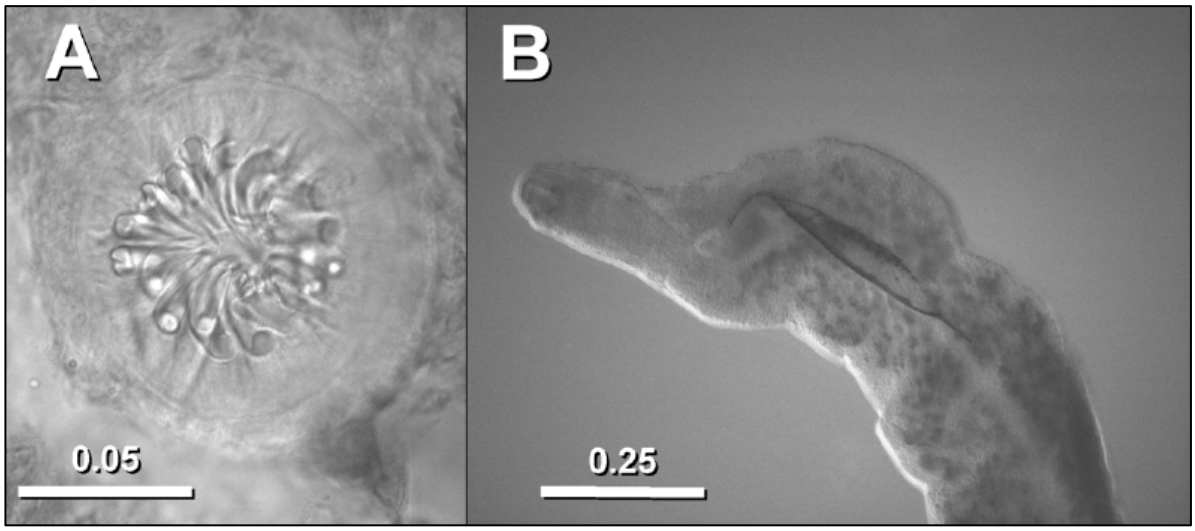

Figure 5.2. *Diclidophora merlangi* on cod, *Gadus morhua*. (A) Terminal male genitalia, consisting in muscular penis with crown of 17 hooks, ventral view. (B) Egg inside the uterus, ventral view. Bars in millimeters.

In order to assess similarity in body proportions between the two forms from cod and *D. merlangi* on whiting, 32 specimens from whiting were studied and measured. Mean testis area of *D. merlangi* on *M. merlangus* was calculated using the mean areas of ten randomly selected post-germarium testes for each specimen. Mean egg length was obtained using the mean lengths of all the eggs of each specimen (12 parasites had eggs, ranging from one to five eggs per specimen). In addition, specimens of other species of *Diclidophora* from the Northeast Atlantic were measured: two specimens of *Diclidophora denticulata* (Olsson, 1876), from pollock, *Pollachius virens* (Linnaeus, 1758); two specimens of *Diclidophora pollachi* (Van Beneden and Hesse, 1863), from pollack, *Pollachius pollachius* (Linnaeus, 1758); and two specimens of *Diclidophora luscae* (Van Beneden and Hesse, 1863) from pouting, *Trisopterus luscus* (Linnaeus, 1758). These additional forms were used as controls providing a scale of relative interspecific morphological similarity to facilitate comparison between the specimens of *D. merlangi* from cod and from whiting. All the specimens used for comparisons belong to the collection of the late Professor G. Rees, University of Wales in Aberystwyth, United Kingdom and had been stained in Malaquite green and Gower's carmine (no collection numbers available).

Size and shape information of all specimens was summarized and compared using Principal Component Analysis (PCA) of the variance-covariance matrix using eight key, non-linearly dependent, log-transformed morphometric variables (Labarbera,1989) (see Figure 5.3 and Table 5.1). The eight variables were selected because they were associated

with shape variability and were homologous among all species (Labarbera,1989). Since the primarily interest was determining whether the shape of *D. merlangi* on cod was more similar to that of *D. merlangi* on whiting than to that of other species of *Diclidophora*, particular attention to the PCA ordination resulting from discarding the first principal component (PC1) was paid, since it is assumed that it mostly represents variation in general size. However, since PC1 may also contain useful size-related shape information (Jungers *et al*., 1995), two additional methods based on Mossimann shape ratios that have proven to satisfactorily control for the effect of isometric size in PCA were also used (Jungers *et al*., 1995). The first technique consisted of substituting the original metric variables by the ratios formed by dividing each variable by the geometric mean of all variables, whereas the second corresponded to the log-transformed version of the first (Darroch and Mossimann, 1985).

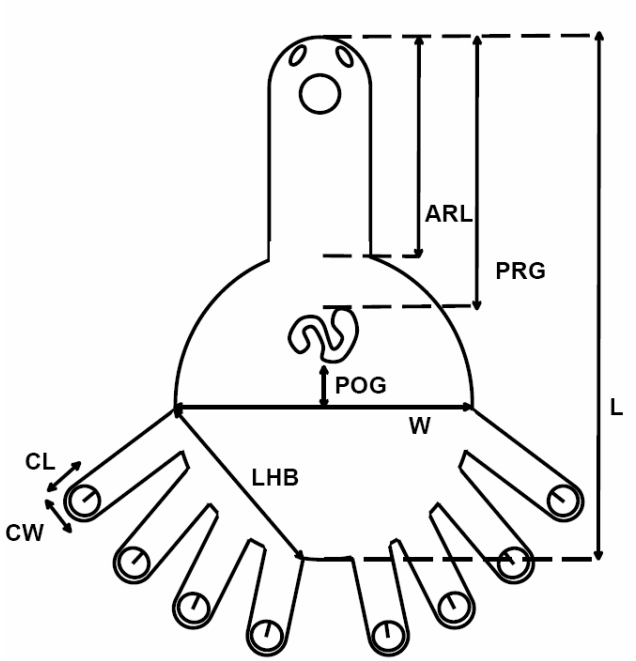

Figure 5.3. Schematic drawing of the metric variables used for principal component analyses: L, body length; W, body width at origin of haptor; ARL, anterior region length; CL, first left clamp length; CW, first left clamp width; LHB, mean lateral haptor "basis" length; POG, post-germarium length; PRG, pre-germarium length.

Table 5.1. Comparative data of *Diclidophora merlangi* on *Gadus morhua*, *Diclidophora merlangi* on *Merlangius merlangus*, *Diclidophora denticulata, Diclidophora luscae* and *Diclidophora pollachi*. Abbreviatons of measures employed in the PCA are shown in parentheses. Mean values, SD and ranges are indicated when more than 2 specimens were measured. All measurements are in millimeters except where otherwise stated. N denotes the number of specimens examined.

	Diclidophora merlangi			*Diclidophora denticulata*	*Diclidophora luscae*	*Diclidophora pollachi*
Host	*Gadus morhua* from North Sea	*Gadus morhua* from Celtic Sea	*Merlangius merlangus*	*Pollachius virens*	*Trisopterus luscus*	*Pollachius pollachius*
N	1	1	32	2	2	2
Body length (L)	2.24	3.30	9.07±1.98 (4.25-13.10)	5.9-9.22	5.44-5.51	11.64-14.04
Body maximum width (W)	1.18	1.06	3.69±0.77 (2.12-5.43)	1.49-2.03	2.31-2.4	3.09-3.35
Anterior region length (ARL)	0.96	1.58	3.61±0.98 (1.37-5.25)	1.05-1.29	0.61-0.73	1.06-1.55
Clamp width (CW)	0.14	0.17	0.28±0.40 (0.18-0.36)	0.40-0.56	0.19-0.23	0.33-0.38
First left clamp length (CL)	0.17	0.22	0.35±0.05 (0.22-0.43)	0.54-0.75	0.24-0.25	0.32-0.40
Mean lateral haptor basis length (LHB)	0.85	1.15	2.68±0.63 (1.35-4.10)	1.40-1.79	2.11-2.57	3.10-3.37
Post-germarium length (POG)	0.22	0.64	1.34±0.39 (0.58-2.23)	2.39-3.62	1.09-1.54	3.89-4.66
Pre-germarium length (PRG)	1.16	1.89	4.93±1.20 (2.68-7.37)	2.8-4.47	3.23-3.73	6.03-8.79
Pharynx length	0.15	0.08	0.27±0.04 (0.15-0.39)	0.17-0.24	0.10-0.12	0.31-0.32
Penis diameter	0.077	0.069	0.12±0.02 (0.08-0.15)	0.11-0.12	0.084	0.13-0.14
No. penis hooks	17	17	17±2 (13-20)	15-18	10-12	11-15
No. testes	223	256	201±31 (167-290)	-	-	-
Testis area (μm^2)	826	908	6,704±3,124 (1,777-14,130)	-	-	-
Germarium length	0.53	0.78	1.96±0.43 (1.00-2.83)	0.95-1.84	1.24-1.31	1.44-1.46
Oötype length	0.17	0.19	0.54±0.13 (0.36-0.76)	-	-	-
Oöcyte area (μm^2)	258	346	1,289±400 (733-2,557)	-	-	-
Egg length	-	0.44	0.42±0.06 (0.34-0.55)	0.43	0.29	0.61-0.66

In order to gain insight into the effect on reproduction of development in a potentially unsuitable host, the size of both the parenchyma cells and oöcytes of the specimens from cod was compared to that of the 32 specimens from whiting (spermatozoa were too small to be measured at light microscopy). Measurements of parenchyma cells provided information about the possible effect of freezing, fixing and staining on the size of all the parasite cells of the forms from cod. In each specimen, the areas of ten oöcytes from the distal part of the germarium and ten parenchyma cells from the clamp peduncles and anterior part of the body were measured. Differences in cell areas between specimens were evaluated by a Mann-Whitney U test (Conover, 1999).

5.3. Description

Diclidophora merlangi (Kuhn, in Nordmann, 1832) Krøyer, 1838

(Figures 5.1, 5.2; Table 5.1).

General diagnosis: General morphology as *D. merlangi* from *M. merlangus*, described by Cerfontaine (1896) with corrections and comments by Rubec & Dronen (1994). Meristic and metric data in Table 5.1. Special traits: Body size smaller than in published descriptions and whiting vouchers from University of Wales. Typical clamp sclerites of *D. merlangi*. Four nodules could be distinguished in the anterior jaw of two clamps from the Celtic Sea specimen (Figure 5.1B). Testes pre-, para- and post-germarium, size smaller than in whiting vouchers. Copulatory organ consisting of muscular penis with crown of 17 very closed grooved and recurved hooks (Figure 5.2A). Oöcytes in germarium relatively smaller than those of voucher specimens from whiting (Figure5.1D). Egg fusiform with two long polar appendages (type I of Kearn, 1986), similar in size and proportions to those of whiting vouchers (Table 5.1 and Figures 5.1A, 5.2B).

5.3.1. Taxonomic summary

Host: Atlantic cod, *Gadus morhua* L. (2 specimens; weight: 472 and 1,400 g; standard length: 34.6 and 45.5 cm).

Localities: North Sea (51º 40.0’ N - 7º 24.5’ W); Celtic Sea (55° 56.9’ N - 01° 08.5’ W)

Infection site: Gills.

Infection parameters: North Sea, intensity = 1, prevalence = 0.67 % (Number of hosts examined, *N* = 149); Celtic Sea, intensity = 1, prevalence = 0.72 % (*N* = 139).

Specimens deposited: 2 vouchers deposited at The Natural History Museum, London, United Kingdom (Reg. No. 2006.2.3.1-2).

5.3.2. Remarks

The morphological traits of the forms from cod conform to those of *D. merlangi* from whiting: the sclerites of dorsal clamp (g1 and g2) are asymmetrical in length (Figure 5.1C); a few small nodules are present in the anterior jaw of the clamps; the uterine bag is absent; the testes are placed pre-, para- and post-germarium; and the egg is type I (2, non-hooked appendages) (Rubec & Dronen, 1994). The main difference between *D. merlangi* from whiting and the 2 specimens from cod concern the substantially smaller body size of the latter (Table 5.1). However, the size does not seem a reliable trait to characterize the species of *Diclidophora*, especially when they are in an alternative host, because, even in the usual host, some individuals can be substantially smaller than the average (Sproston, 1946; Llewellyn & Tully, 1969).

In addition, according to the PCA results the size of the measured structures of the specimens of cod and whiting seemed to be equally proportional relative to their overall body size (Table 5.1). The first PCA indicated that metric differences between the specimens found on cod and those of *D. merlangi* from whiting were mainly associated to PC1 (supposedly associated with body size), whereas variation along PC2 indicated greater similarity between the specimens from cod and those of *D. merlangi* than the other congeneric species (Figure 5.4A). This pattern of higher morphological closeness between the specimens from cod and those of *D. merlangi* is fully supported by the two size-adjusted PCA methods (Figure 5.4B, C).

The testes and germaria were noticeably smaller in the monogeneans from cod. Nevertheless, the number of testes of *D. merlangi* from cod is within the range of those of *D. merlangi* in whiting (Table 5.1) and spermatozoa were observed in the sperm duct. In contrast, the oöcyte areas from the cod parasites were also about three times smaller from those of whiting (Table 5.1). This size difference is significant ($U < 0.0001$, $n = 32$, $p = 0.004$), whereas that of parenchyma cells between the forms from cod and whiting is not ($U = 7$, $n = 34$, $p = 0.07$, and $U = 29$, $n = 34$, $p = 0.86$, for cells from anterior part of the body and from the clamp peduncles respectively). Thus, the different size of the oöcyte cells cannot be attributed to a general smaller cell size of the smaller parasites from cod. The oöcytes seemed degenerated in the cod monogeneans since their cytoplasms appeared translucent under light microscopy. In addition, the oöcyte nuclei of the Celtic Sea

specimen were not visible, whereas those of the North Sea specimen were noticeably smaller than those of the forms from whiting.

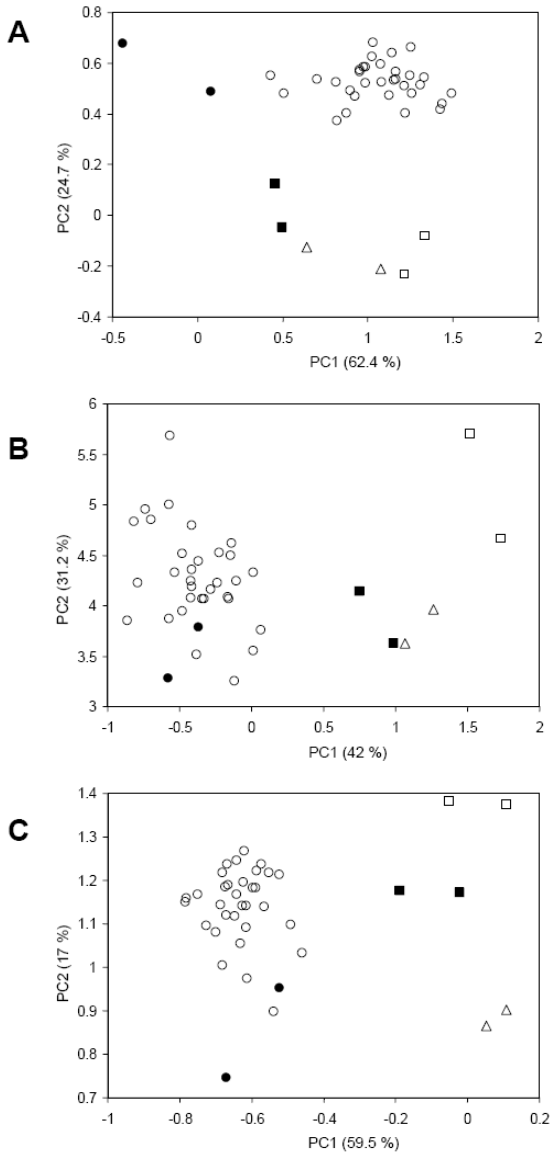

Figure 5.4. Scatterplots of principal component analyses (PCA) on the first 2 principal components (PC1 and PC2) based on morphometric measurements of specimens of *Diclidophora* from the North Atlantic: *Diclidophora denticulata* (Δ); *Diclidophora luscae* (■); *Diclidophora merlangi* on cod, *Gadus morhua* (●); *Diclidophora merlangi* on whiting, *Merlangius merlangus* (○); *Diclidophora pollachi* (□). Percentage of variance explained by PC1 and PC2 in parentheses. (A) PCA with log-transformed variables. (B) Size adjusted PCA based on ratios of each original variable to the geometric mean of all variables. **C.** Size adjusted PCA based on ratios of each log-transformed variable to the geometric mean of all log-transformed variables.

5.4. Discussion

To date *Diclidophora morrhuae* (Van Beneden and Hesse, 1864) has been the only species of the genus known on cod (Hemmingsen & MacKenzie, 2001). Since the original description (and despite the high number of studies of the helminth fauna of Atlantic cod carried out since then) only 2 additional records of *D. morrhuae* are known (Sproston 1946). Moreover, Van Beneden & Hesse (1864) maintained that these forms actually could correspond to *Diclidophora palmata* (Leuckart, 1830), whose usual host is the ling, *Molva*

molva (Linnaeus, 1758), and consequently *D. morrhuae* is invalid. Later reviews of *Diclidophora* have followed this view (Llewellyn, 1958; Llewellyn & Tully, 1969; Mamaev, 1976; Hemmingsen & MacKenzie, 2001).

The morphology of the two specimens studied do not conform to the original description of *D. morrhuae* (Van Beneden & Hesse, 1864) (although no type material exists), revealing that they represent a different species, and thus a new host record. Apparently, it is not the first time that *D. merlangi* have been observed in an unusual host, since Llewellyn (1958) proposed that specimens of *Diclidophora gadi* (Reichenbach-Klinke, 1951) (currently considered invalid [Mamaev, 1976]) on haddock *Melanogrammus aeglefinus* (Linnaeus, 1758) actually represented misshapen specimens of *D. merlangi*.

The extremely low prevalence and abundance of the species of *Diclidophora* so far reported on cod, a fish widely and intensely surveyed for parasites in the last 150 years, is strong evidence for all reported infestations being accidental and caused by species specific to other gadids. Accordingly, in the context of close host-parasite coevolution between species of *Diclidophora* and gadiforms envisaged by Llewellyn & Tully (1969), no extant species would have evolved with Atlantic cod.

This study provides some interesting and new observations on the reproductive consequences of *D. merlangi* colonizing cod. Although it cannot be ruled out that the specimens on cod represent young individuals, thereby their small body size, they were even smaller than the youngest or smallest individuals reported herein or in other studies. Thus the specimens in cod are likely dwarf specimens of *D. merlangi*. Although no negative impact on spermatogenesis could be documented and the number and aspect of the testes were apparently normal, it can be argued that the smaller size of the male and female organs should result in lower fertility. In addition, the previous observations indicated that the female reproductive potential was impaired, because although the oöcytes could mature along the germarium from the distal to the proximal region, they ultimately reached much smaller sizes than those of *D. merlangi* on whiting. This evidence, together with the spoiled aspect of the oöcytes, suggests that *D. merlangi* on cod cannot produce viable ova. Although it can be argued that the degenerate aspect of the oöcytes might have resulted from freezing, all other cells in these specimens looked normal. In addition, in the course of an ongoing study, it had been verified that oöcytes of previously frozen specimens of *Diclidophora* have also normal appearance (personal observation). Paradoxically, one specimen on cod did develop an egg-shell with a normal size and appendages with a normal shape. It would not be the first record of egg formation in species of *Diclidophora* under

unusual conditions, since Llewellyn (1958) observed that egg capsule formation occurred in senescent individuals, although it often resulted in abnormal shapes. Since the normal sized egg of the specimen on cod was formed in an oötype that was about three times smaller than normal, this finding does not support the notion that the egg capsule is exclusively assembled in the oötype, and thus egg size of monogeneans reflects oötype size (Kearn, 1986). Although the oötype is somewhat expansible when eggs are formed, this observation rather sustains that the uterus also participates in the assembly of the egg capsule and that egg shape and size is genetically fixed.

The specimens of *D. merlangi* from this study were found in two cod from distant geographic localities but the effects of these two apparently accidental colonizations were similar: dwarfism and probably female infertility. Cod is generally larger than whiting, but the two specimens infected with *D. merlangi* had standard lengths within the usual range of whiting in the northeast Atlantic (Svetovidov, 1986). Perhaps the presumably smaller size of the gill lamellae of these cod made parasite attachment possible, but the conditions provided by these unusual host prevented full development. Detailed studies relating the morphology of attachment organs with gill morphology within the gadiforms have provided valuable data on the mechanical processes accounting for the high host specificity of species of *Diclidophora* (Llewellyn, 1956; Llewellyn & Tully, 1969; Llewellyn *et al*., 1980; Rubec & Dronen, 1994) and deserve further attention. Future studies studying *in vivo* morphological and physiological changes during the development of monogeneans attached on unusual hosts, especially with phylogenetically close host species, are needed.

6. Composition and structure of parasite communities in *G. morhua* in the NE Atlantic

6. 1. Introduction

To date ecological studies on cod parasites have focused on parasite populations of individual parasites. Some authors have analyzed rigorously the seasonal variations of species prevalence and abundance in order to reveal an infection pattern related to abiotic factors (*i.e*. water temperature) or biotic influence (*i.e.* effect of predation on the host population). Parasite species studied include: the monogenean *Gyrodactylus callariatis* (Appleby, 1996), the copepods *Lernaeocera branchialis* and *Clavella adunca* (Linderby & Thulin, 1983), the acanthocephalan *Echinorhynchus gadi* (Linton, 1933; Möller, 1975; Hemmingsen *et al.*, 1995), the trematodes *Hemiurus communis* (Meskal, 1967; Möller, 1975), *Derogenes varicus* (Meskal, 1967) and *Podocotyle atomon* (Möller, 1975); and the anisakid nematodes *Hysterothylacium aduncum* (Andersen, 1993) and *Anisakis simplex* (Hemmingsen *et al.*, 1995).

Additional work has documented the variation over long periods of time in the levels of parasite infection with anisakid nematodes and acanthocephalans related to population dynamics of cod, their predators and prey. Chandra & Khan (1988) associated the substantial increase in abundance of larval *Pseudoterranova decipiens* and *A. simplex* in cod off eastern Canada, as compared to the data by Templeman *et al.* (1957) with increases in the populations of the definitive host, seals, in the area. Long-term comparison studies on the abundance of larval *P. decipiens* in cod in the NW Atlantic were also reported by Boily & Marcogliese (1995), Brattey *et al.* (1990); McClelland *et al.* (1990) and Hauksson (1989). A substantial increase of the abundance of the larval anisakids *P. decipiens* and *A. simplex* in cod from Scottish waters (as compared to levels observed in 1958) was reported by Rae (1972) and Wootten & Waddell (1977). However, des Clers (1991) analysed these data and found no significant variation in infection levels in 1964-1970.

Myjak *et al.* (1994) found that infections of cod in the southern Baltic Sea with *Contaraecum osculatum* and *Hysterothylacium aduncum* were much lower during 1987-1993 compared to those in the 1960s due to the decrease in the number of seals in the area. Reimer (1995) related the increased levels of infection of cod with *Hysterothylacium aduncum* to the increase of fish prey in the diet of cod due to the decline in crustacean populations. Reimer (1995) and Rokicki (1995) noted a decrease in both prevalence and intensity, of the acanthocephalan *Echinorhynchus gadi* in Baltic cod over periods of 40 and 20 years, respectively, and suggested that salinity and pollution levels and changes in abundance of crustacean intermediate hosts are responsible. The absence of juveniles of

Corynosoma semerme and *C. strumosum* from cod in the southern Baltic Sea was attributed to the decreased number of seals in the area (Rokicki , 1995).

Parasites live as populations that are divided into metapopulations because they are found in spatially discontinuous habitats: the hosts. This is reflected in the theoretical framework for hierarchical organization of parasite populations and communities developed two decades ago (Holmes & Price, 1986; Esch *et al.*, 1990; Guégan *et al.*, 2005). The lowest level of the hierarchy represents the infrapopulation (*i.e*. all members of a given parasite species within a single host individual) and the infracommunity which includes all of the infrapopulations within an individual host. The next hierarchical level includes the metapopulation and the component community (*i.e*. all of the infracommunities within a given host population). The highest level of parasite community organisation is the suprapopulation which includes all individuals of a species (including free-living stages) within an ecosystem. The compound community (or supracommunity), the most encompassing level, includes all suprapopulations of all parasite communities within an ecosystem (Esch *et al.*,1990; Bush *et al.*, 1997). The composition and structure of local parasite faunas and compound communities is dependent on historical and zoogeographic factors and environmental filters acting on parasite dispersal (Holmes, 1990: Esch *et al.* 1990; Guégan et al, 2005). The knowledge of the patterns and processes underlying the structure of parasite communities in marine fish has increased considerably during the last decade (Guégan *et al.*, 1992; Sousa, 1994; Poulin, 1995; Rohde *et al.*, 1995; Poulin, 1996; 2001).

However, studies focusing on parasite communities in marine fish in the NE Atlantic, and in Atlantic cod in particular, are still lacking. This chapter aims to fill this gap by providing a detailed description of the composition and structure of parasite communities in cod from the six NE Atlantic regions studied. This allowed an evaluation of the variability and regional characteristics at two hierarchical levels of community organisation, *i.e.* infracommunities and component communities, to be attempted.

A detailed study on parasite community structure was carried out to test the hypothesis whether faunal structural differences/similarities are also apparent at finer levels of community organisation in NE Atlantic cod, and the three predictions resulting from the faunal comparisons:

(i) Parasite communities in cod from the Baltic Sea and Trondheimsfjord would show much lower richness, abundance, diversity and would exhibit higher variation in composition and structure.

(ii) Parasite communities in cod from the open water regions (Irish, Celtic and North seas and Icelandic waters) would have the highest richness, abundance, diversity and similarity and would be dominated by larval nematodes.

(iii) With 11 species (nearly a fifth of the total number) shared between the six regions there would be a substantial homogenisation in the composition of both the component and infracommunities. *A. simplex*, *H. aduncum* and *D. varicus* would contribute substantially to the structural homogeneity between communities.In particular the

6.2. Materials and methods

6. 2. 1. Host samples

6. 2. 1. 1. Baltic Sea

The Baltic Sea cod, corresponding to the South East Baltic stock (Nielsen *et al.*, 2001; ICES, 2005a), was sampled in two neighbouring areas, Hanö Bight and Öland Island. Fish from the FSS (25-28 February 2002) and from the SSS (4-6 March 2003) were caught in Hanö Bight which is situated to the south-east of the southern Swedish coast and north of Bornholm Island (FSS: 56º12'-55º36' N and 17º56'-14º24'E; SSS: 55º27'-55º53'N and 14º21'-15º34'E) (Figure 6.1A). Fish from the AS (18-20 November 2002) were sampled west of the southern Swedish coast off Öland Island (57º28'-56º33'N and 17º57' 16º54'E). The hydrographical conditions at the Hanö Bight and Öland Island are similar. There is a permanent stratification into an upper low-salinity layer (approximately 7‰) and a deeper saline layer (approximately 12-16 ‰).

Tagging experiments have shown that most of the cod in this area perform seasonal migrations to spawn South-East of Bornholm Island (Aro, 1989; Robichaud & Rose, 2004). Cod that migrate to spawn to the Bornholm Basin come mainly from the feeding grounds in the Hanö Bight (Netzel, 1974). During the feeding period adult cod spread over large areas and may move long distances. In the eastern Baltic, the feeding migration after spawning is in general from deeper waters towards more shallow areas (Aro, 1989; Robichaud & Rose, 2004). However, the homing behaviour is variable and the fish may use different spawning areas in successive years (Aro, 1989).

6. 2. 1. 2. Celtic Sea

Cod from the Celtic Sea were sampled south of Ireland (ICES division VIIg) and belong to the Celtic Sea cod stock that spawns from February to April (on average March). Twenty-three fish comprising the FSS (18-21 and 26 March 2002) were collected at 50º56'-51º43'N

and 7º25'-8º1'W. Fifty-six fish of the AS (19-20 and 23-24 October 2002) and 59 fish of the SSS (18-20 March 2003) were caught in the neighbouring areas (51º30'-51º20'N and 7º36'-7º50'W, and 51º30'-51º54'N and 7º4'-7º25'W, respectively) (Figure 6.1B). The maximum depth in the sampling locations was 100 m. The hydrographical conditions of this area are characterized by the mixture of Atlantic waters and the coastal waters of the Bristol Channel and the Irish Sea. Moreover, Celtic Sea waters are influenced by the water circulation of the North Atlantic Drift and the Frontal systems of the Celtic Sea and Atlantic Seaboard (OSPAR, 2000). The lateness of spawning compared with other stocks may be due to the later occurrence of the production cycle in the area, due to strong tidal mixing (Brander, 1994), and is not influenced primarily by temperature (see also Chapter 3).

6. 2. 1. 3. Icelandic waters

Cod from Icelandic waters were caught in two neighbour areas that correspond to spring (spawning) and autumn (feeding) grounds. The fish belonged to the same spawning population (Pampoulie *et al.* 2006). Forty-five fish comprising the FSS (15-16 April 2002) and 58 fish of the SSS (4-5 April) were caught on the southwest coast (64º16'-64º24'N and 22º27'-22º45'W, and 63º36'-64º15'N and 21º44'-22º15'W, respectively). The AS (3-9 October 2002) included 62 fish caught in an offshore area (66º22'-63º56'N and 22º52'-26º31'W) west of Iceland (Figure 6.1C). The depth in the sampling areas ranged from 100m in the coastal spawning areas, to near 1000 m in the feeding grounds. Despite the existence of two distinct spawning populations of the Icelandic cod stock (*i.e.* NE and SW populations) there is migration in both directions and more genetic differences were found in fish from this location at different depths than at different locations (Pampoulie *et al.*, 2006). Jónsson (1996) observed that both mature and immature Icelandic tagged cod have only been caught in the Icelandic shelf area.

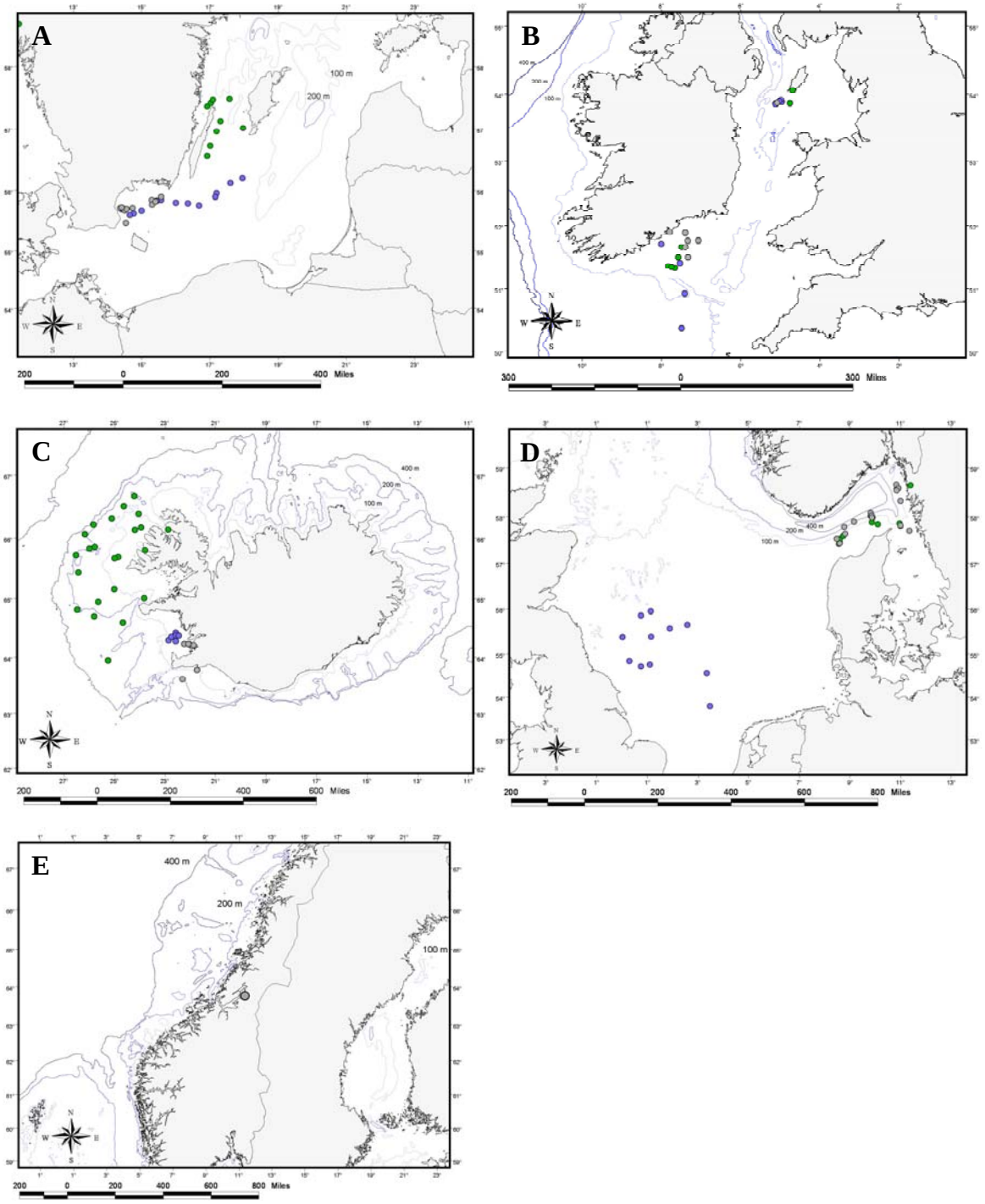

Figure 6.1. Sampling locations on Baltic Sea (A), Celtic and Irish Seas(B), Icelandic waters (C), North Sea (D), and Trondheimsfjord (Norway) (E). FSS, blue; AS,green; SSS, grey.

6. 2. 1. 4. Irish Sea

Irish Sea cod were sampled southward to the Isle of Man (ICES Division VIIa). Sixty fish comprising the FSS (March 2002), 52 fish of the AS (22 and 27 August and 23 September 2002) and 24 fish of the SSS (31 March 2003) were caught in a neighbouring area (53º51'-53º55'N and 04º57'-05º08'W, and 53º52'-54º03'N and 04º42'-04º46'W, and 53º52' N 05º05'W, respectively) (Figure 6.1B). The bathymetry of the sampled area changes in a short step decreasing from 50 to 100 m depth (Sager & Sammler, 1975) and the water column can become stratified. Cod spawning in this area are restricted to the coastal region correlated with the earlier food production. After spawning cod move southwards (ICES, 2005a; see Chapter 3 for details).

6. 2. 1. 5. North Sea

Cod from the North Sea were sampled at two different locations (Dogger Bank and Skagerrak). According to ICES, the fish belong to the North Sea and Skagerrak cod stocks that spawn from January to April (on average February-March). Twenty-seven fish comprising the FSS (8-13 February 2002) were caught at Dogger Bank (Central North Sea), between the Jutland Peninsula and NE England (54º42'-55º57'N and 00º44'-01º08'E). Sixty fish of the AS (2-5 September 2002) and of the SSS (27-30 January 2003) each, were caught at locations close to the Danish side of Skagerrak (57º42'-58º39'N and 08º33'-11º23'E, and 57º41'-58º39'N, 08º48'-11º20'E, respectively) (Figure 6.1D). As described in Chapter 3 the hydrographical conditions of the two sampling locations are very dissimilar.

6. 2. 1. 6. Trondheimsfjord (Norway)

Cod from Trondheimsfjord were caught on one single occasion in the second spring of sampling (5-6 April 2003) inshore of the fjord (63º45'N, 11º22'E). Sixty fish comprised the SSS. These cod belong to the Norwegian Coastal stock, some of which leave the fjord for the outer coastal waters during the feeding season, but the majority return for spawning in March and April (Pedersen, 1984; Godø, 1986; Jakobsen, 1987) (Figure 1E).

6.2.2. Parasite community analyses

Ecological terms follow Bush *et al.* (1997). Species with a prevalence > 10% in any of the samples will further be referred to as common, those with a prevalence ≤10% as rare, and those with prevalence < 3%, as accidental. Species with prevalence ≥ 50% are considered most prevalent. Infection parameters of larva L3 and adult (plus larva L4) of *H. aduncum* are presented and treated separately in relation to the different role of cod in the parasite life-cycle. Analysis of community structure was carried out at both component and infracommunity levels. The measures of component community richness and diversity adopted were the total number of parasite species (species richness); Berger-Parker dominance index; and Shannon-Wiener's diversity index. Infracommunity structure was also assessed by the distributions of species richness, abundance, Berger-Parker index and Brillouin's diversity index. All diversity/dominance indices are defined and calculated as in Krebs (1999) using natural logarithms ($\log_e$) in calculating the formers. The similarity index of Bray-Curtis (Legendre & Legendre, 1998) [following ln (x+1) transformation of abundance data] was calculated at both infra- and component community levels.

The frequency distributions of infracommunity species richness were tested for goodness of fit to the Poisson distribution (Kolmogorov-Smirnov procedure; assumption of the null model is a random distribution) and the null model of Janovy *et al.* (1995) (i.e. χ^2 test; assumption of the null model is that in the absence of associations and interactions between species, the frequency distribution of infracommunity species richness is predicted by prevalence values of all the species comprising the component community).

Due to the overall aggregated distribution of parasites, Spearman rank correlations (r_s) and non-parametric tests (Mann–Whitney and Kruskall–Wallis) were applied for statistical comparisons. Where parametric tests were used, parasite abundance data were ln (x+1) transformed. Prevalences were compared with Fisher's exact test. Intraspecific comparisons of abundance distributions were carried out only for species with prevalence > 30%. Analyses were carried out using SPSS 13.0 (SPSS Inc., 2004) and the programme Quantitative Parasitology 3.0 (Rózsa *et al.*, 2000).

Community composition analyses were carried out with PRIMER v6 software (Clarke & Gorley, 2006) which provides multivariate procedures for analyzing species/samples abundance matrices. Species datasets were analysed using communities in individual fish as replicate samples. First, the ANOSIM procedure which performs randomization tests on similarity matrices was used to test the null hypothesis of no differences in parasite community structure between samples (1-way layout). The

ANOSIM procedure calculates the R-statistic which indicates the magnitude of the difference among/between samples and a significance level that corresponds to the alpha level (probability of Type I error) in traditional ANOVA. The R-statistic ranges from 0 to 1; R>0.75 indicates a substantial difference in overall community structure (i.e. strong separation), whereas values for R<0.25 indicate little separation; intermediate R values reflect varying degrees of overlap but generally different community structure. Following the ANOSIM test for among/between sample differences, the SIMPER procedure was used to identify 'key discriminating' species on the basis of the overall percent contribution of each species to the average dissimilarity between samples.

6.3. Results

6.3.1. Parasite communities in cod in the Baltic Sea

A total of 180 fish was examined. The structure of the three samples by host sex and age is summarized in Table 6.1. The cod were predominantly adults (age class ≥3) and younger individuals (age class 2) were only collected in the AS. However fish of the three samples overlapped in size (Figure 6.2; see Table 6.4 for ranges). Females were more numerous and also bigger and heavier than males (p<0.05) in all samples.

Table 6.1. Structure of cod population sample from Baltic Sea by age and sex of host. For age determination, it was assumed that cod were born in January. NA, age not determined.

Age class (yrs)		2		3		4		5		6		7		8		NA		Totals by sex		Totals
Year	Season	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
2002	FSS			8	9	9	14	6	9		3						1	23	36	59
2002	AS	9	8	13	19	3	2		1	1		1					4	27	34	61
2003	SSS			5	3	10	20	3	9	3	2	1	2		1	1		23	37	60
Totals		9	8	26	31	22	36	9	19	4	5	2	2		1	1	5	73	107	180

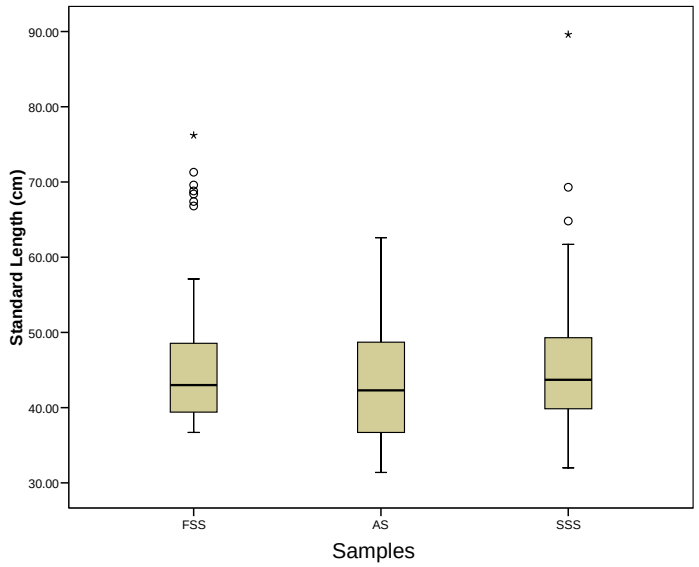

Figure 6.2. Box-plots for standard length of *G. morhua* in the three samples from Baltic Sea. *Abbreviations*: Samples: FS, first spring sample; AS, autumn sample; SSS, second spring sample.

6.3.1.1. Community composition

Species composition, prevalence and mean abundance of each parasite species in the three samples (FSS and SSS from Hanö Bight and AS from Öland Island) are summarized in Table 6.2. Nine species were identified as common. Four species were most prevalent: the acanthocephalan *E. gadi* (all samples) and three nematodes, *C. osculatum*, *H. aduncum* (L3) and *H. rigidum* (Table 6.3). Their abundance differed significantly between samples ($p<0.001$ in all cases). Pairwise comparisons revealed significant differences in the abundance of the four species ($p<0.05$) and the prevalence of *H. aduncum* (L3) and *H. rigidum* ($p<0.001$) between the two spring samples. The comparisons between the autumn (AS) and spring samples showed significant differences in the abundance in all cases ($p<0.05$) except for *H. rigidum* in AS *vs* SSS comparison. The prevalences of the four species were also significantly different in the autumn-spring comparisons ($p<0.05$ in all cases) with the exception of *H. rigidum* in AS *vs* SSS comparison.

Four species (*A. simplex*, *C. gracilis*, *C. semerme* and *C. strumosum*) found with prevalence > 10% in one sample were rare or absent in the other samples (Table 6.2). The prevalences of *A. simplex* and *C. strumosum* differed significantly between samples ($p<0.001$ and $p=0.002$, respectively), the former being more prevalent in the SSS and the latter in the AS. Five other species were rare or absent in some samples (*P. decipiens*, *A. crassicollis*, *L. elongatum* and *H. communis*), the latter accidentally present in SSS.

Table 6.2. Prevalence (P%), mean (MA ± SD) and median (M, shown if >0 only) abundance of parasites in the three samples of *G. morhua* from Baltic Sea (n=sample size).

Parasite species/Sample	Spring 2002 (n=59)	Autumn 2002 (n=61)	Spring 2003 (n=60)
	P (%) MA ± SD (M)	P (%) MA ± SD (M)	P (%) MA ± SD (M)
TREMATODA (adult forms)			
Hemiurus communis			1.7 0.02 ± 0.13
Lepidapedon elongatum	3.4 0.53 ± 2.95		3.3 0.03 ± 0.18
NEMATODA (larval forms)			
Anisakis simplex s.l. (L3)	1.7 0.02 ± 0.13	6.6 0.07 ± 0.25	36.7 7.03 ± 22.34
Contracaecum osculatum s.l. (L3)	35.6 3.08 ± 8.31	72.1 11.46 ± 22.20 (3)	53.3 5.85 ± 13.34 (1)
Hysterothylacium aduncum (L3)	15.2 0.32 ± 1.97	65.6 3.66 ± 8.71 (1)	43.3 1.45 ± 2.76
Hysterothylacium rigidum (L3)		60.7 2.98 ± 4.73 (1)	60.0 15.98 ± 88.18 (1)
Pseudoterranova decipiens s.l. (L3)		4.9 0.11 ± 0.58	6.7 0.08 ± 0.33
NEMATODA (adult forms)			
Ascarophis crassicollis			3.3 0.03 ± 0.18
Capillaria gracilis			11.7 0.38 ± 1.29
Hysterothylacium aduncum	6.8 0.14 ± 0.57	21.3 0.57 ± 1.55	13.3 0.37 ± 1.44
ACANTHOCEPHALA (post-cystacant)			
Corynosoma semerme		31.1 0.67 ± 1.36	
Corynosoma strumosum	1.7 0.03 ± 0.26	14.7 0.38 ± 1.19	1.7 0.02 ± 0.13
ACANTHOCEPHALA (adult forms)			
Echinorhynchus gadi s.l.	94.9 30.00 ± 33.03 (16)	72.1 12.64 ± 19.83 (2)	98.3 54.37 ± 60.95 (32.5)

6.3.1.2. Community structure

Descriptors of component communities in cod sampled in the Baltic Sea are presented in Table 6.3. The total number of species was highest in the SSS. However the AS had the highest number of species present at larval stage, the other two samples exhibiting similar numbers of parasite species present as larvae and adults. The Berger-Parker dominance index was distinctly higher in both spring samples. Shannon-Wiener's diversity index showed lowest values for the FSS and this was related to both the lowest species richness and highest dominance (Table 6.3). Similarity between the three samples was moderately high (61.6-72.6%) with 6-7 (out of 6-11) species shared between communities. However, communities sampled in spring (FSS and SSS) exhibited the lowest similarity.

Table 6.3. Component community descriptors of metazoan communities in *G. morhua* from Baltic Sea.

	Spring 2002 FSS	Autumn 2002 AS	Spring 2003 SSS
Total no. of parasite species	6	8	11
Total no. of spp. in larval assemblages	4	7	6
Total no. of spp. in gastrointestinal assemblages	3	2	6
Total no. of spp. in ectoparasite assemblages	-	-	-
Berger-Parker dominance index	0.88	0.39	0.64
Shannon-Wiener's diversity index	0.46	1.38	1.11
Bray-Curtis similarity index (shared species)			
FSS	-	61.63 (6)	61.56 (6)
AS	61.63 (6)	-	72.63 (7)
Most prevalent species		*C. osculatum* *H. aduncum* L3	*C. osculatum*
		H. rigidum	*H. rigidum*
	E. gadi	*E. gadi*	*E. gadi*

A significant effect of fish size (SL) on total species richness and abundance was detected (range for r_s=0.396-0.733, $p<0.002$ and 0.228-0.498, $p<0.05$, respectively). Of the most prevalent species, only *C. osculatum* and *H. rigidum* exhibited size-dependence, both showing increase in abundance with fish size. The former showed positive correlation in all samples (r_s=0.557, 0.790 and 0.748, respectively; all $p<0.0001$). *H. rigidum* was positively correlated with size in the two samples (AS, r_s=0.486, $p<0.0001$; SSS, r_s=0.346, $p=0.007$). Moreover, these two anisakids showed significant correlations with age in two samples (AS and SSS) (*C. osculatum*, r_s=0.688 and 0.525, $p<0.001$; *H. rigidum*, r_s =0.472 and 0.396, $p\leq0.002$, respectively). The abundance of *H. aduncum* (L3) was only correlated with fish length (SL) but not with age in the SSS (r_s=0.326, $p=0.011$). *A. simplex* was a common

species only in SSS and showed significant correlation with both SL and age (r_s=0.630 and 0.516 respectively, p<0.001).

Infracommunity descriptors of metazoan assemblages from the three samples and the results of the statistical comparisons are shown in Table 6.4. Only three fishes (two from FSS and one from AS) were uninfected. The maximum number of species per fish was higher in the AS and SSS. Species density distributions in all three samples agreed with both the Poisson distribution and the distribution predicted by the null model of Janovy *et al.* (1995).

All infracommunity descriptors (richness, abundance, diversity and dominance) showed significant differences between samples (Table 6.4). These significant differences were maintained when juvenile fish (*c.* 1/3 of AS, see Table 1) were excluded from the comparisons. There were significant differences in parasite richness and abundance between the two spring samples (p<0.001), these parameters being higher in the SSS. These differences were also observed in both larval and gastrointestinal assemblages (p≤0.003). Surprisingly, differences in richness and abundance of parasite species between the autumn and spring samples showed different patterns. Thus, in comparisons with the spring of the same year (*i.e*. AS *vs* FSS) the only non-significant comparisons were for the abundance of total parasite communities and the richness of gastrointestinal assemblages (p<0.001 in the remaining comparisons). On the other hand, in comparisons with the spring of the following year (*i.e*. AS *vs* SSS) the only non-significant comparisons were for the richness of total parasite communities and the abundance of larval assemblages (p≤0.038 in the remaining comparisons).

The most prevalent species in component communities were found to dominate infracommunities in a similar manner in the three samples. The acanthocephalan *E. gadi* and the larval nematode *C. osculatum* dominated 93.2% and 6.8% of the infracommunities in the FSS, respectively. *E. gadi* and three larval nematodes, *H. rigidum, C. osculatum* and *A. simplex*, dominated infracommunities in the SSS (83.3; 8.3; 5.0; and 3.3%, respectively), whereas *E. gadi*, *C. osculatum*, *H. aduncum* and *H. rigidum* were dominant in infracommunities in the AS (37.7; 32.8 and 11.5% respectively). Notably, *E. gadi* was dominant species in a smaller proportion of infracommunities in the AS as compared with both spring samples.

Table 6.4. Infracommunity descriptors of metazoan communities in *G. morhua* from Baltic Sea and significance of differences (K-W test; R of ANOSIM for similarities) between the three samples (ns = not significant).

	Spring 2002 (n =59)	Autumn 2002 (n =61)	Spring 2003 (n =60)	Significance of differences χ^2 (R)	p
Fish length (SL, cm)	36.7-76.2	31.4-62.6	32-89.6	2.307	ns
Total infracommunities					
No. species/fish (range)	0-4	0-7	1-6		
Mean no. of species ± SD	1.59 ± 0.83	3.34 ± 1.40	3.23 ± 1.45	56.248	<0.001
Mean no. of individuals ± SD	34.12 ± 34.50	32.54 ± 29.89	85.62 ± 122.90	26. 159	<0.001
Mean dominance ± SD	0.90 ± 0.15	0.69 ± 0.21	0.79 ± 0.18	36.717	<0.001
Mean diversity ± SD	0.19 ± 0.25	0.60 ± 0.34	0.50 ± 0.36	41.560	<0.001
Mean similarity	58.52	40.88	55.49	0.242	0.001
Larval parasite assemblages					
No. species/fish (range)	0-3	0-6	0-5		
Mean no. of species ± SD	0.54 ± 0.75	2.56 ± 1.37	2.02 ± 1.43	64.160	<0.001
Mean no. of individuals ± SD	3.46 ± 8.43	19.33 ± 26.09	30.42 ± 100.30	45.190	<0.001
Mean similarity	12.57	35.52	26.50	0.242	0.001
Gastrointestinal parasite assemblages					
No. species/fish (range)	0-2	0-2	0-3		
Mean no. of species ± SD	1.05 ± 0.39	0.93 ± 0.63	1.32 ± 0.54	14.449	0.001
Mean no. of individuals ± SD	30.66 ± 34.04	13.21 ± 20.03	55.20 ± 60.88	42.774	<0.001
Mean similarity	67.29	34.43	72.67	0.145	0.001

6.3.1.3. Infracommunity similarity

Levels of infracommunty similarity were generally low (mean ranged between 41-59%, see Table 6.4) for total communities due to the low levels of similarity in larval parasite assemblages, the mean infracommunity similarity being somewhat higher in the spring samples. All species dominating infracommunities contributed to the infracommunity similarity (Table 6.5) and just two species determined more than 50% of the cumulative similarity: *E. gadi* and *C. osculatum* (AS) and *E. gadi* (FSS and SSS). The latter species solely contributed to 93.2% and 74.9% of infracommunity similarity in the two spring samples, respectively.

Table 6. 5. Species that most contribute to the similarity (Bray-Curtis index) between infracommunities in the three samples from Baltic Sea. Mean abundance [ln(x+1)], mean similarity, the ratio similarity to standard deviation, the percent contribution to similarity, and the cumulative percent similarity are given for each species.

Parasite species	Mean abundance	Mean similarity	Similarity/SD	Percent contribution	Cumulative percent similarity
FSS					
E. gadi	2.82	54.55	2.08	93.21	93.21
AS					
E. gadi	1.60	13.38	0.81	32.74	32.74
C. osculatum	1.54	11.68	0.84	28.58	61.32
H. aduncum	1.03	8.75	0.84	21.40	82.72
H. rigidum	0.89	5.64	0.67	13.79	96.51
SSS					
E. gadi	3.47	41.55	2.25	74.88	74.88
H. rigidum	1.06	4.98	0.65	8.97	83.86
C. osculatum	1.03	4.36	0.56	7.86	91.71

ANOSIM procedure revealed little separation between the three samples using infracommunities as replicates, gastrointestinal assemblages exhibiting strongly overlapping composition (Table 6.4). R-value was negligibly small (R=0.238, p=0.001) when only the common species in total communities (*i.e.* P>10%) were used for computing infracommunity similarity, thus suggesting strongly overlapping composition. Pairwise tests revealed only a slightly higher R-value (0.32) for FSS *vs* AS comparison.

The levels of dissimilarity were distinctly higher between the samples from Hanö Bight and Öland Island (FSS *vs* AS and SSS *vs* AS). The two species (*C. osculatum* and *E. gadi*) which contributed most to the within-community similarity were also responsible for more than 50% of the cumulative dissimilarity in the pairwise comparisons of the three samples (Table 6.6).

Table 6.6. Species that most contribute to the dissimilarity (Bray-Curtis index) between infracommunities in the three samples from Baltic Sea. Mean abundance [ln(x+1)], mean dissimilarity, the ratio dissimilarity to standard deviation, the percent contribution to dissimilarity, and the cumulative percent dissimilarity are given for each species. Mean dissimilarities between samples in parentheses.

Parasite species	Mean abundance group 1	Mean abundance group 2	Mean dissimilarity	Dissimilarity/SD	Contribution %	Cumulative %
FSS *vs* AS (mean dissimilarity 64.81%)						
E. gadi	2.82	1.60	23.24	1.20	35.85	35.85
C. osculatum	0.64	1.54	15.67	1.13	24.18	60.04
H. aduncum	0.23	1.03	10.75	1.04	16.59	76.62
H. rigidum	0.00	0.89	8.67	0.96	13.38	90.00
FSS *vs* SSS (mean dissimilarity 49.24%)						
E. gadi	2.82	3.47	15.35	0.98	31.17	31.17
C. osculatum	0.64	1.03	10.06	1.02	20.42	51.59
H. rigidum	0.00	1.06	8.70	0.92	17.68	69.27
H. aduncum	0.23	0.64	5.92	0.86	12.02	81.28
A. simplex	0.01	0.80	5.82	0.64	11.82	93.10
AS *vs* SSS (mean dissimilarity 60.14%)						
E. gadi	1.60	3.47	19.89	1.24	33.08	33.08
C. osculatum	1.54	1.03	11.72	1.19	19.49	52.57
H. rigidum	0.89	1.06	8.93	1.10	14.85	67.42
H. aduncum	1.03	0.64	8.20	1.10	13.63	81.05
A. simplex	0.05	0.80	5.29	0.65	8.80	89.85
C. semerme	0.33	0.00	2.46	0.60	4.09	93.94

6.3.2 Parasite communities in cod in the Celtic Sea

A total of 138 fish was examined. Table 6.7 summarizes the structure of the three samples by host sex and age. Males were better represented than females in all samples. Sample sizes for different age classes did not differ between the samples. Fish sizes of the three samples overlapped and significant differences were only found in the pairwise comparisons of FSS *vs* AS and SSS ($p \leq 0.005$) (see Figure 6.3 and Table 6.10).

Table 6.7. Structure of cod population sample from Celtic Sea by age and sex of host. For age determination, it was assumed that cod were born in January. NA, age not determined.

Age class (yrs)		1		2		3		4		NA		Totals by sex		Totals
Year	Season	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
2002	FSS		1	7	5	5	3		2			12	11	23
2002	AS	2	1	13	8	12	18	2				29	27	56
2003	SSS	1	1	11	8	25	5	4	3	1		42	17	59
Totals		3	3	31	21	42	26	6	5	1		83	55	138

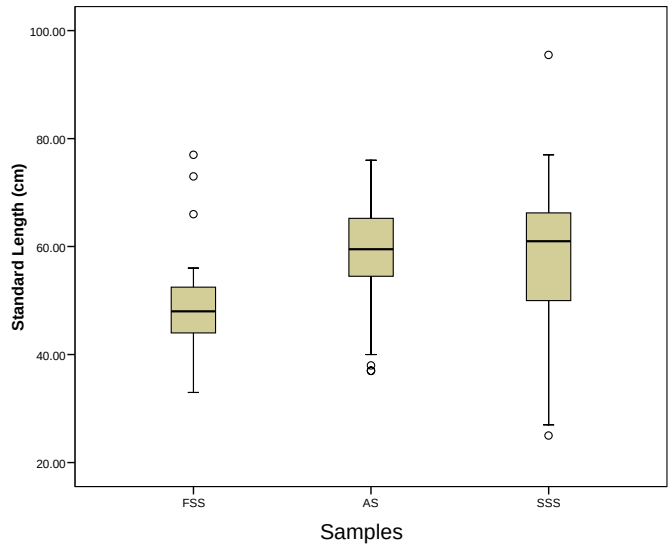

Figure 6.3. Box-plots for standard length of *G. morhua* from 3 samples in Celtic Sea. *Abbreviations*: Samples: FS, first spring sample; AS, autumn sample; SSS, second spring sample.

6.3.2.1. Community composition

Species composition, prevalence and mean abundance of each parasite species in the three samples are summarised in Table 6.8. Of the 39 species recovered, 19 were common and 11 had prevalence > 50% in at least one sample. Of these, five species were most prevalent in all samples: the trematode *D. varicus*, anisakid nematodes *A. simplex*, *C. osculatum* and *H. aduncum* (L3 and adults) and the copepod *C. adunca*. In addition, *H. communis* and *C.*

elongatus were both most prevalent in the SSS and *H. rigidum* and P. *decipiens* in the AS. *C. cirratus* was most prevalent in SSS and AS (Table 6.9). With the exception of *A. simplex* and *C. osculatum,* the abundance of these species differed between samples ($p \leq 0.007$) being greater in SSS. Pairwise comparisons of abundances of the shared most prevalent species between seasons (five species for FSS *vs* AS and two species for AS *vs* SSS comparison) revealed no significant differences. Nearly 40% of the species present in the three samples were rare (all larval trematodes and cestodes; the monogenean *D. merlangi*; the trematode *L. rachion*; the nematode *A. filiformis*; the acanthocephalan *C. semerme*; the copepods *Caligus curtus*, *C. diaphanus* and *C. ornatus*; and the isopod *G. elongata*).

Table 6.8. Prevalence (P%), mean (MA ± SD) and median (M, shown if >0 only) abundance of parasites in the three samples of *G. morhua* from Celtic Sea (n=sampe size).

	Spring 2002 (n = 23)	Autumn 2002 (n = 56)	Spring 2003 (n = 59)
Parasite species/Sample	P% MA ± SD (M)	P% MA ± SD (M)	P% MA ± SD (M)
MONOGENEA			
Diclidophora merlangi			1,7 0,02 ± 0,13
TREMATODA (metacercariae)			
Bucephalinae gen. sp.	8.7 0.26 ± 1.05	8.9 0.11 ± 0.37	8.5 0.08 ± 0.28
Prosorynchoides gracilescens		1.8 0.04 ± 0.27	5.1 0.17 ± 1.05
Prosorhynchus crucibulum		5.4 0.07 ± 0.32	8.5 0.14 ± 0.51
TREMATODA (adult forms)			
Derogenes varicus	78.3 10.65 ± 28.60 (3)	80.4 8.20 ± 12.62 (4)	93.2 23.27 ± 26.52 (13)
Gonocerca phycidis		7.1 0.09 ± 0.35	16.9 0.24 ± 0.57
Hemiurus communis	39.1 4.57 ± 18.24	35.7 1.59 ± 4.48	66.1 4.19 ± 10.03 (1)
Lepidapedon elongatum	4.3 0.04 ± 0.21		
Lepidapedon rachion		1.8 0.02 ± 0.13	3.4 0.12 ± 0.65
Stephanostomum spp.	34.8 5.22 ± 12.02	26.8 0.79 ± 2.14	10.2 0.53 ± 2.49

	Spring 2002 (n = 23)	Autumn 2002 (n = 56)	Spring 2003 (n = 59)
CESTODA (larval forms)			
Hepatoxylon sp.			3.4
			0.07 ± 0.41
Lacistorhynchus sp.		1.8	5.1
		0.02 ± 0.13	0.24 ± 1.19
Pseudophyllidea gen. spp.		5.4	
		0.09 ± 0.39	
Trypanorhyncha gen. spp.	4.3	1.8	6.8
	0.04 ± 0.21	0.02 ± 0.13	0.10 ± 0.44
CESTODA (adult forms)			
Abothrium gadi	4.3	19.6	18.6
	0.04 ± 0.21	0.27 ± 0.59	0.22 ± 0.49
NEMATODA (larval forms)			
Anisakis simplex s.l. (L3)	87.0	94.6	91.5
	85.91 ± 190.30	71.75 ± 139.41	73.58 ± 102.76
	(11)	(29)	(23)
Contracaecum osculatum s.l. (L3)	73.9	71.4	72.9
	3.57 ± 5.19	9.39 ± 16.89	8.85 ± 16.63
	(1))	(3)	(3)
Hysterothylacium aduncum (L3)	56.5	64.3	78.0
	8.57 ± 20.93	6.70 ± 10.79	16.69 ± 26.31
	(1)	(2)	(9)
Hysterothylacium rigidum (L3)	26.1	76.8	39.0
	1.09 ± 3.74	32.21 ± 49.09	3.08 ± 17.01
		(12)	
Pseudoterranova decipiens s.l. (L3)	26.1	67.9	45.8
	1.57 ± 6.01	3.11 ± 4.56	1.66 ± 2.73
		(1)	
NEMATODA (adult forms)			
Ascarophis morrhuae	17.4	19.6	22.0
	1.13 ± 4.78	0.32 ± 0.90	1.85 ± 6.67
Ascarophis crassicollis	13.0	21.4	37.3
	0.17 ± 0.49	0.39 ± 0.87	4.71 ± 17.32
Ascarophis filiformis			1.7
			0.02 ± 0.13
Capillaria gracilis		10.7	6.8
		0.16 ± 0.53	0.08 ± 0.34
Cucullanus cirratus	21.7	87.5	74.6
	0.43 ± 0.99	5.95 ± 10.64	5.41 ± 9.34
		(3)	(2)
Cucullanus sp.			1.7
			0.02 ± 0.13
Hysterothylacium aduncum	91.3	91.1	98.3
	13.52 ± 13.16	17.45 ± 18.11	52.24 ± 51.48
	(8)	(10)	(35)

	Spring 2002 (n = 23)	Autumn 2002 (n = 56)	Spring 2003 (n = 59)
Spinitectus sp.	4.3		10.2
	0.04 ± 0.21		0.29 ± 1.37
ACANTHOCEPHALA (post-cystacant)			
Corynosoma semerme		8.9	
		0.11 ± 0.37	
Corynosoma strumosum	4.3	16.1	27.1
	0.26 ± 1.25	0.27 ± 0.70	0.47 ± 1.18
ACANTHOCEPHALA (adult forms)			
Echinorhynchus gadi s.l.	4.3	3.6	6.8
	0.65 ± 3.13	0.04 ± 0.19	0.08 ± 0.34
COPEPODA			
Caligus curtus			3.4
			0.03 ± 0.18
Caligus diaphanus		1.8	
		0.02 ± 0.13	
Caligus elongatus		1.8	55.9
		0.07 ± 0.53	4.69 ± 7.40
			(1)
Chondracanthus ornatus		1.8	
		0.02 ± 0.13	
Clavella adunca	65.2	64.3	83.0
	1.8 ± 2.58	2.39 ± 3.69	3.97 ± 4.27
	(1)	(1)	(3)
Lernaeocera branchialis	4.3	5.4	8.5
	0.04 ± 0.21	0.07 ± 0.32	0.12 ± 0.46
ISOPODA			
Gnathia elongata			1.7
(praniza larva)			0.02 ± 0.13

6.3.2.2. Community structure

Component community descriptors of the Celtic Sea samples are given in Table 6.9. The total component community richness was high in all three samples and showed a maximum in SSS, which also had the highest number of gastrointestinal parasites, whereas the community sampled in the first spring was poorest. The latter also exhibited the highest dominance and correspondingly, the lowest diversity. The similarity between samples was rather high (68.1-81.5%) with 18-25 (out of 20-32) species shared between communities. The lowest similarity was observed between communities sampled in spring.

A significant effect of fish size (SL) on total species richness and abundance was observed (range for r_s=0.368-0.602, $p<0.05$ and 0.628-0.803, $p\leq0.001$, respectively). The abundance of five of the ten most prevalent species was found to be correlated with fish

size in at least two samples (*A. simplex*, *H. aduncum*, *D. varicus*, *P. decipiens* and *C. cirratus*); the abundance of the first two was significantly associated with size in all samples (r_s=0.712 and 0.784; r_s=0.710 and 0.557; and r_s=0.353 and 0.350, respectively; $p \leq 0.007$ in all cases). The nematodes listed above plus *C. osculatum* and *C. elongatus* were positively correlated with both size and age in at least two samples, whereas P. *decipiens* and *C. elongatus* showed correlation with both size and age in one sample. However, only *A. simplex* exhibited highly significant correlations with age in all three samples (r_s=0.669, 0.468 and 0.659; all $p<0.001$).

Table 6.9. Component community descriptors of metazoan communities in *G. morhua* from Celtic Sea.

	Spring 2002 FSS	Autumn 2002 AS	Spring 2003 SSS
Total no. of parasite species	20	29	32
Total no. of spp. in larval assemblages	8	13	12
Total no. of spp. in gastrointestinal assemblages	11	12	16
Total no. of spp. in ectoparasite assemblages	2	5	5
Berger-Parker dominance index	0.62	0.44	0.36
Shannon-Wiener's diversity index	1.39	1.71	1.78
Bray-Curtis similarity index (shared species)			
FSS	-	75.4 (18)	68.1 (19)
AS	75.4	-	81.5 (25)
Most prevalent species	*D. varicus*	*D. varicus*	*D. varicus*
			H. communis
	A. simplex	*A. simplex*	*A. simplex*
	C. osculatum	*C. osculatum*	*C. osculatum*
	H. aduncum L3	*H. aduncum* L3	*H. aduncum* L3
		P. decipiens	
		C. cirratus	*C. cirratus*
	H. aduncum	*H. aduncum*	*H. aduncum*
			C. elongatus
	C. adunca	*C. adunca*	*C. adunca*

Table 6.10 presents infracommunity descriptors of metazoan assemblages from the three samples and the results of the statistical comparisons. All fish were infected with 2-16 species, the maximum number of species per fish being the highest in the SSS. Species density distributions in all three samples agreed with both the Poisson distribution and the distribution predicted by the null model of Janovy *et al.* (1995).

All infracommunity descriptors exhibited significant differences between samples with the exception of the dominance in total infracommunities, and these differences were also evident in the larval, gastrointestinal and ectoparasite assemblages (Table 6.10). Overall, infracommunities and assemblages from the SSS exhibited higher richness and abundance, especially in comparison with those from the FSS ($p \leq 0.003$ for total communities and $p \leq 0.05$ for the three assemblages). The only non-significant comparisons were for the richness and diversity of total communities (SSS *vs* AS), the abundance of gastrointestinal assemblages and the richness and abundance of ectoparasite assemblages (FSS *vs* AS).

Six of the most prevalent species were frequently found to dominate infracommunities. *A. simplex*, *H. aduncum* and *D. varicus* dominated 39.1%, 30.4% and 13.0% of infracommunities in FSS, respectively; adult *H. aduncum* solely dominating 26.1% of the infracommunities. Infracommunities in SSS were dominated by *H. aduncum* (47.5%; adults only 44.1%), *A. simplex* (25.4%), *D. varicus* (16.9%) and *C. osculatum* (3.4%). Domination exhibited a slightly different pattern in the AS where *A. simplex, H. aduncum* and *H. rigidum*, dominated 37.5%, 25% (adults only 19.6%) and 23.2% of the infracommunities, respectively whereas *D. varicus* and *C. osculatum* were most abundant in 5.4% of the infracommunities each. Occasionally four other species (*H. communis*, *Stephanostomum* spp., *A. crassicollis* and *C. adunca*) were most abundant in a few infracommunities.

Table 6.10. Infracommunity descriptors of metazoan communities in *G. morhua* from Celtic Sea and significance of differences (K-W test; R of ANOSIM for similarities) between the three samples (ns = not significant).

	Spring 2002 (n =23)	Autumn 2002 (n =56)	Spring 2003 (n =59)	Significance of differences χ^2 (R)	p
Fish length (cm)	33.0-77.0	37.0-76.0	25.0-95.5	12.843	0.002
Total infracommunities					
No. species/fish (range)	4-10	3-13	2-16		
Mean no. of species ± SD	6.13 ± 1.60	8.50 ± 2.25	9.37 ± 2.99	26.056	<0.001
Mean no. of individuals ± SD	139.57 ± 210.75	161.70 ± 176.97	207.24 ± 170.08	10.973	0.004
Mean dominance ± SD	0.53 ± 0.19	0.50 ± 0.15	0.53 ± 0.17	0.614	n.s.
Mean diversity ± SD	1.02 ± 0.32	1.27 ± 0.29	1.22 ± 0.39	8.605	0.014
Mean similarity	48.2	56.91	55.99	0.294	0.001
Larval parasite assemblages					
No. species/fish (range)	1-6	1-8	0-9		
Mean no. of species ± SD	2.87 ± 1.18	4.25 ± 1.40	3.92 ± 1.82	13.502	0.001
Mean no. of individuals ± SD	101.26 ± 204.53	123.88 ± 162.71	105.14 ± 119.04	7.567	0.023
Mean similarity	44.3	52.98	48.22	0.157	0.001
Gastrointestinal parasite assemblages					
No. species/fish (range)	1-5	2-7	1-8		
Mean no. of species ± SD	3.13 ± 0.97	4.05 ± 1.23	4.69 ± 1.55	20.550	<0.001
Mean no. of individuals ± SD	36.48 ± 39.08	35.25 ± 27.62	93.27 ± 71.77	35.087	<0.001
Mean similarity	43.51	54.51	61.26	0.215	0.001
Ectoparasite assemblages					
No. species/fish (range)	0-2	0-3	0-3		
Mean no. of species ± SD	0.70 ± 0.56	0.75 ± 0.64	1.53 ± 0.77	35.333	<0.001
Mean no. of individuals ± SD	1.83 ± 2.61	2.57 ± 3.89	8.83 ± 9.36	32.182	<0.001
Mean similarity	35.14	33.42	43.9	0.123	0.001

6.3.2.3. Infracommunity similarity

Infracommunity similarities were generally low (range for means 48-57%) and the three assemblages exhibited a similar pattern (Table 6.10). Only two (FSS) or three (spring samples) dominant species contributed to 60% of the similarity between infracommunities (Table 6.11). These were three nematodes (*A. simplex* and *H. aduncum* in all samples and *H. rigidum* in the AS) and the trematode *D. varicus* (SSS).

Table 6.11. Species that most contribute to the similarity (Bray-Curtis index) between infracommunities in the three samples from Celtic Sea. Mean abundance [ln(x+1)], mean similarity, the ratio similarity to standard deviation, the percent contribution to similarity, and the cumulative percent similarity are given for each species.

Species	Mean abundance	Mean similarity	Similarity/SD	Percent contribution	Cumulative percent similarity
FSS					
H. aduncum	2.56	16.29	1.67	33.80	33.80
A. simplex	2.59	13.03	1.31	27.04	60.84
AS					
H. aduncum	2.82	14.38	2.58	25.26	25.26
A. simplex	3.19	13.22	1.94	23.23	48.49
H. rigidum	2.35	7.18	0.98	12.61	61.10
SSS					
H. aduncum	3.81	18.07	3.05	32.28	32.28
D. varicus	2.58	9.87	1.73	17.63	49.91
A. simplex	3.05	9.77	1.52	17.44	67.35

ANOSIM revealed compositional overlap between infracommunities. which was due to the more homogeneous composition of larval and ectoparasite assemblages (Table 6.10). An analysis restricted to common parasite species revealed somewhat higher separation between samples ($R=0.305$, $p=0.001$). Pairwise tests of the total communities showed that the two spring samples exhibit compositional separation similar to the seasonal comparison (*i.e.* FSS *vs* AS) ($R=0.342$ and $R=0.354$; $p<0.001$, respectively) whereas communities of the AS and SSS exhibited the lowest separation ($R=0.261$; $p<0.001$).

The four species which contributed strongly to the within-community similarity were also contributing to the dissimilarity between samples. Additional differentiating species were: *C. cirratus* (all comparisons); *C. osculatum* (all comparisons); *C. adunca* (FSS *vs* SSS) and *H. communis* (FSS *vs* SSS) (Table 6.12).

Table 6.12. Species that most contribute to the dissimilarity (Bray-Curtis index) between infracommunities in the three samples from Celtic Sea. Mean abundance [ln(x+1)], mean dissimilarity, the ratio dissimilarity to standard deviation, the percent contribution to dissimilarity, and the cumulative percent dissimilarity are given for each species. Mean dissimilarities between samples in parentheses.

Parasite species	Mean abundance group 1	Mean abundance group 2	Mean dissimilarity	Dissimilarity/SD	Percent contribution	Cumulative percent similarity
FSS *vs* AS (mean dissimilarity 52.70%)						
H. rigidum	0.31	2.35	7.54	1.39	14.32	14.32
A. simplex	2.59	3.19	7.49	1.41	14.20	28.52
H. aduncum	2.56	2.82	4.73	1.27	8.97	37.49
C. cirratus	0.23	1.46	4.63	1.60	8.78	46.27
C. osculatum	1.06	1.45	4.58	1.28	8.70	54.97
D. varicus	1.48	1.60	4.58	1.34	8.69	63.66
FSS *vs* SSS (mean dissimilarity 52.78%)						
A. simplex	2.59	3.05	7.43	1.34	14.08	14.08
H. aduncum	2.56	3.81	5.70	1.20	10.80	24.88
D. varicus	1.48	2.58	5.69	1.45	10.78	35.66
C. osculatum	1.06	1.43	4.18	1.25	7.93	43.59
C. cirratus	0.23	1.26	3.85	1.26	7.29	50.88
H. communis	0.56	0.99	3.51	0.98	6.64	57.52
C. adunca	0.75	1.28	3.49	1.15	6.62	64.14
AS *vs* SSS (mean dissimilarity 48.80%)						
H. rigidum	2.35	0.49	6.01	1.34	12.33	12.33
A. simplex	3.19	3.05	5.99	1.27	12.28	24.61
D. varicus	1.60	2.58	4.63	1.33	9.49	34.10
C. osculatum	1.45	1.43	4.11	1.22	8.41	42.52
H. aduncum	2.82	3.81	4.08	1.34	8.36	50.88
C. cirratus	1.46	1.26	3.22	1.32	6.61	57.49
C. adunca	0.86	1.28	2.97	1.18	6.09	63.58

6.3.3. Parasite communities in cod in Icelandic waters

A total of 165 fish was examined. The structure of the three samples by host sex and age is summarized in Table 6.13. Spring samples comprised more male than female individuals. The sample sizes for cod of different ages also differed, particularly in the autumn when the sampled population comprised mostly juveniles (age class 2). Fish sizes of the samples overlapped but significant differences were detected (Figure 6.4; see Table 6.16 for ranges). The AS exhibited the smallest fish size whereas no significant differences in standard length (SL) and age were detected between the two spring samples.

Table 6.13. Structure of cod population sample from Icelandic waters by age and sex of host. For age determination, it was assumed that cod were born in January. NA, age not determined.

Age class (yrs)		2		3		4		5		6		7		8		9		NA		Totals by sex		Totals
Year	Season	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
2002	FSS				1	1	1	5	3	4	3	14	4	6	2				1	30	15	45
2002	AS	4	3	7	9	6	10	7	3	3	2	1	3			1	1		2	29	33	62
2003	SSS			5	2	4	3	8	1	3	5	12	4	8			1		2	40	18	58
Totals		4	3	12	12	11	14	20	7	10	10	27	11	14	2	1	2		5	99	66	165

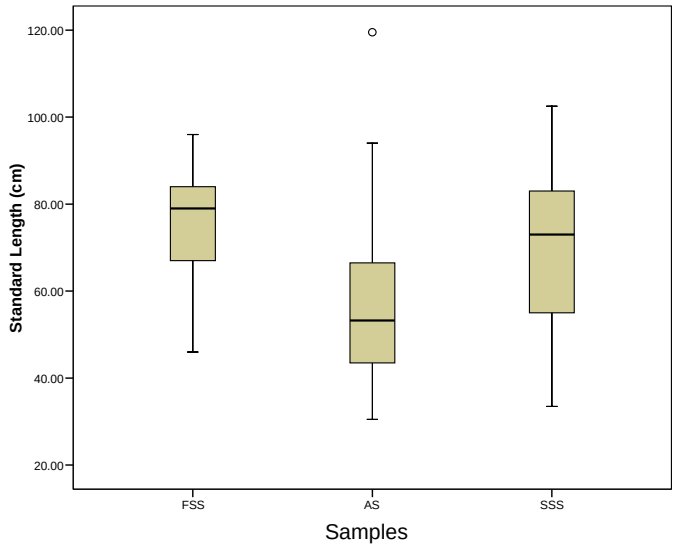

Figure 6.4. Box-plots for standard length of *G. morhua* in three samples from Icelandic waters. *Abbreviations*: Samples: FS, first spring sample; AS, autumn sample; SSS, second spring sample.

6.3.3.1. Community composition

Species composition, prevalence and mean abundance of each parasite species in the three samples are summarized in Table 6.14. A total of 17 species was identified as common. Of these, five species were most prevalent in all samples: the trematode *D. varicus* and the nematodes *A. simplex*, *C. osculatum*, *H. aduncum* (L3 and adults) and *C. cirratus* (Table 6.15) Significant differences were found in the abundance of these species between the three samples ($p \leq 0.02$) except for *H. aduncum* (L3). Abundances of larval nematodes were substantially lower and those of *D. varicus* and *C. cirratus* were greater in the AS.

There were some differences in the composition of the most prevalent species between spring samples (sampled coastal southwest) and AS (sampled offshore west). Thus, *C. gracilis* and *A. morrhuae* occurred with prevalence >50% in SSS and AS, respectively. *P. decipiens*, *E. gadi* and *C. adunca* were most prevalent in both AS and SSS. Assuming that the differences in the composition of the most prevalent species may be due to cod age, distance between the sampling locations and that there are seasonal variations in species distributions, tests for differences in the distributions of the most prevalent species were carried out first between the spring samples.

Eight of the ten species with prevalence >50% in at least one of the spring samples exhibited significant differences. *A. simplex* and *C. osculatum* were more abundant in FSS ($p=0.029$ and $p=0.002$, respectively) whereas *D. varicus*, *P. decipiens*, *C. gracilis*, *C. cirratus*, *H. aduncum* and *E. gadi* showed higher abundance in SSS ($p \leq 0.033$ in all cases). Nevertheless, only two species (*P. decipiens* and *C. gracilis*) had significantly higher prevalence in the SSS ($p=0.002$ and $p=0.0001$, respectively).

Comparisons between FSS and AS revealed that seven of the ten species tested showed significant differences in abundance distributions. *A. simplex* and *C. osculatum* were more abundant in the FSS while *D. varicus*, *P. decipiens*, *A. morrhuae*, *C. gracilis* and *C. cirratus* were more abundant in the AS ($p \leq 0.023$ in all cases). Prevalences showed significant differences for 5 species: *C. osculatum*, *A. morrhuae*, *C. gracilis*, *C. cirratus* and *C. adunca* ($p \leq 0.031$ in all cases); only the first species was more prevalent in the FSS.

Comparisons between SSS and AS demonstrated significant differences in abundance of five species. *A. simplex*, *P. decipiens*, *C. gracilis*, *H. aduncum* and *E. gadi* were more abundant in the SSS (all $p \leq 0.031$), and only *C. cirratus* was most abundant in the AS ($p=0.006$). The prevalences of *D. varicus*, *A. morrhuae* and *C. cirratus* were higher in the AS ($p=0.015$, 0.041 and 0.0001, respectively) while *C. gracilis* was more prevalent in the SSS ($p=0.009$). A large number of rare taxa (16) was found in all three (*Otodistomum*

sp. and *C. strumosum*), two (*L. rachion*, *Stephanostomum* spp., *A. gadi*, *A. crasicollis*, *Spinitectus* sp., *C. curtus*, *G. elongata* and unidentified trypanorhynch larvae) or a single sample (*P. gracilescens*, *O. bacillaris*, *J. arctica*, *S. pleuronectis*, unidentified larval pseudophyllideans and unidentified plerocercoids).

Table 6.14. Prevalence (P%), mean (MA ± SD) and median (M, shown if >0 only) abundance of parasites in the three samples of *G. morhua* from Icelandic waters (n = sample size).

	Spring 2002 (n = 45)	Autumn 2002 (n = 62)	Spring 2003 (n = 58)
Parasite species/sample	P (%) MA ± SD (M)	P (%) MA ± SD (M)	P (%) MA ± SD (M)
TREMATODA (metacercariae)			
Otodistomum sp.	2.2 0.02 ± 0.15	1.6 0.02 ± 0.13	1.7 0.02 ± 0.13
Prosorynchoides gracilescens			1.7 0.03 ± 0.26
TREMATODA (adult forms)			
Derogenes varicus	84.4 5.29 ± 5.13 (4)	79.0 106.98 ± 236.83 (12)	94.8 37.57 ± 68.52 (15)
Fellodistomum sp.			1.7 0.02 ± 0.13
Hemiurus levinseni	2.2 0.07 ± 0.45	16.1 0.82 ± 2.63	3.5 0.03 ± 0.18
Lepidapedon elongatum	4.4 1.04 ± 6.42	1.6 0.03 ± 0.25	22.4 4.03 ± 17.90
Lepidapedon rachion		1.6 0.02 ± 0.13	3.5 0.12 ± 0.70
Opechona bacillaris			1.7 0.02 ± 0.13
Podocotyle reflexa		11.3 0.16 ± 0.58	5.2 0.05 ± 0.22
Stephanostomum spp.	2.2 0.02 ± 0.15	3.2 0.10 ± 0.56	5.2 0.07 ± 0.32
CESTODA (larval forms)			
Scolex pleuronectis		1.6 0.02 ± 0.13	
Pseudophyllidea fam. gen. spp.			1.7 0.02 ± 0.13
Trypanorhyncha fam. gen. spp.	2.2 0.02 ± 0.15	1.6 0.02 ± 0.13	

	Spring 2002 (n = 45)	Autumn 2002 (n = 62)	Spring 2003 (n = 58)
Unidentified plerocercoids			1.7 0.02 ± 0.13
CESTODA (adult forms)			
Abothrium gadi	8.9 0.09 ± 0.29		3.5 0.03 ± 0.18
NEMATODA (larval forms)			
Anisakis simplex s.l. (L3)	100.0 492.91 ± 463.16 (339)	98.4 194.71 ± 383.83 (54.5)	100.0 340.53 ± 418.77 (163.5)
Contracaecum osculatum s.l. (L3)	100.0 75.69 ± 48.37 (73)	88.7 39.23 ± 44.30 (25)	96.5 60.43 ± 82.62 (27.5)
Hysterothylacium aduncum (L3)	97.8 41.16 ± 44.95 (26)	96.8 35.34 ± 32.30 (26)	98.3 36.67 ± 31.25 (31)
Hysterothylacium rigidum (L3)		1.6 0.02 ± 0.13	17.2 1.03 ± 4.11
Pseudoterranova decipiens s.l.(L3)	35.6 0.62 ± 1.03	51.6 4.03 ± 17.24 (1)	67.2 5.19 ± 10.89 (1.5)
NEMATODA (adult forms)			
Ascarophis morrhuae	35.6 1.69 ± 3.91	67.7 14.47 ± 28.20 (2)	48.3 17.24 ± 45.34
Ascarophis crassicollis	4.4 0.07 ± 0.33		1.7 0.03 ± 0.26
Ascarophis filiformis	6.7 0.07 ± 0.25	6.5 0.26 ± 1.55	10.3 0.17 ± 0.57
Capillaria gracilis	6.7 0.16 ± 0.67	30.6 0.66 ± 1.35	55.2 2.41 ± 6.67 (1)
Cucullanus cirratus	75.6 5.27 ± 7.38 (3)	93.5 8.71 ± 10.82 (5)	67.2 5.78 ± 8.34 (2)
Hysterothylacium aduncum	88.9 22.11 ± 35.36 (10)	87.1 19.73 ± 23.62 (11.5)	86.2 35.10 ± 38.83 (21.5)
Spinitectus sp.	4.4 0.04 ± 0.21		
ACANTHOCEPHALA (post-cystacant)			
Corynosoma semerme	2.2 0.04 ± 0.30		
Corynosoma strumosum	2.2 0.02 ± 0.15	9.7 0.15 ± 0.47	8.6 0.09 ± 0.28

	Spring 2002 (n = 45)	Autumn 2002 (n = 62)	Spring 2003 (n = 58)
ACANTHOCEPHALA (adult forms)			
Echinorhynchus gadi s.l.	48.9	50.0	62.1
	3.18 ± 6.76	1.52 ± 2.84	8.84 ± 14.36
		(0.5)	(2)
HIRUDINEA			
Johanssonia arctica		1.6	
		0.02 ± 0.13	
COPEPODA			
Caligus curtus		6.5	3.5
		0.13 ± 0.59	0.03 ± 0.18
Caligus elongatus	2.2	30.6	3.5
	0.04 ± 0.30	1.53 ± 6.17	0.03 ± 0.18
Clavella adunca	44.4	66.1	55.2
	1.38 ± 2.10	2.61 ± 4.18	2.00 ± 3.38
		(1)	(1)
Lernaeocera branchialis	15.6	17.7	24.1
	0.27 ± 0.69	0.26 ± 0.60	0.38 ± 0.77
ISOPODA			
Gnathia elongata	6.7		
	0.09 ± 0.36		

6.3.3.2. Community structure

Component community descriptors of the Icelandic samples are presented in Table 6.15. The total component community richness was high in all three samples and showed a maximum in the SSS, which also had the richest list of larval and gastrointestinal endoparasites. However, the FSS from the same sampling location exhibited the lowest richness. Berger-Parker dominance index was higher in the spring samples. Shannon-Wiener's diversity index showed a maximum in the AS which exhibited the lowest dominance values. With 18-22 species (out of 24-30 species) shared between samples, the similarity between component communities was consistently high (range 77.8-83.33%).

There was a significant positive effect of fish size (SL) on the abundance of all parasites in each infracommunity (range for r_s=0.821-0.871, $p<0.001$) but not on species richness. Three of the most prevalent species were found to be size-dependent in all samples, *A. simplex*, *C osculatum* and *H. aduncum* (range for r_s=0.842-0.859; 0.445-0.608; and 0.358-0.573, respectively; all $p\leq0.016$). The abundance of *D. varicus* was significantly correlated with SL in AS and SSS (r_s=0.352, p=0.007 and r_s=0.302, p=0.017, respectively). However, only the abundance of *A. simplex* and *C. osculatum* was also correlated with host age in all samples (r_s=0.781, 0.792, 0.781 and r_s=0.392, 0.478 and 0.547; all $p<0.001$

respectively). *A. simplex* exhibited the strongest correlation thus confirming its accumulation with age.

Table 6.15. Component community descriptors of metazoan communities in *G. morhua* from Icelandic waters.

	Spring 2002 FSS	Autumn 2002 AS	Spring 2003 SSS
Total no. of parasites species	24	25	30
Total no. of spp. in larval assemblages	8	9	11
Total no. of spp. in gastrointestinal assemblages	13	12	16
Total no. of spp. in ectoparasite assemblages	4	5	4
Berger-Parker dominance index	0.76	0.45	0.61
Shannon-Wiener's diversity index	0.85	1.54	1.36
Bray-Curtis similarity index (shared species)			
FSS	-	77.8 (18)	80.28 (22)
AS	77.8	-	83.33 (18)
Most prevalent species	*D. varicus* *A. simplex* *C. osculatum* *H. aduncum* L3 *C. cirratus* *H. aduncum*	*D. varicus* *A. simplex* *C. osculatum* *H. aduncum* L3 *P. decipiens* *A. morrhuae* *C. cirratus* *H. aduncum* *E. gadi* *C. adunca*	*D. varicus* *A. simplex* *C. osculatum* *H. aduncum* L3 *P. decipiens* *C. gracilis* *C. cirratus* *H. aduncum* *E. gadi* *C. adunca*

Infracommunity descriptors of metazoan assemblages from the three samples and the results of statistical comparisons are shown in Table 6.16. Infracommunities in all three samples were rich and abundant: fish were infected with 5-14 species and the lowest mean abundance was >400 parasites. However, species density distributions in all three samples agreed with both the Poisson distribution and the distribution predicted by the null model of Janovy *et al.* (1995).

The five descriptors of total infracommunities (mean species richness, mean abundance, mean dominance, mean diversity and mean similarity) varied significantly between samples due to the significant differences in the assemblages of larval and gastrointestinal parasites (Table 6.16). When juvenile fish (*c.* more than 1/3 of AS, see Table 6.13) were excluded from the comparisons, the same significant differences for all the descriptors were detected (all $p \leq 0.040$) except for the mean abundance of total infracommunities.

Table 6.16. Infracommunity descriptors of metazoan communities in *G. morhua* from Icelandic waters and significance of differences (K-W test; R of ANOSIM for similarities) between the three samples (ns = not significant).

	Spring 2002 (n =45)	Autumn 2002 (n =62)	Spring 2003 (n =58)	Significance of differences χ^2 (R)	p
Fish length (cm)	46.0-96.0	30.5-119.5	33.5-102.5	34.705	0.000
Total infracommunities					
No. species/fish (range)	5-11	5-14	5-13		
Mean no. of species ± SD	6.98 ± 1.34	8.37 ± 1.89	8.72 ± 2.07	23.113	<0.001
Mean no. of individuals ± SD	651.36 ± 470.94	431.52 ± 504.12	558.05 ± 476.20	10.932	0.004
Mean dominance ± SD	0.65 ± 0.20	0.53 ± 0.16	0.56 ± 0.19	8.585	0.014
Mean diversity ± SD	0.88 ± 0.37	1.19 ± 0.28	1.17 ± 0.39	19.163	<0.001
Mean similarity	72.88	62.41	62.16	0.109	0.001
Larval parasite assemblages					
No. species/fish (range)	2-5	2-5	3-6		
Mean no. of species ± SD	3.42 ± 0.62	3.52 ± 0.78	3.98 ± 0.83	13.594	0.001
Mean no. of individuals ± SD	610.49 ± 471.14	273.52 ± 415.24	444.07 ± 451.42	22.416	<0.001
Mean similarity	82.54	71.5	72.17	0.041	0.006
Gastrointestinal parasite assemblages					
No. species/fish (range)	2-6	2-8	1-7		
Mean no. of species ± SD	3.73 ± 1.18	4.48 ± 1.33	4.72 ± 1.32	14.984	0.001
Mean no. of individuals ± SD	39.09 ± 39.60	153.45 ± 243.99	111.53 ± 104.07	26.687	<0.001
Mean similarity	52.29	53	52.77	0.115	0.001
Ectoparasite assemblages					
No. species/fish (range)	0-2	0-4	0-3		
Mean no. of species ± SD	0.69 ± 0.70	1.23 ± 0.91	0.86 ± 0.74	10.475	0.005
Mean no. of individuals ± SD	1.78 ± 2.23	4.55 ± 8.26	2.45 ± 3.67	7.492	0.024
Mean similarity	17.16	29.46	24.28	0.044	0.001

Comparisons between spring samples revealed significant differences in the majority of community descriptors of total infracommunities as well as of larval and gastrointestinal assemblages (all $p \leq 0.028$) except for the mean abundance of total infracommunities. When comparing infracommunities from FSS with those of AS, only the richness of larval assemblages did not show significant differences ($p \leq 0.019$ for all other descriptors in total communities and the three assemblages). On the other hand, the SSS only differed significantly from the AS in the abundance of total infracommunities and the richness and abundance of larval and ectoparasite assemblages.

Six of the most post prevalent species were frequently found to dominate infracommunities and a similar pattern was observed in all samples. *A. simplex* and *H. aduncum* dominated infracommunities of all three samples (80% and 13.3% in FSS; 37.1% and 22.6% in AS; and 53.4% and 20.7% in SSS, respectively). *C. osculatum* dominated 6.7% of the infracommunities in FSS, whereas *A. morrhuae*, *C. osculatum* and *D. varicus* were the most abundant species in 12.1%, 10.3% and 3.4% of infracommunities in SSS, respectively. Finally, four species had the highest abundance in infracommunities from the AS: *D.* varicus (22.6%), *C. osculatum* (8.1%), *A. morrhuae* (4.8%), and *C. cirratus* (4.8%).

6.3.3.3. Infracommunity similarity

Infracommunities exhibited similarly to component communities high similarity values (Table 6.16) which were generally due to higher similarities of gastrointestinal assemblages. Three nematode species, *A. simplex*, *C. osculatum* and *H. aduncum* contributed to the similarity between infracommunities (Table 6.17). The two first contributed to over 60% of the similarity in FSS, whereas *A. simplex* and *H. aduncum* cumulated *c.* 50% of the similarity in the AS and SSS.

ANOSIM procedure revealed a strongly overlapping composition of infracommunities between the three samples (Table 4). When juvenile fish were excluded from the analysis a similar negligibly small value for R was obtained ($R=0.145$, $p=0.001$). The analysis restricted to common parasite species revealed even higher homogeneity of the samples ($R=0.103$, $p=0.001$). Overall, the three nematode species which contributed to the within-community similarity were also important in between-sample differentiation. However, a number of additional species also contributed to the latter: *D. varicus*, *A. morrhuae* and *C. cirratus* (all comparisons); and *E. gadi* (showing much higher abundance in SSS *vs* FSS and AS) (Table 6.18).

Table 6.17. Species that most contribute to the similarity (Bray-Curtis index) between infracommunities in the three samples from Icelandic waters. Mean abundance [ln(x+1)], mean similarity, the ratio similarity to standard deviation, the percent contribution to similarity, and the cumulative percent similarity are given for each species.

Species	Mean abundance	Mean similarity	Similarity/SD	Percent contribution	Cumulative percent similarity
FSS					
A. simplex	5.58	25.41	4.52	34.87	34.87
C. osculatum	4.07	18.91	4.67	25.95	60.82
AS					
H. aduncum	3.67	15.58	2.86	24.96	24.96
A. simplex	3.99	14.59	2.31	23.38	48.34
C. osculatum	2.97	10.52	1.50	16.86	65.20
SSS					
A. simplex	4.72	16.20	2.19	26.06	26.06
H. aduncum	3.94	15.67	3.40	25.21	51.27
C. osculatum	3.19	10.14	1.89	16.31	67.58

Table 6.18. Species that most contribute to the dissimilarity (Bray-Curtis index) between infracommunities in the three samples from Icelandic waters. Mean abundance [ln(x+1)], mean dissimilarity, the ratio dissimilarity to standard deviation, the percent contribution to dissimilarity, and the cumulative percent dissimilarity are given for each species. Mean dissimilarities between samples in parentheses.

Parasite species	Mean abundance group 1	Mean abundance group 2	Mean dissimilarity	Dissimilarity /SD	Percent contribution	Cumulative percent similarity
FSS *vs* AS (mean dissimilarity 36.35%)						
A. simplex	5.58	3.99	5.82	1.29	16.02	16.02
D. varicus	1.46	2.70	5.01	1.37	13.79	29.80
C. osculatum	4.07	2.97	4.14	1.12	11.38	41.19
A. morrhuae	0.51	1.57	3.77	1.16	10.36	51.55
C. cirratus	1.32	1.79	3.13	1.30	8.61	60.16
H. aduncum	3.71	3.67	2.92	1.21	8.04	68.20
FSS *vs* SSS (mean dissimilarity 35.92%)						
A. simplex	5.58	4.72	4.93	1.16	13.72	13.72
D. varicus	1.46	2.78	4.19	1.50	11.66	25.38
C. osculatum	4.07	3.19	4.03	1.20	11.23	36.61
E. gadi	0.79	1.39	3.33	1.20	9.28	45.88
A. morrhuae	0.51	1.22	3.13	0.92	8.72	54.60
C. cirratus	1.32	1.24	3.02	1.31	8.41	63.01
AS *vs* SSS (mean dissimilarity 39.41%)						
A. simplex	3.99	4.72	5.32	1.34	13.50	13.50
D. varicus	2.70	2.78	4.83	1.41	12.26	25.76
C. osculatum	2.97	3.19	4.21	1.25	10.69	36.44
A. morrhuae	1.57	1.22	4.05	1.20	10.29	46.73
C. cirratus	1.79	1.24	3.24	1.32	8.22	54.95
E. gadi	0.60	1.39	3.14	1.17	7.96	62.91
H. aduncum	3.67	3.94	2.61	1.08	6.62	69.53

6.3.4. Parasite communities in cod in the Irish Sea

A total of 147 fish was examined. The structure of the three samples by host sex and age is summarized in Table 6.19. Males were better represented than females in the spring samples and there were marked differences between sexes. Males and females differed significantly with respect to standard length (SL) and weight in all samples. The sample sizes for cod of different ages also differed, and particularly in autumn when the population sampled were comprised of more juveniles (age class 1). Fish sizes of the three samples overlapped but significant differences were detected (Figure 6.5; see Table 6.22 for ranges) between the AS and the spring samples (p=0.0001 in both comparisons).

Table 6.19. Structure of cod population sample from Irish Sea by age and sex of host. For age determination, it was assumed that cod were born in January. NA, age not determined.

Age class (yrs)		1		2		3		4		NA		Totals by sex		Totals
Year	Season	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
2002	FSS			14	5	19	15	3	3	1		37	23	60
2002	AS	20	29	1	1						1	21	31	52
2003	SSS			13		7	1	1		1	1	22	2	24
Totals		20	29	28	6	26	16	4	3	2	2	80	56	136

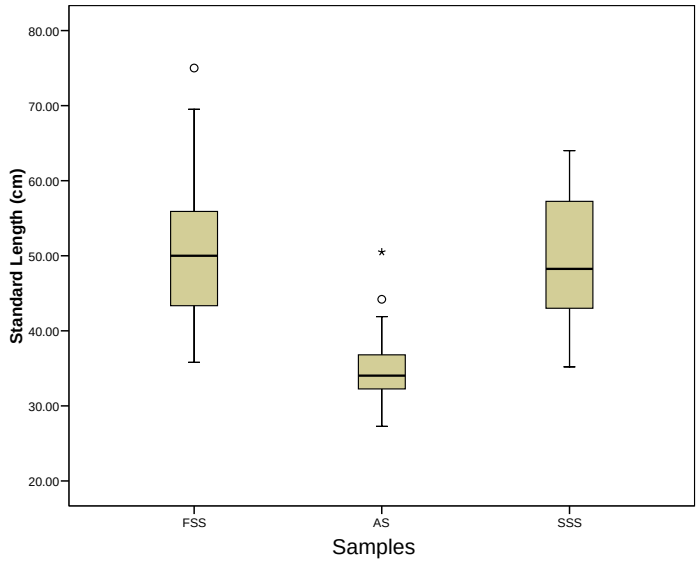

Figure 6.5. Box-plots for standard length of *G. morhua* in three samples from Irish Sea. *Abbreviations*: Samples: FS, first spring sample; AS, autumn sample; SSS, second spring sample.

6.3.4.1. Community composition

Species composition, prevalence and mean abundance of each parasite species in the three samples are given in Table 6.20. Of the 37 species recovered 23 were common in at least one of the three samples. Of these, four species were most prevalent in all samples: the trematodes *D. varicus* and *H. communis* and the nematodes *H. aduncum* (L3) and *A. morrhuae* (Table 6.21). Significant differences were found in the abundance of these species between the three samples ($p \leq 0.004$) except for *A. morrhuae*, the mean abundance of the first three species being lower in AS than in both spring samples (all $p \leq 0.022$). Three nematodes *C. osculatum*, *C. cirratus* and *H. aduncum* were also most prevalent in the spring samples. *C. adunca* was most prevalent in the FSS and AS; *A. crassicollis* in the AS and SSS; and *A. simplex* was only found with prevalence >50% in SSS (Table 6.20).

Table 6.20. Prevalence (P%), mean (MA ± SD) and median (M, shown if >0 only) abundance of parasites in the three samples of *G. morhua* from Irish Sea (n = sample size).

	Spring 2002 (n = 60)	Autumn 2002 (n = 52)	Spring 2003 (n = 24)
Parasite species/Sample	P (%) MA ± SD (M)	P (%) MA ± SD (M)	P (%) MA ± SD (M)
TREMATODA (metacercariae)			
Bucephalinae gen. sp.	23.3 2.05 ± 8.22	5.8 0.06 ± 0.24	
Prosorynchoides gracilescens			4.2 0.08 ± 0.41
Prosorhynchus crucibulum	1.7 0.02 ± 0.13	1.9 0.02 ± 0.14	8.3 0.08 ± 0.28
Rhipidocotyle sp.		1.9 0.02 ± 0.14	
TREMATODA (adult forms)			
Derogenes varicus	100.0 52.53 ± 55.24 (39)	100.0 14.85 ± 17.57 (9.5)	100.0 34.38 ± 27.70 (26.5)
Gonocerca phycidis	15.0 0.80 ± 3.06	25.0 0.46 ± 0.96	41.7 3.04 ± 8.17
Hemiurus communis	91.7 14.48 ± 36.13 (4)	50.0 1.17 ± 2.41 (0.5)	87.5 8.88 ± 19.76 (3)
Hemiurus luehei		13.5 0.25 ± 0.68	
Lecithaster ?gibbosus			4.2 0.17 ± 0.82
Lepidapedon elongatum	5.0 0.15 ± 0.82	3.8 0.15 ± 0.87	12.5 0.25 ± 0.85

	Spring 2002 (n = 60)	Autumn 2002 (n = 52)	Spring 2003 (n = 24)
Lepidapedon rachion	1.7	1.9	4.2
	0.03 ± 0.26	0.02 ± 0.14	0.17 ± 0.82
Opechona bacillaris		1.9	
		0.02 ± 0.14	
Stephanostomum sp.	38.3	26.9	12.5
	1.23 ± 2.53	3.13 ± 11.49	0.58 ± 2.26
CESTODA (larval forms)			
Lacistorhynchus sp.	10.0		4.2
	0.12 ± 0.37		0.04 ± 0.20
Scolex pleuronectis	5.0		
	0.05 ± 0.22		
Trypanorhyncha gen. spp.	10.0		4.2
	0.13 ± 0.43		0.04 ± 0.20
CESTODA (adult forms)			
Abothrium gadi	25.0	11.5	37.5
	0.42 ± 0.83	0.15 ± 0.46	0.38 ± 0.49
NEMATODA (larval forms)			
Anisakis simplex s.l. (L3)	48.3	15.4	50.0
	9.78 ± 63.76	0.31 ± 1.08	1.21 ± 1.82
			(0.5)
Contracaecum osculatum s.l. (L3)	91.7	17.3	87.5
	17.63 ± 24.83	0.54 ± 1.32	16.75 ± 35.09
	(9.5)		(6.5)
Hysterothylacium aduncum (L3)	76.7	69.2	70.8
	16.88 ± 26.02	4.25 ± 8.13	15.75 ± 20.27
	(5.5)	(2)	(9)
Hysterothylacium rigidum (L3)		13.5	16.7
		0.21 ± 0.67	0.67 ± 1.99
Pseudoterranova decipiens s.l. (L3)	26.7	9.6	37.5
	1.07 ± 3.43	0.12 ± 0.38	1.96 ± 4.46
NEMATODA (adult forms)			
Ascarophis morrhuae	71.7	63.5	62.5
	12.58 ± 29.44	3.83 ± 6.08	5.33 ± 9.68
	(2.5)	(1.5)	(1.5)
Ascarophis crassicollis	36.7	53.8	50.0
	2.40 ± 4.73	3.60 ± 7.32	5.38 ± 14.14
		(1)	(0.5)
Ascarophis filiformis	6.7		
	0.07 ± 0.25		
Capillaria gracilis		1.9	4.2
		0.02 ± 0.14	0.04 ± 0.20
Cucullanus cirratus	71.7	21.2	79.2
	5.38 ± 14.51	0.33 ± 0.79	4.96 ± 6.81
	(3)		(2)

	Spring 2002 (n = 60)	Autumn 2002 (n = 52)	Spring 2003 (n = 24)
Hysterothylacium aduncum	100.0	46.2	100.0
	42.07 ± 45.39	2.65 ± 5.06	34.67 ± 36.53
	(25.5)		(21.5)
Spinitectus sp.			8.3
			0.13 ± 0.45
ACANTHOCEPHALA (post-cystacant)			
Corynosoma semerme		1.9	
		0.02 ± 0.14	
Corynosoma strumosum	25.0	1.9	12.5
	0.52 ± 1.85	0.02 ± 0.14	0.13 ± 0.34
ACANTHOCEPHALA (adult forms)			
Echinorhynchus gadi s.l.	16.7	3.8	20.8
	0.52 ± 2.10	0.04 ± 0.19	0.25 ± 0.53
HIRUDINEA			
Calliobdella nodulifera	1.7		
	0.02 ± 0.13		
COPEPODA			
Acanthochondria soleae			4.2
			0.04 ± 0.20
Caligus curtus	31.7	5.8	
	1.42 ± 4.37	0.06 ± 0.24	
Caligus elongatus	21.7	15.4	8.3
	0.47 ± 1.33	0.48 ± 2.25	0.25 ± 0.90
Clavella adunca	71.7	75.0	41.7
	3.92 ± 7.34	2.25 ± 2.35	0.88 ± 1.26
	(2)	(2)	
Lernaeocera branchialis	8.3	1.9	
	0.08 ± 0.28	0.02 ± 0.14	

Of the nine most prevalent species in at least one of the spring samples [*i.e*. *A. simplex*, *C. osculatum*, *H. aduncum* (L3 and adults), *D. varicus, H. communis*, *A. crassicollis*, *A. morrhuae*, *C. cirratus* and *C. adunca*] only the last listed was more abundant and prevalent in FSS (p=0.003). The remaining exhibited similar abundance distributions and prevalences in FSS and SSS.

Comparisons between AS and the spring samples showed a similar pattern. All of the nine species tested exhibited significant differences in abundance ($p \leq 0.002$ in all AS *vs* FSS comparisons and $p \leq 0.022$ in all AS *vs* SSS comparisons) except for *A. crassicollis* and *A. morrhuae* in both comparisons and *C. adunca* in AS *vs* FSS comparison. Only 5 species of the 9 most prevalent [*A. simplex*, *C. osculatum*, *H. aduncum* (adults), *H. communis* and

C. cirratus] had significantly different prevalences in the seasonal comparisons ($p \leq 0.004$ in AS *vs* FSS and AS *vs* SSS comparisons). *C. adunca* had also significantly higher prevalence in AS (compared with SSS; $p=0.009$).

6.3.4.2. Community structure

Descriptors of component communities in cod sampled in Irish Sea are shown in Table 6.21. The total component community richness was high in all three samples and showed a maximum in the AS. FSS had the lowest richness of gastrointestinal parasites and only two ectoparasite species were found in the SSS. Overall, the Berger-Parker dominance index was very low (highest value in AS) and, correspondingly, the Shannon-Wiener's diversity index was high in all three samples (with a maximum in the AS). Between-community similarities were also high (range 71.6-78.3%) due to the large number of species in common between samples (21-22 out of 26-28 species).

Table 6.21. Component community descriptors of metazoan communities in *G. morhua* from the three samples in Irish Sea.

	Spring 2002 FSS	Autumn 2002 AS	Spring 2003 SSS
Total no. of parasites species	27	28	26
Total no. of spp. in larval assemblages	10	10	10
Total no. of spp. in gastrointestinal assemblages	13	15	15
Total no. of spp. in ectoparasite assemblages	5	4	2
Berger-Parker dominance index	0.28	0.38	0.25
Shannon-Wiener's diversity index	1.98	2.02	1.89
Bray-Curtis similarity index (shared species)			
FSS	-	71.6 (22)	75.4 (21)
AS	71.6	-	78.3 (21)
Most prevalent species	*D. varicus* *H. communis*	*D. varicus* *H. communis*	*D. varicus* *H. communis* *A. simplex*
	C. osculatum *H. aduncum* L3 *A. morrhuae*	*H. aduncum* L3 *A. morrhuae* *A. crassicollis*	*C. osculatum* *H. aduncum* L3 *A. morrhuae* *A. crassicollis*
	C. cirratus *H. aduncum* *C. adunca*	*C. adunca*	*C. cirratus* *H. aduncum*

A significant positive effect of fish size (SL) on the richness and abundance of the total parasite infracommunities was detected in all 3 samples (range for $r_s=0.302$-0.539 and 0.245-0.544, respectively; $p<0.05$) except for the richness in SSS. Two of the most prevalent species were found to be size-dependent in all samples (*A. simplex* and *C. osculatum* ($r_s=0.526$, 0.360 and 0.412; respectively; all $p<0.05$). Other four species were

significantly correlated with SL in a single sample: *C. cirratus* in the FSS, *D. varicus* in the AS and *H. communis* and *A. crassicollis* in the SSS (r_s=0.382, 0.293, 0.509 and -0.520, respectively; all $p \leq 0.011$).

Infracommunity descriptors of metazoan assemblages from the three samples and the results of the statistical comparisons are shown in Table 6.22. The number of species per fish ranged from 3 to 14 and the mean species richness of total communities and gastrointestinal assemblages was notably high. However, species density distributions in all three samples agreed with both the Poisson distribution and the distribution predicted by the null model of Janovy *et al.* (1995).

The majority of the community descriptors of total infracommunities (richness, abundance and diversity) differed significantly between samples, the dominance index exhibiting generally low and similar values (Table 6.22). These significant differences were maintained in larval and adult endoparasite and ectoparasite assemblages. Comparison between spring samples revealed significant differences in richness and abundance of ectoparasite assemblages only (both p=0.0001). Comparisons between the AS and the spring samples showed significant differences in richness and abundance of total infracommunities and in the three assemblages ($p<0.04$ in all cases). The diversity distributions of total infracommunities and the three assemblages were also significantly different in both comparisons ($p \leq 0.012$) except for ectoparasite assemblages in AS *vs* SSS comparison.

Seven of the most prevalent species were found to dominate infracommunities. *H. aduncum*, *D. varicus* and *C. osculatum* dominated in both spring samples (48.3%; 35%; and 6.7% of the infracommunities of the FSS; and 45.8%; 37.5%; and 8.3% of the infracommunities of the SSS, respectively). Adult *H. aduncum* alone dominated 43.3% of the infracommunities in the FSS and 37.5% in SSS, respectively. Infracommunities of the FSS were also dominated by *H. communis* (5%) and *A. simplex*, *A. morrhuae* and *C. cirratus* (1.7% each). Infracommunities of the SSS were dominated by *H. communis* and *A. morrhuae* (4.2% each). The AS exhibited a slightly different pattern in that *D. varicus* dominated 46.1% of the infracommunities and *H. aduncum*, *A. morrhuae*, *Stephanostomum* spp., *A. crasicollis* and *H. communis* were the most abundant species in 25%, 11.5%, 7.75, 5.8% and 1.9% of communities, respectively. In contrast to the observation in the spring samples, larval *H. aduncum* dominated in more infracommunities than adult (21.2% *vs* 3.8% respectively).

Table 6.22. Infracommunity descriptors of metazoan communities in *G. morhua* from Irish Sea and significance of differences (K-W test; R of ANOSIM for similarities) between the three samples (ns = not significant).

	Spring 2002 (n =60)	Autumn 2002 (n =52)	Spring 2003 (n =24)	Significance of differences χ^2 (R)	p
Fish length (cm)	35.8-75.0	27.3-50.5	35.2-64.00	82.738	0.000
Total infracommunities					
No. species/fish (range)	4-14	3-13	5-14		
Mean no. of species ± SD	9.57 ± 2.36	6.31 ± 2.52	9.00 ± 2.34	40.284	<0.001
Mean no. of individuals ± SD	186.82 ± 147.72	39.04 ± 30.77	136.42 ± 86.90	72.777	<0.001
Mean dominance ± SD	0.48 ± 0.15	0.50 ± 0.76	0.45 ± 0.13	0. 963	ns
Mean diversity ± SD	1.34 ± 0.33	1.09 ± 0.33	1.34 ± 0.27	15.815	0.000
Mean similarity	59.84	47.08	57.75	0.37	0.001
Larval parasite assemblages					
No. species/fish (range)	0-7	0-5	0-5		
Mean no. of species ± SD	3.18 ± 1.32	1.38 ± 1.16	2.96 ± 1.43	45.265	0.000
Mean no. of individuals ± SD	48.25 ± 76.76	5.56 ± 8.49	36.13 ± 40.46	60.689	0.000
Mean similarity	48.42	28.13	41.45	0.236	0.001
Gastrointestinal parasite assemblages					
No. species/fish (range)	2-9	2-11	4-10		
Mean no. of species ± SD	5.80 ± 1.25	4.25 ± 1.97	6.25 ± 1.65	28.421	0.000
Mean no. of individuals ± SD	132.67 ± 94.03	30.67 ± 26.95	98.58 ± 60.22	65.067	0.000
Mean similarity	65.47	45.46	62.94	0.324	0.001
Ectoparasite assemblages					
No. species/fish (range)	0-4	0-2	0-2		
Mean no. of species ± SD	1.35 ± 0.94	0.98 ± 0.58	0.50 ± 0.59	19.338	0.000
Mean no. of individuals ± SD	5.90 ± 8.74	2.81 ± 3.70	1.13 ± 1.45	16.367	0.000
Mean similarity	32.17	41.92	17.25	0.087	0.002

6.3.4.3. Infracommunity similarity

Infracommunities showed generally low similarities due to the low and variable similarity of larval and ectoparasite assemblages (Table 6.22). The three species that dominated most of the infracommunities contributed substantially to the similarity between them: *H. aduncum*, *D. varicus* and *C. osculatum* in both spring samples and the first two in the AS (Table 6.23).

Table 6.23. Species that most contribute to the similarity (Bray-Curtis index) between infracommunities in the three samples from Irish Sea. Mean abundance [ln(x+1)], mean similarity, the ratio similarity to standard deviation, the percentage contribution to similarity, and the cumulative percent similarity are given for each species.

Species	Mean abundance	Mean similarity	Similarity/SD	Percent contribution	Cumulative percent similarity
FSS					
H .aduncum	3.70	16.87	3.51	28.19	28.19
D. varicus	3.54	15.29	3.44	25.54	53.73
C. osculatum	2.22	7.53	1.56	12.59	66.32
SSS					
D. varicus	3.32	17.11	6.00	29.63	29.63
H .aduncum	3.38	15.65	2.79	27.10	56.74
C. osculatum	1.91	6.61	1.29	11.45	68.18
AS					
D. varicus	2.31	18.97	2.73	40.29	40.29
H. aduncum	1.53	9.79	1.19	20.80	61.10

Overall, ANOSIM procedure revealed overlapping community composition between the three samples using infracommunities as replicates, the adult parasite assemblages showing somewhat higher value for R whereas larval assemblages and especially ectoparasite assemblages were most homogenous (Table 6.22). An analysis restricted to common parasite species revealed a similar result ($R=0.381$, $p=0.001$) suggesting that they contribute substantially to the homogeneity. Pairwise tests indicated somewhat higher compositional differences in total infracommunities between FSS and AS ($R=0.527$; $p<0.001$).

The two spring samples exhibited the lowest dissimilarity (42.15%) with *C. osculatum*, *A. morrhuae* and *H. communis* contributing most to it (Table 6.24). The dissimilarity between the AS and the spring samples exhibited comparable values. The most important parasite species generating the highest dissimilarity between communities of AS and spring samples were: *H. aduncum*, *D. varicus*, *H. communis*, *A. morrhuae*, *C. cirratus* and *A. crassicollis*. The most consistent species in both comparisons were *H. aduncum* and *D. varicus* because they exhibited the highest ratio of dissimilarity/SD (Table 6.24).

Table 6.24. Species that most contribute to the dissimilarity (Bray-Curtis index) between infracommunities in the three samples from Irish Sea. Mean abundance [ln(x+1)], mean dissimilarity, the ratio dissimilarity to standard deviation, the percent contribution to dissimilarity, and the cumulative percent dissimilarity are given for each species. Mean dissimilarities between samples in parentheses.

Parasite species	Mean abundance group 1	Mean abundance group 2	Mean dissimilarity	Dissimilarity/SD	Percent contribution	Cumulative percent similarity
FSS vs AS (mean dissimilarity 58.36%)						
H. aduncum	3.70	1.53	8.31	1.55	14.25	14.25
C. osculatum	2.22	0.23	7.16	1.66	12.28	26.52
D. varicus	3.54	2.31	5.65	1.37	9.68	36.20
H. communis	1.86	0.52	5.42	1.25	9.28	45.48
A. morrhuae	1.53	1.05	4.79	1.28	8.21	53.69
C. cirratus	1.21	0.19	4.03	1.22	6.90	60.60
A. crassicollis	0.65	0.86	3.56	1.03	6.09	66.69
FSS vs SSS (mean dissimilarity 42.15%)						
C. osculatum	2.22	1.91	4.08	1.25	9.68	9.68
A. morrhuae	1.53	1.13	3.87	1.27	9.18	18.86
H. communis	1.86	1.55	3.50	1.15	8.31	27.16
H. aduncum	3.70	3.38	3.42	1.20	8.12	35.28
C. cirratus	1.21	1.30	3.06	1.31	7.25	42.53
A. crassicollis	0.65	0.89	2.96	0.95	7.01	49.55
D. varicus	3.54	3.32	2.87	1.25	6.82	56.37
C. adunca	1.09	0.45	2.66	1.19	6.31	62.67
AS vs SSS (mean dissimilarity 57.80%)						
H. aduncum	1.53	3.38	8.06	1.51	13.95	13.95
C. osculatum	0.23	1.91	6.77	1.35	11.71	25.66
D. varicus	2.31	3.32	5.09	1.26	8.81	34.46
H. communis	0.52	1.55	4.77	1.29	8.25	42.71
C. cirratus	0.19	1.30	4.64	1.29	8.03	50.74
A. morrhuae	1.05	1.13	4.52	1.21	7.82	58.56
A. crassicollis	0.86	0.89	4.28	1.02	7.40	65.96

6.3.5. Parasite communities in cod in the North Sea

A total of 147 fish was examined. The structure of the three samples by host sex and age is summarized in Table 6.25. Females were better represented than males in all samples but there were no marked differences. The sample sizes for cod of different ages also differed, and particularly in the autumn sample when the sampled population comprised more juveniles (age class 1). Fish sizes (SL) of the three samples overlapped and no significant differences were detected (Figure 6.6; see Table 6.28 for ranges).

Table 6.25. Structure of cod population sample from North Sea by age and sex of host. For age determination, it was assumed that cod were born in January, NA, age not determined.

Age class (yrs)		1		2		3		4		5		6		9		NA		Totals by sex		Totals
Year	Season	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
2002	FSS	1		4	1	4	7	4	5				1					13	14	27
2002	AS	12	15	8	11	5	5		1		1						2	25	35	60
2003	SSS			22	19	1	8	3	3	2			1		1			28	32	60
Totals		13	15	34	31	10	20	7	9	2	1		2		1		2	66	81	147

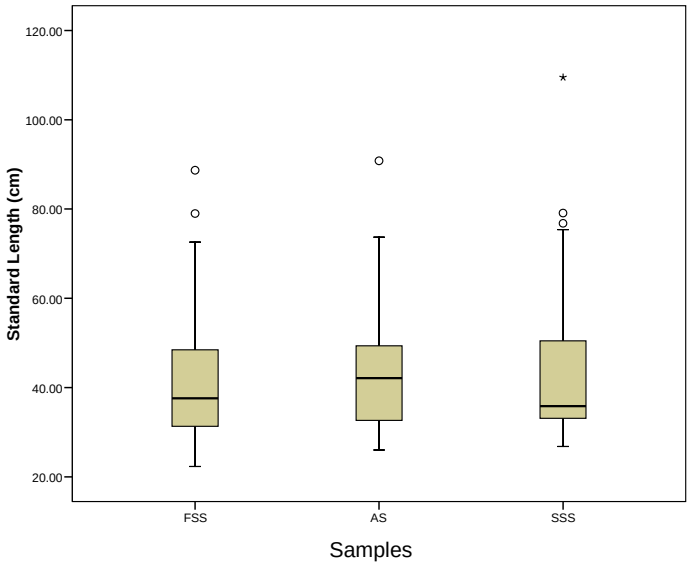

Figure 6.5. Box-plots for standard length of *G. morhua* in three samples from North Sea. *Abbreviations*: Samples: FS, first spring sample; AS, autumn sample; SSS, second spring sample.

6.3.5.1. Community composition

Species composition, prevalence and mean abundance of each parasite species in the three samples (FSS from Dogger Bank and AS and SSS from Skagerrak) are summarized in Table 6.26. A total of 19 species were common in at least one of the three samples. Of these, three species were most prevalent in all samples: the trematode *D. varicus*, the anisakid nematode *H. aduncum* (L3 and adults) and the copepod *C. adunca* (Table 6.27). No significant differences were found in the abundance of these species between the three samples except for *H. aduncum* (adults) (p=0.001), its mean abundance being greater in SSS (Skagerrak). *A. simplex* and *C. cirratus* were both most prevalent in the spring samples and *A. crassicolis* in the AS. Four fish (SL range 50.8-79.0 cm) from FSS were infected with more than a hundred individuals of *D. varicus* (between 160-281 trematodes per fish).

Table 6.26. Prevalence (P%), mean (MA ± SD) and median (M, shown if >0 only) abundance of parasites in the three samples of *G. morhua* from North Sea (n = sample size).

Parasite species/Sample	Dogger Bank Spring 2002 (n = 27)	Skagerrak Autumn 2002 (n = 60)	Skagerrak Spring 2003 (n = 60)
	P (%) MA ± SD (M)	P (%) MA ± SD (M)	P (%) MA ± SD (M)
MONOGENEA (adult forms)			
Diclidophora merlangi	3.7 0.04 ± 0.19		
DIGENEA (metacercariae)			
Bucephalinae gen. sp.		1.7 0.03 ± 0.26	3.3 0.17 ± 1.06
Cryptocotyle lingua		3.3 0.03 ± 0.18	
Otodistomum sp.			6.7 0.83 ± 3.82
DIGENEA (adult forms)			
Derogenes varicus	77.8 40.07 ± 79.77 (2)	86.7 9.43 ± 14.25 (5)	91.7 8.87 ± 15.85 (4)
Gonocerca phycidis			1.7 0.02 ± 0.13
Hemiurus communis	40.7 3.59 ± 7.96	48.3 1.83 ± 3.97	51.7 8.13 ± 30.88 (1)
Hemiurus luehei		23.3 1.87 ± 6.20	3.3 0.03 ± 0.18
Lecithaster ?*gibbosus*		1.7 0.05 ± 0.39	

Parasite species/Sample	Dogger Bank Spring 2002 (n = 27)	Skagerrak Autumn 2002 (n = 60)	Skagerrak Spring 2003 (n = 60)
Lepidapedon elongatum		3.3 0.50 ± 2.93	1.7 0.02 ± 0.13
Stephanostomum spp.	51.8 6.59 ± 15.07 (1)	43.3 6.87 ± 20.03	31.7 1.65 ± 4.05
Steringotrema sp.		1.7 0.02 ± 0.13	
CESTODA (larval forms)			
Grillotia sp.	3.7 0.15 ± 0.77		
Lacistorhynchus sp.	3.7 0.04 ± 0.19	1.7 0.02 ± 0.13	1.7 0.02 ± 0.13
Trypanorhyncha gen. spp.			8.3 0.33 ± 1.64
Unidentified plerocercoids			3.3 0.05 ± 0.29
CESTODA (adult forms)			
Abothrium gadi	7.4 0.07 ± 0.27	1.7 0.02 ± 0.13	8.3 0.08 ± 0.28
NEMATODA (larval forms)			
Anisakis simplex s.l. (L3)	88.9 80.63 ± 135.78 (15)	31.7 1.18 ± 3.02	51.7 46.65 ± 171.88 (1)
Contracaecum osculatum s.l. (L3)	59.3 6.56 ± 12.16 (2)	5.0 0.05 ± 0.22	6.7 0.15 ± 0.58
Hysterothylacium aduncum (L3)	70.4 23.74 ± 85.08 (3)	81.7 5.30 ± 7.48 (3)	78.3 13.30 ± 21.92 (4.5)
Hysterothylacium rigidum (L3)	18.5 0.59 ± 1.42	11.7 0.75 ± 3.71	36.7 2.25 ± 10.57
Pseudoterranova decipiens s.l. (L3)	25.9 0.63 ± 1.18	8.3 0.17 ± 0.62	11.7 2.93 ± 15.20
Rhapidascaris sp. (L3)			1.7 0.02 ± 0.13
NEMATODA - adults			
Ascarophis morrhuae	55.6 4.70 ± 7.84 (1)	15.0 0.25 ± 0.70	10.0 0.12 ± 0.37
Ascarophis crassicollis	18.5 0.67 ± 1.73	56.7 26.65 ± 56.06 (3)	11.7 0.97 ± 3.90
Capillaria gracilis	7.4 0.07 ± 0.27	1.7 0.05 ± 0.39	6.7 0.13 ± 0.54

Parasite species/Sample	Dogger Bank Spring 2002 (n = 27)	Skagerrak Autumn 2002 (n = 60)	Skagerrak Spring 2003 (n = 60)
Cucullanus cirratus	74.1 4.96 ± 10.32 (2)	43.3 1.35 ± 4.04	58.3 4.35 ± 7.69 (1)
Hysterothylacium aduncum	77.8 20.85 ± 67.72 (2)	83.3 7.72 ± 10.07 (4)	91.7 22.90 ± 28.79 (10.5)
ACANTHOCEPHALA (post-cystacant)			
Corynosoma semerme	3.7 0.04 ± 0.19		
Corynosoma strumosum	37.0 5.85 ± 13.93	6.7 0.22 ± 1.19	11.7 0.18 ± 0.54
ACANTHOCEPHALA (adult forms)			
Echinorhynchus gadi s.l.	11.1 0.15 ± 0.46	46.7 4.85 ± 13.56	18.3 0.85 ± 2.48
HIRUDINEA			
Calliobdella nodulifera	7.4 0.07 ± 0.27		1.7 0.02 ± 0.13
COPEPODA			
Caligus curtus		8.3 0.12 ± 0.42	15.0 0.55 ± 2.38
Caligus elongatus	25.9 3.70 ± 10.49	25.0 1.95 ± 6.58	13.3 0.50 ± 2.73
Clavella adunca	70.4 3.70 ± 7.29 (1)	66.7 1.88 ± 2.88 (1)	75.0 2.23 ± 2.58 (1)
Lernaeocera branchialis	14.8 0.19 ± 0.48	18.3 0.45 ± 1.38	16.7 0.20 ± 0.48
AMPHIPODA			
Lafystius morhuanus	3.7 6.93 ± 35.99		

There were differences in the most prevalent species between samples from Dogger Bank and Skagerrak. The list of these species at the former also included *Stephanostomum* spp., *A. morrhuae*, *C. osculatum* while that of the latter included *H. communis* (SSS) and *A. crassicollis* (AS). Assuming that the difference in the composition of the most prevalent species may be due to geographical distance between the sampling locations and that there are seasonal variations in species distributions, the distributions of the most prevalent species at Skagerrak were first tested. Only four species showed significant differences. *A. simplex*, *C. cirratus* and *H. aduncum* (adults) were more abundant in the spring sample ($p<0.01$) whereas *A. crassicollis* showed higher abundance in the autumn sample

($p<0.001$). Prevalences showed the same trend for *A. simplex* ($p<0.05$) and *A. crassicollis* ($p<0.001$) and did not differ for the other 2 species. The differences in abundance of *A. simplex* remained no more significant when juvenile fish (age class 1) were excluded from the comparisons.

Comparison of the distribution of the most prevalent species between spring samples from Dogger Bank and Skagerrak showed that four of the nine species tested had significantly different infection parameters (except for the prevalence of *H. aduncum* (adults). *A. simplex*, *C. osculatum* and *A. morrhuae* were more prevalent and abundant in the sample from Dogger Bank (FSS, all $p\leq0.001$; see Table 6.26) whereas *H. aduncum* (adults) was more abundant in the sample from Skagerrak ($p=0.008$).

6.3.5.1. Community structure

Component community descriptors of the North Sea samples are given in Table 6.27. Total component community richness was high in all three samples and showed a maximum in SSS (Skagerrak), which also had the richest list of larval parasites. The lowest total species richness was observed in FSS (Dogger Bank) which also had lowest number of gastrointestinal species. The Berger-Parker dominance index had similar and low values, while Shannon-Wiener's index was correspondingly high and showed a maximum in the AS. With 20-23 (out of 25-29) species shared, the similarity between component communities was high (range 72.4-76.0%).

There was a significant positive effect of fish size (SL) on the species richness and abundance of total parasite infracommunities (range for $r_s=0.514$-0.717 and 0.586-0.811, respectively; $p < 0.001$). Six of the most prevalent species were found to be size-dependent in at least 2 samples (*D. varicus*, *A. simplex*, *H. communis*, *A. crassicollis*, *C. cirratus* and *H. aduncum* (L3 and adults); the abundances of the first two species were significantly correlated with SL in all samples ($r_s=0.746$, 0.333, 0.339 and 0.624, 0.313, 0.784, respectively; all $p<0.01$). However, only few correlations with both size and age were found: *A. simplex* in all samples; *A. crassicollis* and *H. communis* in both samples from Skagerrak, *C. cirratus* in FSS, *H. aduncum* (adults) in SSS. Interestingly, among the larval anisakids assumed to be accumulated with age of fish, only *A. simplex* showed highly significant correlations with age ($r_s=0.509$, 0.339 and 0.720 for FSS, AS and SSS, respectively; $p<0.001$).

Table 6.27. Component community descriptors of metazoan communities in *G. morhua* from North Sea.

	Dogger Bank (Spring 2002) FSS	Skagerrak (Autumn 2002) AS	Skagerrak (Spring 2003) SSS
Total no. of parasites species	25	26	29
Total no. of spp. in larval assemblages	9	9	12
Total no. of spp. in gastrointestinal assemblages	11	14	13
Total no. of spp. in ectoparasite assemblages	5	4	5
Berger-Parker dominance index	0.38	0.36	0.39
Shannon-Wiener's diversity index	1.89	2.05	1.77
Bray-Curtis similarity index (shared species)			
FSS	-	72.4 (20)	73.6 (21)
AS	72.4	-	76.0 (23)
Most prevalent species	*D. varicus*	*D. varicus*	*D. varicus*
			H. communis
	Stephanostomum spp.		
	A. simplex		*A. simplex*
	C. osculatum		
	H. aduncum L3	*H. aduncum*	*H. aduncum* L3
	A. morrhuae	L3	
	C. cirratus	*A. crassicollis*	*C. cirratus*
	H. aduncum		*H. aduncum*
	C. adunca	*H. aduncum*	*C. adunca*
		C. adunca	

Infracommunity descriptors of metazoan assemblages from the three samples are shown in Table 6.28. The number of species per fish ranged from 1 to 17 and the mean species richness was high. Species density distributions in all samples agreed with Poisson distribution. The density distributions of species in one of the samples (SSS) departed (χ^2=41.55, p=0.02) whereas those in the FSS and AS agreed with the distribution predicted by the null model of Janovy *et al.* (1995). Mean species richness was the only descriptor of total infracommunities that varied significantly between samples due to the significant differences in the larval assemblages (Table 6.28). The assemblages of gastrointestinal parasites and ectoparasites did not show significant differences between samples.

Table 6.28. Infracommunity descriptors of metazoan communities in *G. morhua* from North Sea and significance of differences (K-W test; R of ANOSIM for similarities) between the three samples (ns = not significant).

	Dogger Bank (Spring 2002) (n =27)	Skagerrak (Autumn 2002) (n =60)	Skagerrak (Spring 2003) (n =60)	Significance of differences χ^2 (R)	p
Fish length (cm)	22.3-88.7	26-90.8	26.8-109.5	0.384	ns
Total infracommunities					
No. species/fish (range)	1-12	3-15	1-17		
Mean no. of species ± SD	8.15 ± 2.60	6.57 ± 2.50	6.55 ± 3.20	9.940	0.007
Mean no. of individuals ± SD	214.59 ± 296.71	73.60 ± 74.11	118.48 ± 225.95	4.374	ns
Mean dominance ± SD	0.57 ± 0.17	0.54 ± 0.17	0.57 ± 0.19	0.785	ns
Mean diversity ± SD	1.12 ± 0.35	1.09 ± 0.36	0.98 ± 0.36	3.761	ns
Mean similarity	40.45	43.58	45.97	0.25	0.001
Larval parasite assemblages					
No. species/fish (range)	0-5	0-5	0-8		
Mean no. of species ± SD	3.11 ± 1.22	1.52 ± 1.14	2.22 ± 1.71	27.553	0.000
Mean no. of individuals ± SD	118.22 ± 192.76	7.75 ± 11.19	66.88 ± 187.04	30.491	0.000
Mean similarity	42.74	39.79	32.90	0.123	0.001
Gastrointestinal parasite assemblages					
No. species/fish (range)	0-7	1-8	1-9		
Mean no. of species ± SD	4.26 ± 1.68	4.57 ± 1.75	3.87 ± 1.72	5.501	ns
Mean no. of individuals ± SD	81.78 ± 125.79	61.45 ± 72.58	48.12 ± 63.27	1.169	ns
Mean similarity	35.29	41.99	50.37	0.2	0.001
Ectoparasite assemblages					
No. species/fish (range)	0-3	0-3	0-3		
Mean no. of species ± SD	1.22 ± 0.89	1.18 ± 0.83	1.22 ± 0.88	0.013	ns
Mean no. of individuals ± SD	14.59 ± 37.66	4.40 ± 7.67	3.50 ± 0.88	0.840	ns
Mean similarity	27.08	28.48	36.15	0.01	ns

Comparisons between the samples from Skagerrak (AS *vs* SSS) revealed significant differences in richness, abundance and diversity of larval assemblages (p=0.01, 0.002 and 0.006, respectively) and in the richness of assemblages of gastrointestinal parasites (p=0.026). When juvenile fish (*c.* 1/2 of AS, see Table 6.25) were excluded from the comparisons, significant differences between the two samples were detected in total infracommunity richness, abundance and diversity ($p<0.05$ in all cases) and in gastrointestinal parasite assemblages ($p<0.005$). On the other hand, comparisons between Dogger Bank (FSS) and Skagerrak (SSS) revealed only differences in richness (p=0.005) and abundance (p=0.058) of total communities which were due to the significant differences in richness (p=0.001) and abundance (p=0.003) of larval assemblages; the latter also showed differences in diversity (p=0.001).

Six of the most prevalent species were frequently found to dominate infracommunities in cod from the three samples. *A. simplex*, *D. varicus* and *H. aduncum* dominated 44.4%, 14.8% and 11.11% of the infracommunities in the FSS, respectively. Larval *H. aduncum* alone dominated 7.4% of the infracommunities. Infracommunities in the SSS were dominated by *H. aduncum*, *D. varicus* and *C. cirratus* (56.7%, 11.7% and 10%, respectively). In this sample, adults of *H. aduncum* alone dominated 36.7% of the infracommunities. The AS exhibited a different pattern in that *A. crasicollis* dominated 31.7% of the infracommunities and *H. aduncum* and *D. varicus* were the most abundant species in 23.3% and 15% of communities, respectively. Similarly to the SSS adult *H. aduncum* alone dominated in more infracommunities than larval *H. aduncum* (L3) (18.3% *vs* 6.7% respectively). Finally, *Stephanostomum* spp. had the highest abundance in 13.3% of the infracommunities in this sample. Occasionally nine other species were most abundant in a few infracommunities: *C. adunca*, *C. osculatum*, *P. decipiens*, *C. strumosum*, *H. communis*, *L. elongatum*, *A. morrhuae*, *C. elongatus* and *L. morhuanus*.

6.3.5.1. Infracommunity similarity

Infracommunities showed generally low similarity (Table 6.28). Almost all dominant species cited above contributed to the similarity between infracommunities (Table 6.29). In the samples from Skagerrak (AS and SSS) *H. aduncum* and *D. varicus* contributed most to the similarity within each sample whereas in the FSS (Dogger Bank) the species that most contributed to the mean similarity were *A. simplex, H. aduncum, D. varicus* and *C. adunca* (Table 6.29).

Table 6.29. Species that most contribute to similarity (Bray-Curtis index) between infracommunities in the three samples from North Sea. Mean abundance [ln(x+1)], mean similarity, the ratio similarity to standard deviation, the percent contribution to similarity, and the cumulative percent similarity are given for each species.

Species	Mean abundance	Mean similarity	Similarity/SD	Percent contribution	Cumulative percent similarity
FSS					
A. simplex	2.91	10.24	1.41	25.31	25.31
H. aduncum	2.26	8.66	1.70	21.40	46.72
D. varicus	1.87	4.64	0.82	11.48	58.19
C. adunca	0.99	3.41	0.78	8.43	66.62
AS					
H. aduncum	2.24	15.47	2.12	35.67	35.67
D. varicus	1.76	10.20	1.41	23.52	59.19
A. crassicollis	1.70	5.06	0.57	11.67	70.86
SSS					
H. aduncum	2.93	19.83	1.97	43.15	43.15
D. varicus	1.70	11.32	1.41	24.64	67.78

Overall, ANOSIM procedure revealed little separation between the three samples using infracommunities as replicates, the ectoparasite assemblages being most homogenous (Table 6.28). An analysis restricted to common parasite species revealed a poorer result (ANOSIM R=0.235, p=0.001) suggesting a higher compositional homogeneity of the infracommunities; the mean similarities for each sample were also lower in this analysis (FSS, 39.93%; AS, 42.24%; and SSS, 46.06%).

Pairwise tests of the total communities showed that the two samples (AS and SSS) from Skagerrak showed less compositional separation (AS *vs* SSS, R=0.146; $p<0.001$) than in comparisons with FSS from Dogger Bank (FSS *vs* AS, R=0.415; FSS *vs* SSS, R=0.329; $p<0.001$). The two samples from Skagerrak (AS and SSS) exhibited the lowest dissimilarity (59.1%) with *A. crassicollis* and *H. aduncum* and *D. varicus* contributing most to it; the latter was most consistent species in the entire sample because its ratio of dissimilarity/SD was the highest (1.25) (Table 6.30).

The level of dissimilarity between the two areas of sampling was somewhat lower in spring (FSS *vs* AS: 63.7 *vs* 68%). The most important parasite species generating the highest dissimilarity between communities of Dogger Bank and Skagerrak were: *A. simplex*, *H. aduncum*, *D. varicus* and *A. crassicollis*) (Table 6.30).

Table 6.30. Species that most contribute to the dissimilarity (Bray-Curtis index) between infracommunities in the three samples from North Sea. Mean abundance [ln(x+1)], mean dissimilarity, the ratio dissimilarity to standard deviation, the percent contribution to dissimilarity, and the cumulative percent dissimilarity are given for each species. Mean dissimilarities between samples in parentheses.

Parasite species	Mean abundance group 1	Mean abundance group 2	Mean dissimilarity	Dissimilarity /SD	Percent contribution	Cumulative percent similarity
AS *vs* SSS (mean dissimilarity 59.06%)						
A. crassicollis	1.70	0.21	7.35	0.90	12.44	12.44
H. aduncum	2.24	2.93	6.93	1.19	11.73	24.17
D. varicus	1.76	1.70	5.47	1.25	9.26	33.43
A. simplex	0.42	1.24	4.89	0.93	8.29	41.72
C. cirratus	0.48	1.04	4.82	1.01	8.17	49.88
Stephanostomum spp.	0.83	0.48	4.72	0.79	7.99	57.87
H. communis	0.64	0.79	3.87	1.08	6.56	64.43
FSS *vs* SSS (mean dissimilarity 63.73%)						
A. simplex	2.91	1.24	9.27	1.56	14.54	14.54
H. aduncum	2.26	2.93	7.19	1.12	11.29	25.83
D. varicus	1.87	1.70	6.72	1.27	10.55	36.38
C. cirratus	1.14	1.04	4.68	1.09	7.34	43.73
C. osculatum	1.24	0.08	4.60	0.99	7.22	50.94
Stephanostomum spp.	0.88	0.48	3.80	0.90	5.95	56.90
A. morrhuae	1.01	0.08	3.76	0.84	5.89	62.79
FSS *vs* AS (mean dissimilarity 68%)						
A. simplex	2.91	0.42	9.21	1.71	13.54	13.54
D. varicus	1.87	1.76	6.79	1.31	9.99	23.52
A. crassicollis	0.27	1.70	6.26	0.90	9.21	32.73
H. aduncum	2.26	2.24	5.61	1.10	8.25	40.98
Stephanostomum spp.	0.88	0.83	4.50	0.89	6.62	47.60
C. osculatum	1.24	0.03	4.48	1.01	6.59	54.20
C .cirratus	1.14	0.48	3.95	1.07	5.81	60.01

6.3.6. Parasite communities in cod in Trondheimsfjord (Norway)

A total of 60 fish was examined. The structure of the sample by host sex and age is summarized in Table 6.31. Males were better represented than females but there were no marked differences. The sample sizes for cod of different ages also differed since *c.* half of the cod were 2 years-old. The sizes of males and females overlapped and no significant differences were detected (Figure 6.7; see Table 6.34 for total size range).

Table 6.31. Structure of cod population sample from Trondheimsfjord (Norway) Sea by age and sex of host. For age determination, it was assumed that cod were born in January. NA, age not determined.

Age class (yrs)		1		2		3		4		5		7		Totals by sex		Totals
Year	Season	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
2003	SSS	2		13	13	5	3	9	4	6	4	1		36	24	60

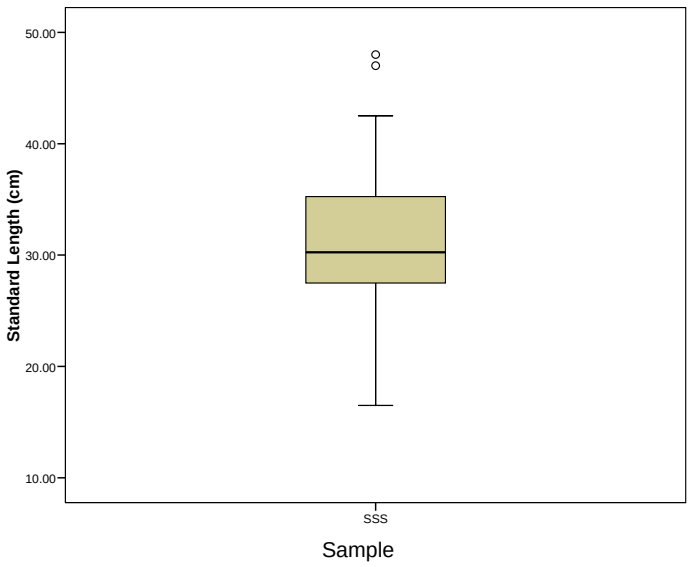

Figure 6.7. Box-plot of standard length of *G. morhua* from Trondheimsfjord (Norway). (*Abbreviation*: Sample: SSS, second spring sample.

6.3.6.1. Community composition

Species composition, prevalence and mean abundance of each parasite species are presented in Table 6.32. Ten species were common and nine rare. Of the common species five had prevalence >50%: the trematodes *H. communis* and *L. rachion* and the nematodes *H. aduncum* (L3), *C. gracilis* and *C. cirratus*.

Table 6.32. Prevalence (P%), mean (MA ± SD) and median (M, shown if >0 only) abundance of parasites in *G. morhua* from Trondheimsfjord (Norway) (n = sample size).

Parasite species/Sample	Spring 2003 (n = 60)	Parasite species/Sample	Spring 2003 (n = 60)
	P% MA ± SD (M)		P% MA ± SD (M)
TREMATODA (metacercariae)		NEMATODA (adult forms)	
	1.7	*Ascarophis morrhuae*	1.7
Prosorhynchus crucibulum	0.02 ± 0.13		0.02 ± 0.13
TREMATODA (adult forms)		*Capillaria gracilis*	88.3 18.25 ± 38.34 (8)
Derogenes varicus	30.0 0.48 ± 0.93	*Cucullanus cirratus*	93.3 14.32 ± 19.43 (8)
Hemiurus communis	50.0 1.90 ± 3.12 (0.5)	*Hysterothylacium aduncum*	5.0 0.12 ± 0.58
Lepidapedon elongatum	60.0 177.47 ± 585.76 (2)	ACANTHOCEPHALA (post-cystacant)	
Lepidapedon rachion	45.0 49.42 ± 191.24	*Corynosoma semerme*	1.7 0.02 ± 0.13
NEMATODA (larval forms)		ACANTHOCEPHALA (adult forms)	
Anisakis simplex s.l. (L3)	5.0 0.05 ± 0.22	*Echinorhynchus gadi* s.l.	30.0 0.48 ± 1.02
Contracaecum osculatum s.l. (L3)	8.3 0.23 ± 0.96	COPEPODA (adult forms)	
Hysterothylacium aduncum (L3)	65.0 1.20 ± 1.47 (1)	*Clavella adunca*	43.3 0.92 ± 1.41
Hysterothylacium rigidum (L3)	8.3 0.12 ± 0.42	*Holobomolochus confusus*	1.7 0.02 ± 0.13
Pseudoterranova decipiens s.l. (L3)	1.7 0.02 ± 0.13	*Lernaeocera branchialis*	21.7 0.33 ± 0.73

6.3.6.2. Community structure

Descriptors of the component community sampled at Trondheimsfjord are given in Table 6.33. Total component community richness was not very high and there were only three ectoparasite species. The Berger-Parker dominance index was high and Shannon-Wiener's index relatively high.

Table 6.33. Component community descriptors of metazoan communities in *G. morhua* from Trondheimsfjord (Norway).

	Spring 2003 SSS
Total no. of parasites species	18
Total no. of spp. in larval assemblages	7
Total no. of spp. in gastrointestinal assemblages	9
Total no. of spp. in ectoparasite assemblages	3
Berger-Parker dominance index	0.67
Shannon-Wiener's diversity index	1.05
Bray-Curtis similarity index(shared species)	*H. communis* *L. elongatum* *H. aduncum* L3 *C. gracilis* *C. cirratus*

There was a significant positive effect of fish size (SL) on the species richness and abundance of total parasite infracommunities (r_s=0.518 and r_s=0.586, respectively; $p<0.001$). Four of the five most prevalent species (*H. communis*, *L. elongatum*, *C. gracilis* and *C. cirratus*) were found to be size-dependent (r_s=0.397; 0.301; 0.322; and 0.619, respectively; all $p<0.02$). Moreover the abundance of these species was also positively correlated with fish age (r_s=0.312; 0.377; 0.319; and 0.584, respectively; all $p<0.02$).

Infracommunity descriptors of the metazoan assemblages from Trondheimsfjord are shown in Table 6.34. Infracommunities were rich and abundant, the number of species per fish ranging from 1 to 10. However, larval and ectoparasite assemblages were notably poor. Species density distributions in all three samples agreed with both the Poisson distribution and the distribution predicted by the null model of Janovy *et al.* (1995).

Three of the most post prevalent species frequently dominated infracommunities in cod from Trondheimsfjord sample. *C. cirratus* dominated 35% of the infracommunities and *L. elongatum* and *C. gracilis* were the most abundant species in 28.3% of infracommunities each. Occasionally three other species, *L. rachion*, *H. aduncum* and *E. gadi*, dominated few infracommunities (5%, 1.7% and 1.7%, respectively).

Table 6.34. Infracommunity descriptors of metazoan communities in *G. morhua* from Trondheimsfjord (Norway).

	Spring 2003 (n =60)
Fish length (cm)	16.5-48.0
Total infracommunities	
No. species/fish (range)	1-10
Mean no. of species ± SD	5.57 ± 2.06
Mean no. of individuals ± SD	265.37 ± 718.50
Mean dominance ± SD	0.61 ± 0.18
Mean diversity ± SD	0.84 ± 0.33
Mean similarity	44.18
Larval parasite assemblages	
No. species/fish (range)	0-3
Mean no. of species ± SD	0.92 ± 0.67
Mean no. of individuals ± SD	1.65 ± 1.74
Mean similarity	31.94
Gastrointestinal parasite assemblages	
No. species/fish (range)	1-7
Mean no. of species ± SD	4.03 ± 1.57
Mean no. of individuals ± SD	262.45 ± 718.36
Mean similarity	46.01
Ectoparasite assemblages	
No. species/fish (range)	0-2
Mean no. of species ± SD	0.67 ± 0.66
Mean no. of individuals ± SD	1.27 ± 1.60
Mean similarity	18.97

6.3.6.3. Infracommunity similarity

Infracommunities showed rather low similarity levels; these were notably low for ectoparasite assemblages. The three dominant species cited above largely contributed to the similarity between infracommunities (Table 6.35). *C. cirratus* and *C. gracilis* showed similar contribution whereas *L. elongatum* contributed less to the similarity because its abundance was lower. Consequently it was the least consistent species because its ratio of similarity/SD was the smallest (0.62).

Table 6.35. Species that most contribute to (Bray-Curtis index) between infracommunities in Trondheimsfjord (Norway). Mean abundance [ln(x+1)], mean similarity, the ratio similarity to standard deviation, the percentage contribution to similarity, and the cumulative percent similarity are given for each species.

Species	Mean abundance	Mean similarity	Similarity/SD	Percent contribution	Cumulative percent similarity
SSS					
C. cirratus	2.06	14.30	1.45	32.37	32.37
C. gracilis	2.06	13.27	1.35	30.03	62.40
L. elongatum	1.97	5.68	0.62	12.86	75.25

6. 4. Discussion

The present results agree well with the predictions based on the comparative analysis of the higher level taxonomical structure of the regional parasite faunas in cod formulated in Chapter 4. Thus, parasite communities in cod from the Baltic Sea and Trondheimsfjord exhibited the lowest levels of richness, abundance and diversity of total infracommunities and both larval and ectoparasite assemblages (the latter lacking in the Baltic Sea). The only departure was the higher richness and abundance of the gastrointestinal helminth assemblages studied at Trondheimsfjord, the mean richness being within the lower range for assemblages sampled in the open water regions and the mean abundance being well above the upper limits observed in any region. As expected, communities from the low-salinity regions also showed a higher heterogeneity of infracommunity composition and structure which resulted in mean similarity levels at the lower range, associated with considerable variation in larval helminth and ectoparasite assemblages.

Therefore, as expected, the low salinity of the Baltic Sea which limits the distribution of ectoparasites and many intermediate hosts for parasites with complex life-cycles, is reflected in the composition and structure of parasite communities in cod from this region. The majority of the species reported here agree with the species list given by Reimer & Walter (1993). Three species listed by these authors, *Brachyphallus crenatus*, *Bothriocephalus scorpii* and *Pomphorhynchus laevis*, were not recovered in the present study which revealed three other species not reported by Reimer & Walter (1993) (*C. osculatum*, *C. gracilis* and *Corynosoma* spp.). The present study recorded higher prevalence of anisakids than reported by Myjak *et al.* (1994) and also higher prevalences of *E. gadi* and *H. aduncum* than those recorded by Pilecka-Rapacz & Sobecka (2004). The record of *H. communis* in a single fish from the SSS is outside the boundary lines for the distribution of this species (Reimer, 1970). However, this fact does not indicate that *H. communis* is expanding its distribution eastwards; rather the infected fish had migrated from the neighbouring Kattegat feeding area. The latter suggestion agrees with the report of this species by Möller (1975) in Kiel Fjord.

E. gadi was the most prevalent species in all samples from Baltic Sea although showing some differences between samples. This acanthocephalan is a generalist parasite with regard to both intermediate (benthic crustaceans) and final hosts (fishes) (Zander, 1998) and is the most frequently reported parasite of fish from the Baltic Sea (*e.g.* Möller, 1975; Reimer & Walter, 1993; Zander, 1998; Kesting & Zander, 2000; Hastein *et al.*, 2001; Zander & Reimer, 2002; Pilecka-Rapacz & Sobecka, 2004). Recently, Zander *et al.* (2000)

found that the main hosts in the life-cycles of *Hysterothylacium* sp. and *E. gadi* from Salzhaff (southern Baltic Sea) were amphipods and that the amphipod *Gammarus salinus* harbours both species. Eutrophication was suggested as a leading factor for the massive abundances of generalist parasites in the host populations as well as in the host individuals in the Baltic Sea (Zander, 1998; Kesting & Zander, 2000; Zander & Reimer, 2002). This suggestion is supported by the present study since three of the four dominant species in component communities in cod (*E. gadi*, *C. osculatum* and *H. aduncum*) are generalist parasites; the first two were also found to dominate more than one third of infracommunities (Table 6.36). It is also possible that *E. gadi* and *H. aduncum* are transmitted to cod *via* concomitant infections of the intermediate hosts.

Unexpectedly, parasite communities sampled from Trondheimsfjord exhibited relatively high richness and abundance due to the gastrointestinal parasite assemblages which were the major contributors to the high mean abundance of the total parasite communities. Several species of trematodes are acquired by cod in the first year of life through feeding on small invertebrates which serve as intermediate hosts of the parasites. *L. elongatum* was assumed to be predominantly a parasite of juvenile cod showing decreased infection levels with cod age (Hemmingsen & MacKenzie, 2001). However, the infection levels of this trematode, as well as those of *H. communis* and *D. varicus,* exhibited an increase with fish age in the sample from Trondheimsfjord. Moreover, *L. elongatum*, together with the nematodes *C. cirratus* and *C. gracilis* , were found to dominate infracommunities only in this sample (Table 6.36). Final hosts of *C. gracilis* and *C. cirratus* are mainly gadoids (Moravec, 1994; Køie, 2000; 2001). The family Gadidae is well represented in Trondheimsfjord (10 species, J.A. Sneli pers. comm.). Therefore, the higher richness/abundance of the final hosts at this location may explain the higher levels of infection and dominance of the two nematodes in infracommunities in cod.

Table 6.36. Comparative table of the composition of the most prevalent species in communities in *G. morhua* from the six regions of NE Atlantic. Species found to dominate more than 30% of infracommunities are indicated with (IC).

	Baltic Sea	**Celtic Sea**	**Icelandic waters**	**Irish Sea**	**North Sea**	**Trondheimsfjord**
Larval nematodes	*C. osculatum* (**IC**)	*C. osculatum*	*C. osculatum*	*C. osculatum*	*C. osculatum*	
	H. aduncum	*H. aduncum*	*H. aduncum*	*H. aduncum*	*H. aduncum*	*H. aduncum*
		A. simplex (**IC**)	*A. simplex* (**IC**)	*A. simplex*	*A. simplex* (**IC**)	
		P. decipiens	*P. decipiens*			
Adult nematodes		*H. aduncum* (**IC**)	*H. aduncum* (**IC**)	*H. aduncum* (**IC**)	*H. aduncum* (**IC**)	
	H. rigidum					
		C. cirratus	*C. cirratus*	*C. cirratus*	*C. cirratus*	*C. cirratus* (**IC**)
			A. morrhuae	*A. morrhuae*	*A. morrhuae*	
				A. crassicollis	*A. crassicollis* (**IC**)	
			C. gracilis			*C. gracilis* (**IC**)
Trematodes		*D. varicus*	*D. varicus* (**IC**)	*D. varicus* (**IC**)	*D. varicus*	
		H. communis		*H. communis*	*H. communis*	*H. communis*
					Stephanostomum spp.	
						L. elongatum (**IC**)
Acanthocephalans	*E. gadi* (**IC**)		*E. gadi*			
Copepods		*C. adunca*	*C. adunca*	*C. adunca*	*C. adunca*	
		C. elongatus				

As suggested in Chapter 4 both component and infracommunities in cod from the open water regions (Irish, Celtic and North seas and Icelandic waters) were more diverse and abundant compared with low-salinity regions. However, infracommunities exhibited large variations between regions. Total parasite communities sampled in Icelandic waters were both rich and abundant, showing the highest mean values for the latter parameter, and this was associated with the highest richness and abundance observed in larval helminth assemblages. On the other hand, although variable, communities in cod from Icelandic waters showed the second highest mean abundance (one sample) of the gastrointestinal parasite assemblages. This was largely due to the high infection levels with the trematode *D. varicus* and the nematode *C. cirratus*. These two species were dominant in the communities sampled in autumn and this agrees with the increase in the intermediate hosts of both species (crustaceans) at the end of summer (Køie, 1979; 2000). Despite the seasonal prey availability of crustaceans, young cod feed more on crustaceans than on small fish (ICES, 2005a).

Another characteristic feature of parasite communities in cod from Icelandic waters was the strong domination of the larval nematodes which contributed to nearly 50% of the mean richness and to 63-74% of the mean abundance of the total communities. Thus, the prediction that communities from open water locations would be dominated by larval nematodes was fully met in this region. Communities from the other three regions exhibited much wider variation of the relative representation of the larval anisakids, which was generally higher in fish from the Celtic Sea (42-50% of the mean richness and 51-78% of the mean abundance of total communities) and the lowest in samples from the Irish Sea (22-33% of the mean richness and 14-26% of the mean abundance of total communities). This is also reflected in the dominance patterns: larval *A. simplex* dominated more infracommunities in cod from the Celtic Sea whereas *D. varicus* and adult *H. aduncum* dominated those from the Irish Sea.

The contrasting patterns observed in larval helminth assemblages from the two regions appear associated with an opposing contribution of the gastrointestinal helminth assemblages, *i.e.* notably high representation of the latter in communities from the Irish Sea (61-69% of the mean richness and 71-79% of the mean abundance of total communities) *vs* relatively low representation in communities from the Celtic Sea (48-51% of the mean richness and 22-45% of the mean abundance of total communities). Cod in the Irish Sea utilise the full depth range (until a depth of 154 m) through out the year (Righton *et al.*, 2001). This ensures a diverse range of prey and consequently diverse infections with

parasites utilising trophic transmission. Moreover, the prey of younger cod include larger quantities of crustaceans and decapods (ICES, 2005a and references therein). These groups serve as intermediate hosts of many parasite species and explain in particular, the dominance of *D. varicus*, larval *H. aduncum* and *A. crassicollis* in infracommunities of the autumn sample (Hemmingsen & MacKenzie, 2001).

Communities in cod sampled in the North Sea exhibited a variable contribution of the two assemblages (*i.e*. larval and gastrointestinal parasites) to the total richness and abundance but no significant pattern related to the two different sampling areas (Dogger Bank and Skagerrak) could be discerned. However, there was a notably high contribution of the ectoparasite assemblages which contributed to 15-19% of the mean richness and 3-7% of the mean abundance of total communities in cod from this region (*vs* a range of 9-16 and 0.2-4% in the other three regions).

The third hypothesis based on the structure of the regional faunas (Chapter 4) was only partially met since significant compositional homogenisation (within each region) was observed in component communities whereas infracommunities exhibited much higher variation within each sample (Table 6.37). Thus, as expected the overall range of the variation of within-region similarity between component communities was 62-83%, similarity being highest between communities sampled in Icelandic waters (78-83%) and the lowest between communities sampled in the Baltic Sea (62-73%). Furthermore, the three species, *H. aduncum*, *A. simplex* and *D. varicus* expected to contribute substantially to the structural homogeneity between communities were dominant in the component communities in all six (the first species) and the four open water regions (the latter). *H. aduncum* was also found to dominate a substantial proportion of the infracommunities in the samples from all four open-water regions, *A. simplex* – in 3 (Celtic Sea, North Sea and Icelandic waters) and *D. varicus* – in 2 (Irish Sea and Icelandic waters), respectively (Table 6.36).

Table 6.37. Comparative table for infracommunity descriptors (within-region ranges for means) of total communities, larval, gastrointestinal and ectoparasite assemblages in *G. morhua* in the six regions of NE Atlantic.

	Baltic Sea	Celtic Sea	Icelandic waters	Irish Sea	North Sea	Trondheimsfjord
Total infracommunities						
No. species/fish (range)	0-7	4-16	5-14	3-14	1-17	1-10
Mean no. of species	1.59 – 3.34	6.13-9.37	6.98-8.72	6.31-9.57	6.55-8.15	5.57
Mean no. of individuals	32.54 - 85.62	139.57-207.21	431.52-651.36	39.04-186.82	73.60-214.59	265.37
Mean dominance	0.69- 0.90	0.50-0.53	0.53-0.65	0.45-0.50	0.54-0.57	0.61
Mean diversity	0.19- 0.60	1.02-1.27	0.88-1.19	1.09-1.34	0.98-1.12	0.84
Mean similarity	41-59	48-57	62-73	47-60	40-46	44
Larval parasite assemblages						
No. species/fish (range)	0-6	1-9	2-6	0-7	0-8	0-3
Mean no. of species	0.54 -2.56	2.87-4.25	3.42-3.98	1.38-3.18	1.52-3.11	0.92
Mean no. of individuals	3.46 -30.42	101.26-123.88	273.52-610.49	5.56-48.25	7.75-118.22	1.65
Mean similarity	13-36	44-53	72-83	28-48	33-42	31
Gastrointestinal parasite assemblages						
No. species/fish (range)	0-3	1-8	2-8	2-11	0-9	1-7
Mean no. of species	0.93-1.32	3.13-4.69	3.73-4.72	4.25-6.25	3.87-4.57	4.03
Mean no. of individuals	13.21- 55.20	35.23-93.27	30.09-153.45	30.67-132.67	48.12-81.78	262.45
Mean similarity	34-73	43-61	52-53	45-65	35-50	46
Ectoparasite assemblages						
No. species/fish (range)		0-3	0-4	0-4	0-3	0-2
Mean no. of species		0.70-1.53	0.69-1.23	0.50-1.35	1.18-1.22	0.67
Mean no. of individuals		1.83-8.83	1.78-4.55	1.13-5.90	3.50-14.59	1.27
Mean similarity		33-44	17-29	17-32	27-36	19

However, the within-sample infacommunity similarities exhibited lower levels (overall range 40-73%) thus suggesting somewhat lower predictability at this level of community organisation, infracommunities in cod from Icelandic waters exhibiting again the highest range values (62-73%). The high homogeneity of both component and infracommunities in cod from Icelandic waters can be related to the fact that the same spawning population although sampled in the southwest coastal (spring samples) and west offshore (autumn sample), was studied (ICES, 2005a; Pampoulie *et al.*, 2006). Among the most prevalent species in the three samples, *A. simplex*, *C. osculatum* and *H. aduncum* dominated both the component communities and infracommunities and contributed to the similarity within each sample and dissimilarity between samples. *D. varicus* was also found to be important in the autumn sample. Finally, the within-sample similarities were high due to the high abundance and dominance in the infracommunities of the larval anisakids. Thus, the highest similarity values in the FSS is probably related to the highest dominance of *A. simplex* and *C. osculatum* homogenising infracommunity composition and structure. The comparable values of similarity between AS and SSS could be related to the larger size of the autumn sampling area, which may have increased the heterogeneity of the infracommunities.

Overall, the higher variability in composition and structure observed at the infracommunity level, could be associated with the fact that only a small portion of the parasite species dominating component communities was also most abundant in the infracommunities. In addition to the three widespread dominant species mentioned above, six other species were important at the lower scale of the analysis. Five of these were found to dominate only infracommunities in the low-salinity regions: *C. osculatum* and *E. gadi* in cod from the Baltic Sea and *L. elongatum*, *C. cirratus* and *C. gracilis* in cod from Trondheimsfjord (Table 6.36). This stresses again the peculiar characteristics of these two regions as opposed to the open water regions.

7. Patterns in parasite community structure in *G. morhua* in the NE Atlantic

7.1. Introduction

A central theme in community ecology is the search for order, *i.e.* search for non-random patterns in the species composition and structure of naturally occurring assemblages, and for the ecological processes responsible for those patterns (Poulin, 2005). The search for structure in parasite communities is enhanced by their hierarchical organisation so that comparative analyses can be carried out at several nested spatial scales. (see Chapter 6). Parasite communities in marine fish are generally richer than those in freshwater fish due to wider distributional ranges of parasites in the marine environment and to the longer food chains involving long-lived paratenic hosts (Marcogliese, 2007). These characteristics of marine environments favour parasite cumulative evolution, a process by which parasites continuously diversify to inhabit a wider range of host species (Palm & Klimpel, 2007; Marcogliese, 2007). Kalm & Klimpel (2007) suggested that the addition of an extra-host species at any given point in the life-cycle (lateral incorporation) by originally generalist parasites, followed by further specialization, is the principle responsible for the huge diversity of parasites of marine fish.

This high diversity of parasite species could favour interspecific interactions between parasites. However, the "aggregation model of coexistence" (Shorrocks, 1996) postulates that species coexistence is facilitated when the distribution of species leads to the reduction of interspecific aggregation relative to intraspecific aggregation. This model implies saturation of ecological communities with species, which means that there is saturation of local species richness (*e.g.* number of species in an infracommunity) independent of the size of the regional pool of species (component parasite species) (Morand & Simkova, 2005).

Parasite species occurring within the regional pool (component community) should affect the composition of every local community (infracommunity) although every species is not expected to occur at local scale (Guégan *et al.*, 2005). An approach for recognition of the regional and local processes is the regression of regional species richness against local species richness (Cornell & Lawton, 1992; Srivastava, 1999). Two patterns are recognisable: (i) a linear relationship that indicates non-saturation *i.e.* dependence of infracommunity richness on component community richness; (ii) a curvilinear relationship when there is a limit to infracommunity parasite species richness with increasing component community richness. Local-regional richness relationship has been investigated in some parasite communities in freshwater fish and this has resulted in detection of both saturated and non-saturated patterns of species richness (Kennedy & Guégan, 1994; 1996;

Barker *et al.*, 1996). However, Rohde (1998) has shown that an asymptotic relationship between infracommunity and component community richness is a consequence of the differential likelihoods of parasite species to appear in an infracommunity as determined by transmission rates and intrinsic life-spans and colonisation probabilities. Rohde (2002, 2005) pointed out that the majority of marine host-parasite systems have not reached a ceiling of diversity (*i.e.* non-saturated with parasite species) and marine parasite communities follow mainly the random assortment model (Poulin, 2005 and references therein) which indicates that species abundances are independent from each other and interspecific competition is unimportant over evolutionary time. Morand *et al.* (1999) examined the effects of interspecific aggregation in infracommunities, and demonstrated that interspecific interactions are reduced relative to intraspecific interactions thus facilitating species coexistence in rich communities.

Focusing on species composition of naturally occurring assemblages, nested subset analyses can test for species random structure *vs* order in parasite communities. Non-random structure is present if species-poor communities are distinct subsets of progressively richer parasite communities. Nested subset analyses can be carried out at both infracommunity and component community level (e.g. Simkova *et al.*, 2003; González & Poulin, 2005a). The first is defining the pool of locally available parasite species from which infracommunities can acquire species *i.e.* if infracommunities are random subsets of the component communities. Finding significant nested patterns in fish parasite communities is mainly an exception according to Poulin (2005) and may reflect the heterogeneity among fish (*i.e.* sampling artefacts) rather than non-random structure (Poulin & Valtonen, 2001). Nestedness has been investigated extensively in communities of ectoparasites of marine fish (*e.g.* Worthen & Rohde, 1996; Rohde *et al*., 1998) and some studies have reported significant nested structure in parasite infracommunities in marine hosts (Timi & Poulin, 2003; Vidal-Martínez & Poulin, 2003; González & Poulin, 2005b; Pérez del Olmo *et al.*, 2007). Regardless of the methodological problems in the study of nested subset patterns, recently evaluated by Timi & Poulin (2008), the analysis illustrates in a comprehensive manner how parasite species co-occur in the parasite communities.

Nested subset analyses of parasite communities are also useful tools for revealing structure in both space and time (Carney & Dick, 2000; Poulin & Valtonen, 2002; Timi & Poulin, 2003; González & Poulin, 2005b; González & Oliva, 2006). Overall, studies on temporal and spatial variability of parasite communities suggest that non-random patterns are both ephemeral and unpredictable (Poulin, 2005). Despite the non-equilibrium state of

marine parasite communities (*i.e.* unsaturated non-interactive communities with mainly random species co-occurrence patterns, see Rohde, 2005), repeatability has been revealed in parasite communities in the same marine fish host species when several populations have been studied (*e.g.* Timi & Poulin, 2003; Vidal-Martínez & Poulin, 2003; González & Poulin, 2005b; González *et al.*, 2006; González & Oliva, 2006).

Geographical distance is one of the main factors that contributes to the compositional variation between parasite communities (Poulin & Morand, 1999). This variation can be quantified when similarity values obtained from pairwise comparisons between parasite communities are regressed against geographical distances. The rate of decay of similarity with distance can shed light to the processes influencing the biological similarity of parasite communities in a given host. However, it is not necessarily associated with the vagility of the fish host (Poulin, 2003).

To summarise, the search for order has been an important theme in parasite community ecology in the last decade. Although a number of non-random patterns have been described and discussed in the recent literature, studies focusing on the larger scale of community organisation (*i.e.* component community level) that may reveal the action of large-scale biogeographical processes, are still few. The present study attempts to fill this gap by a comparative assessment of the compositional and structural similarity in parasite component communities in cod focusing on the search for non-random 'macroecological' patterns associated with parasite faunas and component communities in this host in the NE Atlantic.

7.2. Materials and methods

All analyses in this chapter utilise the data on the parasite faunas and component communities in the six NE Atlantic regions studied. A total of 16 component community samples were considered which include both spatial (six regions) and temporal (two spring and one autumn) replicates (see Chapter 3 for details on sampling design and sample sizes).

7.2.1. Similarity patterns in parasite component communities in cod

Community composition analyses were carried out with PRIMER v5 software (Clarke & Gorley, 2006) due to its ample assortment of graphical and multivariate procedures for analyzing species/samples abundance matrices. Two sets of data were analysed using component communities/assemblages as independent observations: Analysis 1: entire dataset; and Analysis 2: dataset restricted to communities in adult fish (SL range 40-70

cm). Further, the parasite community was divided into 3 groups: (i) gastrointestinal helminth assemblages comprised of adult helminths only; (ii) larval helminth assemblages; and (iii) ectoparasite assemblages. All analyses were carried out on total community and on the above subgroups separately and in two variants: *i.e*. using both the mean abundance and the prevalence of parasites in the 16 component communities.

First, non-metric multi-dimensional scaling (MDS) ordination was performed on the matrix of Bray-Curtis similarity index values to visualise the low-dimensional relationships among component communities based on relative similarity in composition. Square-root transformation was chosen to provide deeper community comparison by a moderate down-weighting the contribution of the numerically dominant taxa; it also represents an adequate transformation for prevalence data.

Secondly, hierarchical cluster analysis (group average linkage option) was used to identify groups of communities/assemblages (the latter superimposed on the MDS plots in Figure 7.1 and 7.2). To obtain statistically significant evidence of genuine clusters, a permutation test (1000 permutations) was carried out with the SIMPROF procedure which tests whether each node of the complete dendrogram has significant internal structure.

Thirdly, the ANOSIM procedure which performs randomization tests on similarity matrices, was used to test the null hypothesis of no differences in parasite component community/assemblage structure between regions (one-way layout).

Because communities were studied in three samples (FSS, AS and SSS) and there were no replicates for one of the regions, a two-way crossed layout with no replicates was adopted to test for sample sequence effects (if any) on differences in community composition between the six regions.

This analysis utilises a different permutation procedure. In this procedure the statistic obtained is a measure of how well the regional patterns for the different sample match; this statistic is then recomputed under all possible permutations of the region labels within each sample. The test makes no assumption about the absence of temporal effects; between-sample similarities are irrelevant to a statistic based only on agreement in within-sample patterns. The similarity matrices between localities are obtained for each sample. The rank similarities for each sample are compared. If there are n localities and thus $N=n(n-1)/2$ similarities within a sample, the Spearman correlation coefficient shows the agreement of two samples, j and k

$$\rho_{jk} = 1 - \frac{6}{N(N^2-1)} \sum_{i=1}^{N} (r_{ij} - r_{ik})^2$$

between the matching elements of the two rank similarity matrices $\{r_{ij}, r_{ik}; i=1,\ldots;N\}$. The coefficients are averaged across all $b(b-1)/2$ pairs from the b samples, to obtain an overall measure of agreement ρ_{av} on which the test is based. The procedure can be reversed to provide a test for temporal effects (but allowing the possibility for seasonal effects). As in all correlation coefficients, ρ_{av} takes values in the range (-1,1). Perfect agreement is implied by ρ_{av}=1 whereas the null hypothesis of no regional differences allowing the possibility for seasonal effects is accepted when $\rho_{av} \approx 0$. The departure from zero of this agreement measure is testable by permutation (p-value obtained in the test, see Clarke & Gorley, 2006 for details).

Since communities were sampled in two seasons (spring and autumn), a two-way crossed layout was performed to test for effect of season on differences in community composition between the six regions. The procedure tests the null hypothesis that there are no community differences between regions, allowing for the fact that there may be seasonal differences. The procedure was then reversed thus testing the hypothesis for no differences due to factor 'season' allowing for the fact that there might be regional differences in community composition. For each separate region an R statistic is calculated as if for the simple one-way layout and the resulting values are averaged to give R_{av}. Its permutation is generated by examining all simultaneous re-orderings of the regions within each season (and the reverse).

7.2.2. Decay of similarity with distance

Rates of similarity decay were calculated among the six faunas and 16 component communities by regressing matrices of inter-region/sampling location distance against matrices of inter-faunal/inter-community similarity (Bray-Curtis index based on abundance data computed for all possible pairs). Geographical distances (in nautical miles) were estimated along the coastal line between all regions/sampling locations or using the shortest straight-line distance in the absence of geographical barriers using Google Earth (eye height 1435.62 km). Since cod from each sample were caught in a range of coordinates the distances were measured from the most representative point (*i.e.* where most cod were caught or from the centre of the sampling area).

Simple linear, exponential (semi-ln-transformed data) and power function models (ln-ln-transformed data) were fitted for each dataset in order to examine the best fit of distance-similarity relationship. The significance of the best regression models was

determined by Mantel test (999 permutations, see Manly, 1997) using RT 2.1 program (Western EcoSystems Technology, Inc., Cheyenne, Wyoming).

7.2.3. Regional-local richness relationship

The present study applies the procedure adopted for examination of the relationship between regional and local species richness by Aho (1990), Cornell (1994), Kennedy & Guégan (1994; 1996) and Krasnov *et al.* (2006). The shape of the local-regional relationship was fitted to untransformed, exponential and power function models and the model that accounted for the greatest proportion of the variance and best linearized the relationship was accepted as the best model. In the case when more models linearized the relationship, the one with highest r and F-test values was accepted as the best. The tests of 'local' *vs* 'regional' richness were performed at two spatial scales: (i) between component communities and regional faunas; and (ii) between infracommunities and component communities. A second analysis was performed at the latter scale in which the data for the two low-salinity regions (Baltic Sea and Trondheimsfjord) were excluded. Variables used in the regressions (*i.e.* richness measures) were: maximum infracommunity richness (ICR), component community richness (CCR, samples from each region considered as distinct component communities) and regional richness (RR), estimated as the total faunal richness recorded in a region during the study (see Chapter 4). The relationship between parasite mean abundance and CCR was analysed with linear regression (ln-transformed data) to test for density compensation in cod parasite communities.

7.2.4. Test for non-random parasite community composition

Nested subset analyses were carried out for the total parasite communities and separately for the separate matrices containing either endo- or ectoparasite species using the Nestedness Temperature Calculator Program (NTC) of Atmar & Patterson (1995).

Matrices (parasite species presence/absence in regional faunas/component communities) were packed maximally and the nestedness metric "temperature" (T) was calculated. T measures the 'heat of disorder' *i.e.* the entropy of the system. The "temperature" of a matrix depends on the manner in which species are distributed within it. A matrix T of perfect order assumes the attributes of a frozen liquid where complete order exists only at 0ºC. At the opposite end, at 100ºC the presence-absence matrix is assumed to possess attributes of a free gas. Variations in T between 0º and 100ºC are assumed to be continuous (Atmar & Patterson, 1995).

For each matrix, the observed value of T was compared with the T-values of 1000 randomly generated presence-absence matrices generated by Monte-Carlo simulations (no row or column constraints), to assess the probability of randomly obtaining a matrix with the same or higher degree of order. NTC also provides a graphical output of the packed matrix where the vertical gradient represents the communities ordered from the richest (top) to the poorest (bottom) and the horizontal gradient represents the species ordered by their frequency of occurrence in communities; species/community order is given in reorganization vectors output.

The analyses were carried out on the six regional faunas and the 16 component communities. First, nested subset analysis was carried out on data for the total parasite faunas and for endoparasite and ectoparasite faunas separately. Secondly, the analysis was performed considering the 16 population samples as independent observations. An identical series of analyses was also performed on a restricted dataset including only data from adult fish (SL range 40-70 cm).

7.3. Results

7.3.1. Similarity patterns in parasite component communities in cod

Figures 7.1 and 7.2 present MDS ordinations of the total communities, gastrointestinal, larval and ectoparasite assemblages obtained in Analysis 1. The overlaid cluster boundaries (50, 60 and 80% similarity) indicated an overall very good agreement between the two techniques. MDS plots for total communities based on mean species abundance provided excellent representation of community separation in all ordinations (see Figure 7.1A; plots for restricted set not shown). The cluster analysis for total communities indicated clear spatial segregation of communities in cod from Baltic Sea, Trondheimsfjord and Icelandic waters (Figure 7.1A). SIMPROF procedure identified three significantly structured clusters: (i) all communities in Baltic Sea cod; (ii) communities in cod sampled in autumn in North and Irish seas; and (iii) all communities in cod from Icelandic waters plus all spring samples from Celtic, Irish and North seas and the autumn sample from Celtic Sea. The single sample from Trondheimsfjord appeared separated at very low similarity level.

Gastrointestinal helminth assemblages contributed substantially to the pattern observed in total communities due to the strong separation of assemblages from Baltic Sea and Trondheimsfjord cod which forced a very tight packing of the remaining assemblages resulting in the lowest stress value (stress=0) (Figure 7.1B). When assemblages from Baltic Sea and Trondheimsfjord cod were removed from the analysis the ordination had similar

stress value (0.07) to that of total communities and exhibited the grouping observed in the latter (Figure 7.1C).

Larval helminth assemblages showed a good ordination with the same stress value (0.07) (Figure 7.2A). The strong grouping pattern discriminated well Baltic and Icelandic cod assemblages from the remaining. However, assemblages sampled in autumn from Irish and North Sea appeared closer to those from Trondheimsfjord. The remaining assemblages appeared more closely associated but the three assemblages from Icelandic waters were tightly grouped. Ordination of ectoparasite assemblages was performed excluding communities from Baltic Sea cod, which lacked ectoparasites. No specific regional pattern was observed although the stress was low (0.06) and assemblages in cod from North Sea appeared most distinct (Figure 7.2B).

Ordinations and cluster analyses performed on parasite prevalence data exhibited roughly similar patterns to the above and the stress values differed slightly. Total parasite communities showed an excellent representation (stress=0.01). SIMPROF procedure identified three significantly structured clusters: (i) all communities in Baltic Sea cod; (ii) the community from Trondheimsfjord; and (iii) all communities in cod from Icelandic waters plus the remaining communities from Celtic, Irish and North seas. However, all communities from open water regions appeared strongly overlapped in the MDS plot (Figure 7.1D). Excluding communities in cod from Baltic Sea and Trondheimsfjord resulted in a good ordination which depicted a greater variability (increased stress value, 0.11) in community structure of the open water localities, since only Icelandic communities showed a well-defined group (plot not shown).

Assemblages of gastrointestinal helminths exhibited good representation (stress=0.01) of the distinctness of those in cod from Baltic Sea cod which were clearly separated from the remaining (Figure 1E). The stress slightly increased after excluding assemblages in cod from Baltic and Trondheimsfjord (stress=0.07). A pattern similar to that based on abundance but with a tighter grouping of assemblages in cod from Icelandic waters (Figure 7.1F). Assemblages of larval helminths exhibited similar to the one based on abundance grouping but two Baltic Sea assemblages were clustered together with those from the open water regions (Figure 7.2C). As in the analysis based on abundance, ectoparasite assemblages showed the least recognisable grouping pattern of graphical discrimination (Figure 7.2D).

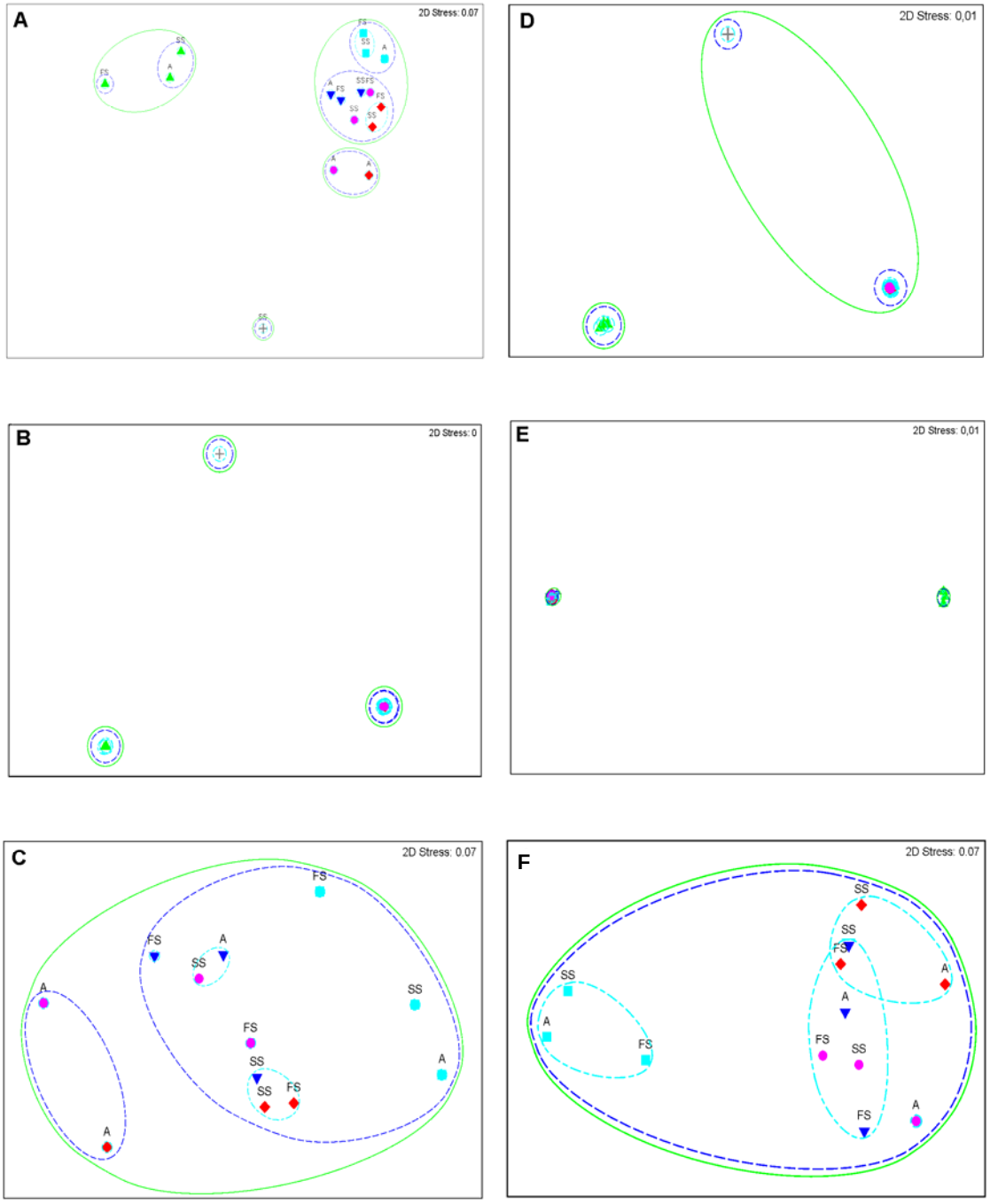

Figure 7.1. Multidimensional scaling ordinations of total communities (A, D) and gastrointestinal helminth assemblages (B, C, E, F) in *G. morhua* from the six regions studied. Similarity matrices based on abundance (A-C) and prevalence (D-F). Samples indicated by different colours: Baltic Sea, green; Celtic Sea, dark blue; Icelandic waters, light blue; Irish Sea, red; North Sea, pink; Trondheimsfjord, grey. Cluster analyses boundaries overlaid (50%, green; 60%, dark blue; 80%, light blue). Baltic Sea and Trondheimsfjord excluded from analyses for gastrointestinal helminth assemblages (C, F), see text for details.

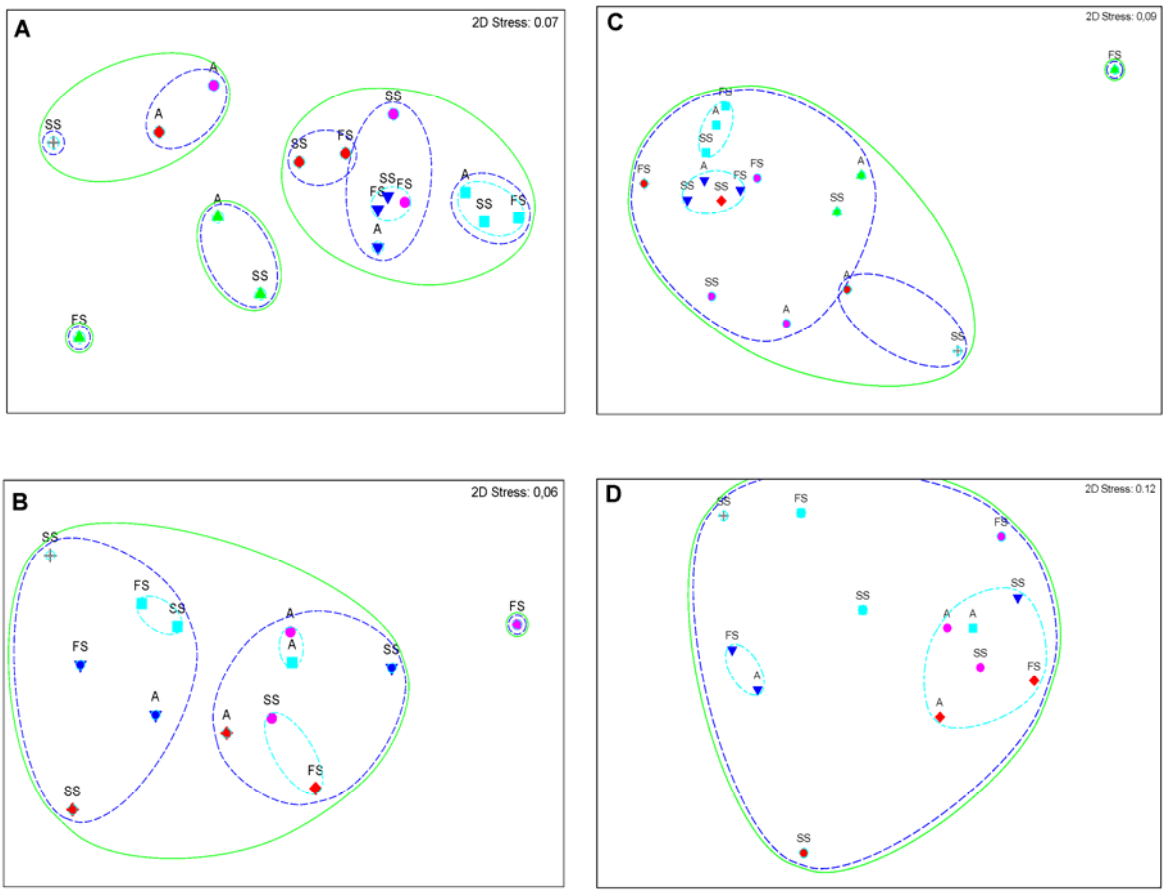

Figure 7.2. Multidimensional scaling ordinations of larval (A, C) and ectoparasite assemblages (B, D) in *G. morhua* from the six regions studied. Similarity matrices based on abundance (A, B) and prevalence (C, D). Samples indicated by different colours: Baltic Sea, green; Celtic Sea, dark blue; Icelandic waters, light blue; Irish Sea, red; North Sea, pink; Trondheimsfjord, grey. Cluster analyses boundaries overlaid (50%, green; 60%, dark blue; 80%, light blue). Baltic Sea excluded from analyses for ectoparasite assemblages (B, D) due to the lack of ectoparasites.

Analysis 2 on the restricted set of communities/assemblages in adult fish revealed patterns of grouping of communities similar to Analysis 1 (plots not shown). The ordinations and clusters based on mean abundance data showed similar differentiation of communities between regions and similar plots for total communities, gastrointestinal and larval helminth assemblages. On the other hand, ectoparasite assemblages exhibited less differentiation between regions. Analyses on prevalence data were also very similar to those in Analysis 1 for total parasites and all three assemblages. However, Icelandic assemblages appeared strongly differentiated along the first axis of the ordination of larval helminth assemblages probably due to the higher prevalence of larval forms (plots not shown).

The high stress values obtained for MDS ordinations and the clustering patterns which indicated significant regional differentiation of parasite communities/assemblages in cod were confirmed in ANOSIM tests which exhibited overall high R values for analyses with both mean abundance and prevalence data (Table 7.1). In the one-way procedure the null hypothesis for no differences in community composition with respect to region of sampling was rejected in both analyses (1 and 2) run on both abundance and prevalence data. Notable exceptions were the ectoparasite assemblages which did not show significant differences in composition between the five regions (*i.e.* Celtic, Irish and North seas, Trondheimsfjord and Icelandic waters) in both analyses. The significance obtained in the test including Baltic Sea assemblages in the analysis was due to the absence of ectoparasites in communities in cod from this region (Table 7.1).

The two-way procedure also revealed an overall good agreement, which resulted in the rejection of the null hypothesis of no regional differences allowing the possibility for 'sample' effects (both Analysis 1 and 2, see Table 7.1). The reverse hypothesis, *i.e.* for no significantly different composition and structure due to 'sample' allowing for differences between regions was accepted in both analyses and all assemblages except for total communities (prevalence data) in Analysis 2 (r_s=0.55, p=0.044). Two-way crossed ANOSIM procedure carried out on both abundance and prevalence data did not reveal significant effect of the factor 'season' on community composition in all comparisons (Table 7.2), the only difference from the analysis for 'sample' effects being the fact that regional differences between gastrointestinal helminth assemblages allowing the possibility for seasonal effects, were not significant.

Another interesting aspect of the regional similarity patterns was depicted in the separate analyses on gastrointestinal helminth assemblages. Overall, the regional differences in composition between these assemblages contributed to the significant differentiation of total parasite communities. However, the higher degree of overlap found between communities from open water locations in cluster analyses and two-dimensional ordination, was confirmed by the tests in the full-dimensional space (*i.e.* ANOSIM, see Table 7.1). The low R values indicated a generally similar composition and structure of these assemblages and a possible sample influence in both analyses (1 and 2, see Table 7.1). Finally, mid-range values of R were obtained for larval helminth assemblages indicating a lower degree of regional differences in their composition and structure.

Table 7.1. Summary of the ANOSIM results: one-way and two-way crossed layout without replicates.

	Mean abundance				Prevalence			
	One-way (region)		Two-way crossed (region & sample)		One-way (locality)		Two-way crossed (region & sample)	
	R	p	ρ	p	R	p	ρ	p
Analysis 1 (entire dataset)								
Total communities	0.738	0.001	0.842	0.003	0.778	0.001	0.887	0.002
Gastrointestinal helminth assemblages	0.658	0.001	0.826	0.003	0.823	0.001	0.911	0.002
Gastrointestinal helminth assemblages (4 regions)	0.321	0.018	0.41	ns	0.738	0.002	0.733	0.048
Larval helminth assemblages	0.524	0.001	0.354	0.049	0.436	0.001	0.147	ns
Ectoparasite assemblages	0.425	0.003	0.72	ns	0.527	0.002	0.798	0.011
Ectoparasite assemblages (5 regions)	0.086	ns	-0.238	ns	0.164	ns	0.048	ns
Analysis 2 (restricted dataset)								
Total communities	0.689	0.001	0.798	0.002	0.719	0.001	0.895	0.001
Gastrointestinal helminth assemblages	0.727	0.001	0.859	0.001	0.737	0.001	0.871	0.002
Gastrointestinal helminth assemblages (4 regions)	0.426	0.009	0.524	ns	0.611	0.003	0.429	ns
Larval helminth assemblages	0.464	0.002	0.119	ns	0.371	0.003	0.523	0.017
Ectoparasite assemblages	0.459	0.002	0.725	ns	0.513	0.001	0.751	0.017
Ectoparasite assemblages (5 regions)	0.139	ns	-0.219	ns	0.225	ns	-0.105	ns

Table 7.2. Summary of the ANOSIM results: two-way crossed layout.

	Mean abundance				Prevalence			
	Two-way crossed				Two-way crossed			
	Region (across seasons)		Season (across regions)		Regions (across seasons)		Season (across regions)	
	R	p	R	p	R	p	R	p
Total communities	0.776	0.003	0.4	ns	0.696	0.001	-0.2	ns
Gastrointestinal helminth assemblages	0.704	0.003	0.4	ns	0.824	0.001	0.2	ns
Gastrointestinal helminth assemblages (4 regions)	0.333	ns	0.25	ns	0.708	0.048	0.25	ns
Larval helminth assemblages	0.688	0.003	0.6	ns	0.48	0.003	-0.2	ns
Ectoparasite assemblages	0.27	ns	-0.5	ns	0.43	0.047	-0.75	ns
Ectoparasite assemblages (5 regions)	-0.141	ns	-0.5	ns	0	ns	-0.75	ns

7.3.2. Exploring 'macroecological' patterns: Decay of similarity with distance

The composition of the regional parasite faunas in cod did not show significant spatial autocorrelation (Figure 7.3A). The explanatory power of both regressions of faunal similarities on geographical distance was very low (*i.e.* 7-11% of the variation in faunal similarity being attributed to distance; Table 7.3).

However, component communities in cod exhibited highly significant spatial autocorrelation. Although exponential function provided a good regression model, the relationship of similarity and geographical distance was best explained using untransformed variables (Table 7.3; Figure 7.3B). However, only a small portion of the variation (*c.* 35%) in community similarity was explained by distance.

The scatter of points suggests that although similarity tends to decrease with distance, there is a large variation at mid-range distances (*i.e.* 500-1200 nm; see Figure 7.3B) so that both low (<40%) and high (>60%) similarities between communities were observed irrespective of distance within this range. This variation chiefly contributed to the low explanatory power of the model.

Table 7.3. Regression statistics for the decay of similarity with distance in parasite faunas and component communities in *G. morhua* in the NE Atlantic. Intercepts are in units of similarity and ln(similarity), and slope values are in units of similarity and ln(similarity) per nautical miles distance. N, number of samples; n, number of parasite contrasts.

	N	n	R^2	Slope	Intercept	p
Faunas						
Similarity *vs.* distance	6	15	0.108	-0.022	65.22	ns
Ln (similarity) *vs.* distance	6	15	0.070	-0.000483	4.11	ns
Component communities						
Similarity *vs.* distance	16	120	0.349	-0.023	66.48	0.0001
Ln (similarity) *vs.* distance	16	120	0.300	-0.000580	4.21	0.0001

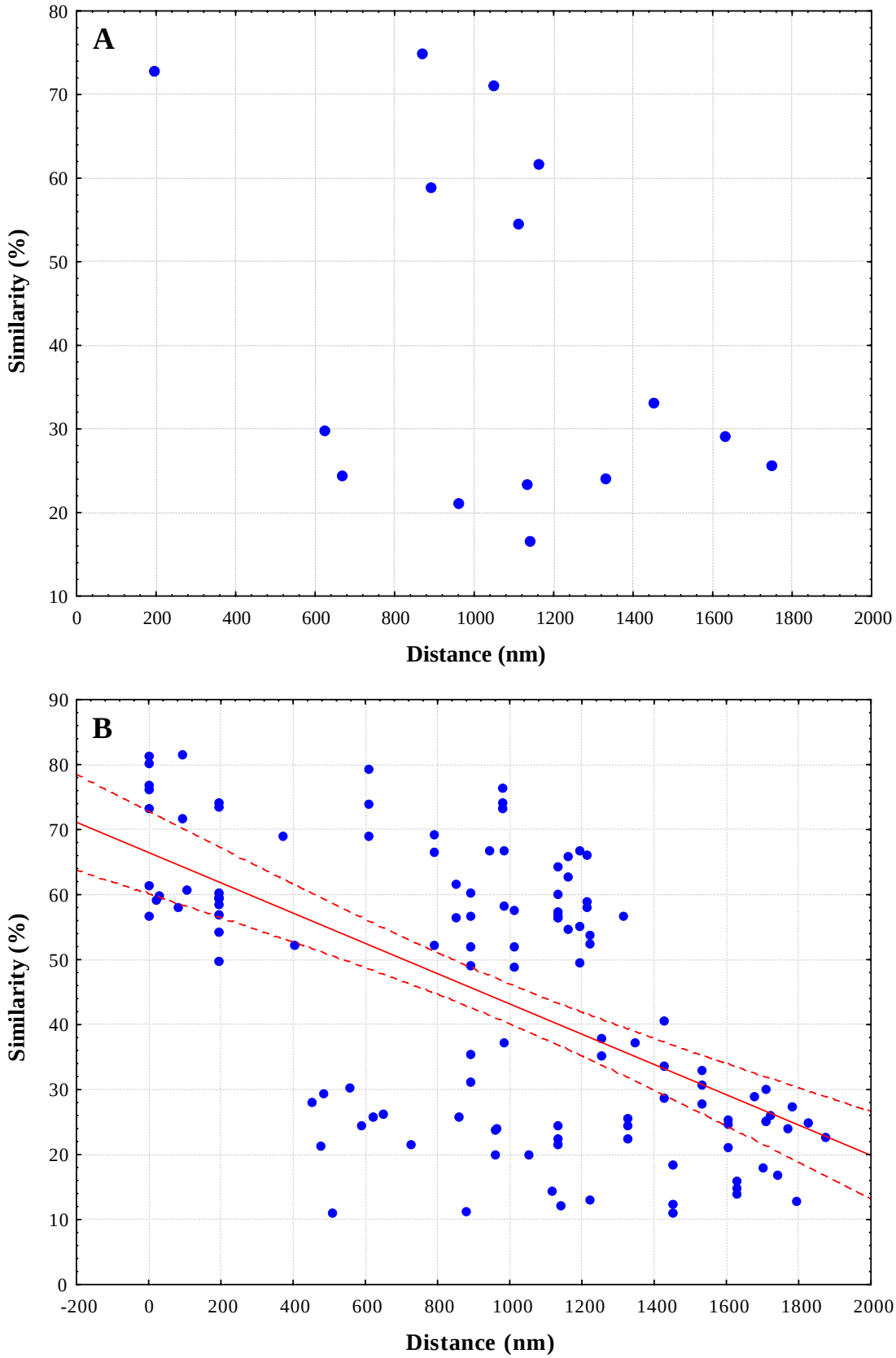

Figure 7.3. The decay of similarity over geographical distance in regional faunas (A) and component communities (B) in *G. morhua* from NE Atlantic. Distance in nautical miles.

7.3.3. Exploring 'macroecological' patterns: Regional-local richness relationship

In the present analyses the existence of proportional sampling was accepted as a null hypothesis following Cornell (1994) and Kennedy & Guégan (1994; 1996). The latter is indicated by a linear relationship with a slope ≤ 1. Direct linear dependence of local on regional richness is assumed if all points fall along the line of equality ('boundary line' of Cornell & Lawton, 1992; *i.e*. relationship with a slope = 1). On the other hand, if points fall below the boundary line and the relationship is best described by a power function, the local richness becomes increasingly independent of regional richness, indicating that infracommunities/component communities become saturated at levels below component/faunal richness.

All raw richness measures varied within a wide range: RR (12-37 species); CCR (6-32 species); and maximum ICR (4-17 species), the parasite fauna and communities sampled in the Baltic Sea being the most depauperate. Due to this, a significant correlation was observed between the richness of component communities and regional faunas (CCR and RR). All points fell below the boundary line and although linear and semi-logarithmic functions provided good fit for the relationship, the data were best fitted by a power function (Figure 7.4A; Table 7.4). This curvilinear relationship was still significant ($F_{(1, 11)}$=8.66, p=0.013) although explaining poorly the variation of the data (adjusted r^2=0.390) when component communities/faunas from Baltic Sea were excluded from the analysis and not significant when data from both low-salinity regions were excluded.

Table 7.4. Relationships between component community (CCR) and regional richness (RR), and between maximum infracommnity richness (max ICR) and component community richness (CCR) for *G. morhua* in NE Atlantic.

	r^2	Slope	Intercept	F	p
Faunas					
CCR - RR	0.833	0.715	0.841	75.90	<0.0001
CCR - Ln RR	0.850	16.16	-31.29	85.27	<0.0001
Ln CCR - RR	0.835	0.045	1.659	77.13	<0.0001
Ln CCR - Ln RR	0.864	1.02	-0.379	96.57	<0.0001
Component communities (6 regions)					
Max ICR - CCR	0.868	0.426	2.143	99.30	<0.0001
Max ICR - Ln CCR	0.837	6.69	-8.457	77.86	<0.0001
Ln max ICR - CCR	0.888	0.046	1.360	110.74	<0.0001
Ln max ICR - Ln CCR	0.906	0.748	0.144	144.77	<0.0001
Component communities (4 regions)					
Max ICR - CCR	0.458	0.436	1.872	10.29	0.0094
Max ICR - Ln CCR	0.475	11.386	-23.803	10.97	0.0078
Ln max ICR - CCR	0.492	0.034	1.686	11.67	0.0066
Ln max ICR - Ln CCR	0.518	0.892	-0.331	12.81	0.0050

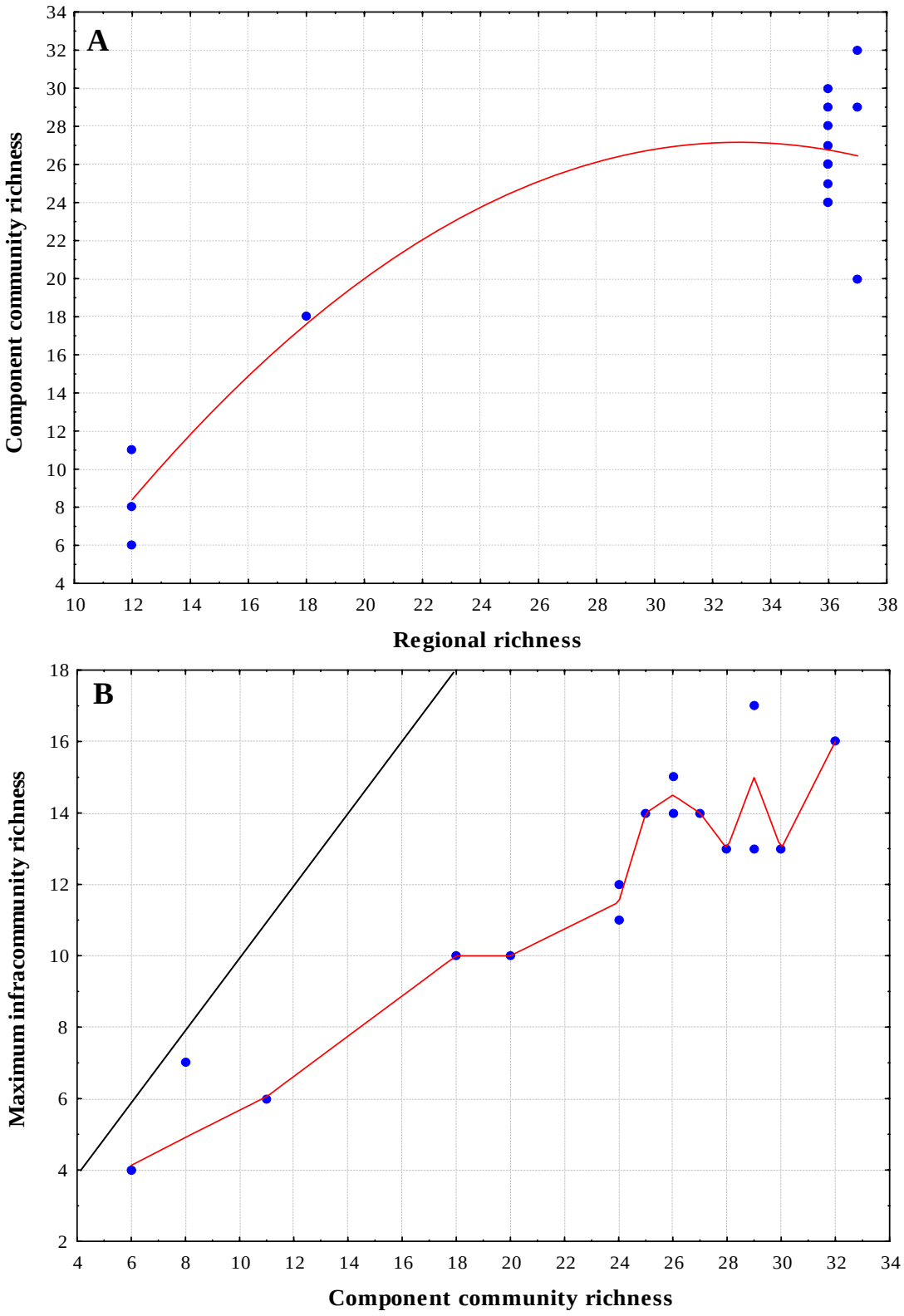

Figure 7.4. Relationship between regional and component community richness (A) and between component community richness and maximum infracommunity richness (B) in *G. morhua* from the six regions in NE Atlantic. Scatter diagrams on non-transformed data. Curve in B indicates median trends fitted to a lowess function. Boundary line (line of equality) in black.

The tests for the relationship between regional and local richness at the lower scale, i.e. between CCR and maximum ICR are shown in Table 7.4. Similar to the larger-scale comparisons above, all points fell well below the boundary line (drawn in black in Figure 7.4B). In this figure the median trend of the curve is fitted to a lowess function which gives a clearer picture of the overall shape of the relationship between the two variables. The relationship between maximum ICR and CCR was positive and best described by a power function in both datasets (i.e. the entire dataset and the subset in which samples from Baltic Sea and Trondheimsfjord were omitted).

The regression of mean abundance on CCR revealed an overall poor explanation of the variation of the data but significant positive relationship (r^2=0.298; $F_{(1,\ 14)}$=7.37; p<0.017) (Figure 7.5; trend fitted to a lowess function). However, no significant relationship was found when the samples from Baltic Sea and Trondheimsfjord were excluded from the analysis.

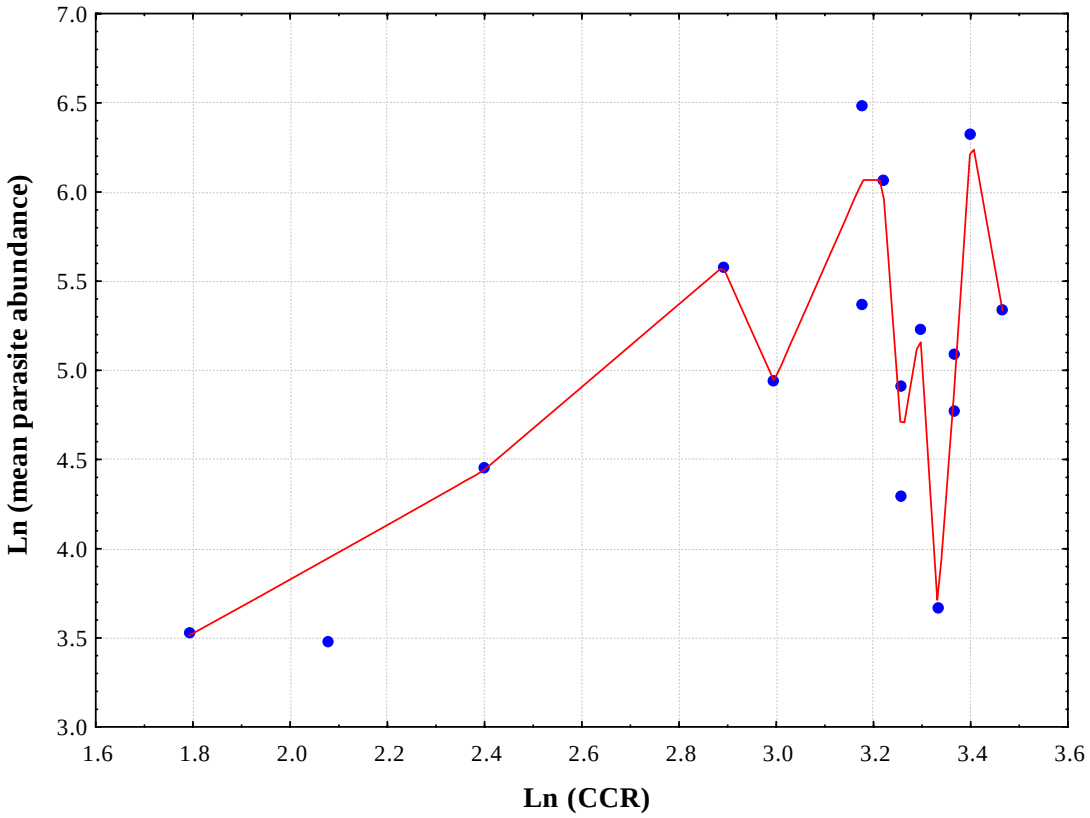

Figure 7.5. Relationship between mean parasite abundance and component community richness (CCR) in 16 component communities in *G. morhua* from the six regions studied. Trend fitted to a lowess function.

7.3.4. Exploring 'macroecological' patterns: Test for non-random parasite community composition

Table 7.5 shows the results of a number of runs of NTC for the cod parasite datasets (see also Materials & Methods section). All the datasets were significantly nested except for the one comprising ectoparasite faunas. Total parasite and endoparasite faunas of cod from the six regions exhibited clear nestedness (*i.e.* poor faunas are nested in the richer ones) and the order (poorest to richest) appeared to follow a longitudinal gradient (*i.e.*, Baltic Sea → Trondheimsfjord → North Sea → Irish Sea → Iceland → Celtic Sea), the only exception being the fauna of cod in the Celtic Sea which exhibited highest species richness. Three regional faunas (*i.e.* those in Celtic and Irish Seas and Trondheimsfjord) contributed much more to the noise than the remainder as indicated by their idiosyncratic temperatures.

Table 7.5. Summary of the results of nestedness analyses on parasite faunas and component communities in *G. morhua* in the six regions of NE Atlantic.

	N	Matrix fill (%)	Matrix T (°)	Simulated T(°) (Mean ± SD)	p
Faunas					
Entire dataset					
Total parasites	6	45.0	23.17	48.15 ± 5.83	<0.0001
Endoparasites	6	46.6	20.98	46.00 ± 6.32	<0.0001
Ectoparasites	6	43.6	23.14	34.59 ± 11.03	<0.15
Restricted dataset					
Total parasites	6	47.5	16.87	47.67 ± 5.96	<0.0001
Endoparasites	6	47.9	19.95	46.65 ± 6.45	0.00002
Ectoparasites	6	50.0	11.27	34.66 ± 12.27	0.03
Component communities					
Entire dataset					
All communities	16	37.8	18.37	63.65 ± 4.08	<0.0001
Baltic Sea excluded	13	38.2	35.81	60.59 ± 4.68	<0.0001
Low-salinity regions excluded	12	37.8	39.45	58.58 ± 4.97	<0.0001
Restricted dataset					
All communities	16	39.9	18.44	63.19 ± 3.91	<0.0001

Nine parasite species were common for the six faunas: the trematode *L. elongatum*; the nematodes *A. simplex*, *C. gracilis*, *C. osculatum*, *H. aduncum*, *H. rigidum* and *P. decipiens*; and the acanthocephalans *C. semerme* and *E. gadi* (all species with rank=1 in the packed matrix). Seven additional species (four nematodes, one trematode, one

acanthocephalan and one copepod) were present in five of the six faunas: *A. morrhuae, C. adunca, A. crassicollis, D. varicus, C. cirratus, C. strumosum* and *L. branchialis* (listed in rank order, 2 to 8). Analysis on the restricted dataset including only parasite occurrence data in adult fish revealed non-random structure of all faunal subsets (*i.e*. all parasites and endo- and ectoparasites), all packed matrices exhibiting temperatures lower than those observed in the analyses of the entire dataset (Table 7.5).

Significant nested subset patterns were observed among total component communities of cod in the NE Atlantic (Table 7.5). Analysis of the entire dataset showed that, as in the case of parasite faunas, the depauperate communities in cod from Trondheimsfjord and Baltic Sea had highest ranks in the packed matrix. However, the order of the communities from open water locations provided indication of a temporal effect on parasite composition. Thus, three communities sampled in spring 2003 (SSS, Celtic Sea → North Sea → Iceland) had highest ranks followed by three communities sampled in autumn 2002 (AS, Celtic Sea → Irish Sea → North Sea). Two communities represented exceptions from this subset pattern, the ones in cod sampled from Irish Sea in spring 2003 and from Icelandic waters in autumn 2002. The latter were based on samples with high representation of juvenile fish (59.1 and 81.7%, respectively). Further, three communities sampled in spring 2002 (FSS, North Sea → Iceland → Celtic Sea) formed the penultimate group in the matrix, whereas the two communities sampled in Irish Sea in spring and the one sampled in autumn in Iceland occupied intermediate position (Figure 7.6).

This order of component communities in the packed matrix was tested for correlations with the following variables: sample size; mean and median length (SL); mean and median age of cod; proportion of juvenile fish in the sample (using both the percentage of fish < 30 cm and < 3 year-olds); latitude, longitude and salinity of sampling locations; season and sampling sequence. Of these, salinity and the proportion of juvenile fish (*i.e.* younger than 3 years) were the only variables which correlated significantly with the rank position in the packed matrix of the component communities (r_s=-0.750, p=0.001 and r_s=-0.500, p=0.048, respectively). Analysis of the matrix after excluding communities from Baltic Sea revealed a nested pattern with a higher temperature; however, none of the above correlations remained significant. Thus it appears that the composition of communities in this region forced the negative correlation due to the low salinity and the lowest representation of juvenile fish (0-29.8%) in the samples.

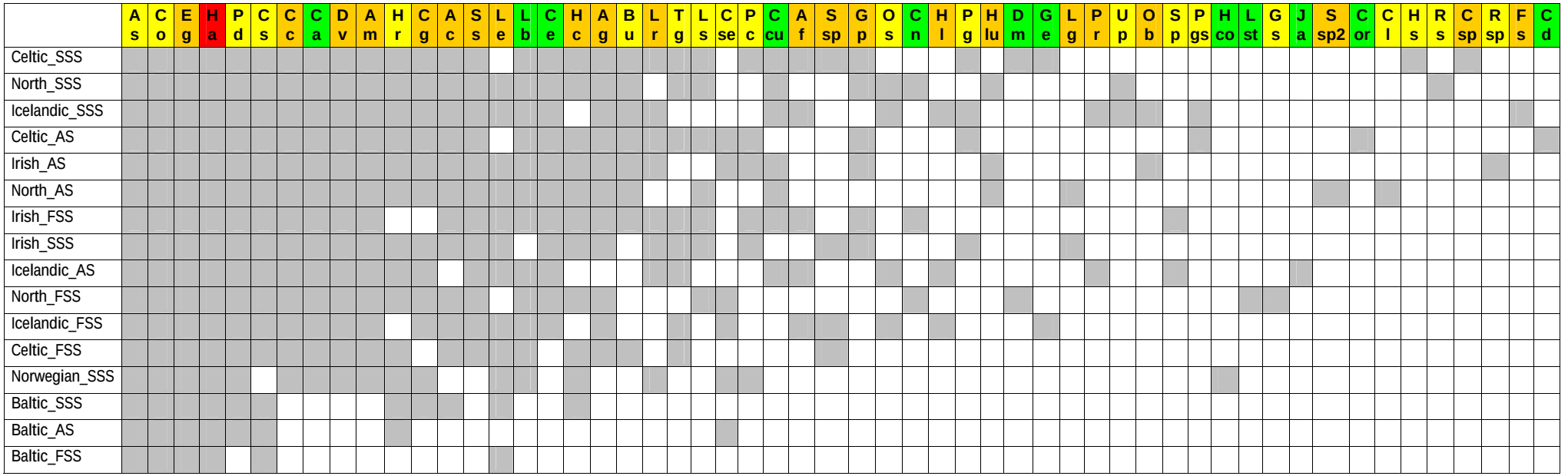

Figure 7.6. Packed matrix of component communities of total parasites in the entire dataset (16 communities in six regions of NE Atlantic; labels in first column). Species (first row) are labelled by first letters of the generic and specific names. Larval helminths marked in yellow; gastrointestinal helminths in orange; *Hysterothylacium aduncum* L3, L4 and adults in red; ectoparasites in green. *Abbreviations*: Samples: FS, first spring sample; SSS, second spring sample; AS, autumn sample. Species: *As, A. simplex*; Co, *C. osculatum*; Eg, *E. gadi*; Ha, *H. aduncum*; Pd, *P. decipiens*; Cs, *C.strumosum*; Cc, *C. cirratus*; Ca, *C. adunca*; Dv, *D. varicus*; Am, *A. morrhuae*; Hr, *H. rigidum*, Cg, *C. gracilis*; Ac, *A. crassicollis*; Ss, *Stephanostomum* spp.; Le, *L. elongatum*; Lb, *L. branchialis*; Ce, *C. elongatus*, Hc, *H. communis*; Ag, *A. gadi*; *Bu, Bucephalinae* gen. sp.; Lr, *L. rachion*; Tg, *Trypanorhyncha* fam. gen. sp.; Ls, *Lacistorhynchus* sp.; Cse, *C. semerme*; Pc, *P. crucibulum*; Ccu, *C. curtus*; Af, *A. filiformis*; Ssp, *Spinitectus* sp., Gp, *G. phycidis*; Os, *Otodistomum*sp.; Cn, *C. nodulifera*; Hl, *H. levinseni*; Pg, *P. gracilescens*; Hlu, *H. luehei*; Dm, *D. merlangi*; Ge, *G. elongata*; Lg, *L.?gibbosus*; Pr, *P. reflexa*; Up, Unidentified plerocercoids; Ob, *O. bacillaris*; Sp, *S. pleuronectis*; Pgs, *Pseudophylidea* gen. sp.; Hco, *H. confusus*; Lst, *L. sturionis*, Gs, *Grillotia* sp.; Ja, *J. arctica*; Ssp2, *Steringotrema* sp.; Cor, *C. ornatus*; Cl, *C. lingua*; Hs, *Hepatoxylon* sp.; Rs, *Rhapidascaris* sp.; Csp, *Cucullanus* sp.; Rsp, *Rhipidocotyle* sp.; Fs, *Fellodistomum* sp.; Cd, *C. diaphanus*.

On the other hand, analyses of a matrix comprised of communities from open water high-salinity regions only (*i.e.* excluding those from Baltic Sea and Trondheimsfjord) revealed significant nestedness and a significant negative correlation between the rank position of communities in the matrix and sampling sequence (r_s =-0.650 p=0.022), thus confirming the temporal trend described above (*i.e.* the sequence from poorest to richest component communities: spring 2002 → autumn 2002 → spring 2003, see Figure 7.6).

Only four parasite species were common for all component communities: three nematodes, *A. simplex*, *C. osculatum* and *H. aduncum*; and the acanthocephalan *E. gadi* (all species with rank=1 in the packed matrix). Twelve species were present in at least twelve of the component communities: *P. decipiens, C. strumosum, C. cirratus, C. adunca, D. varicus, A. morrhuae, H. rigidum, C. gracilis, A. crassicollis, S. caducum* and *L. elongatum*) (species listed according to their rank order in the packed matrix, 2 to 13). However, there were many species that exhibited unexpected presences (*i.e.* in poorer communities) the most remarkable species being the trematodes *L. elongatum*, *H. communis*, *Fellodistomum* sp. and *Rhipidocotyle* sp.; the acanthocephalans *C. strumosum* and *C. semerme*; the nematode *H. rigidum*; and the copepod *C. diaphanus* (Figure 7.6).

Finally, there was a strong negative correlation between component population sizes of the parasite species and their rank order in the packed matrices (r_s ranging between -0.502 and -0.806 depending on the component community; all p<0.001 in all cases) *i.e*. the best colonisers of component communities in cod also were the most abundant species. Pairwise tests of the rank order in the packed matrices of larval *vs* adult forms and endo- *vs* ectoparasites did not reveal significant differences (M-W test, Z= -0.853, p=0.394 and Z=-1.406, p=0.160, respectively).

Analyses performed on the restricted dataset also revealed significant nested subset paterns both among total, ecto- and endoparasite faunas and among parasite communities (Table 7.5). Only two species were common for all 16 communities (*H. aduncum* and *C. osculatum*) whereas nine were present in at least 12 communities: *P. decipiens, A. simplex, E. gadi, D. varicus, C. cirratus, C. adunca, C. strumosum*, and *H.rigidum* (species listed according to their rank order in the packed matrix, 2 to 10).

7.4. Discussion

Kennedy & Bush (1994) stressed the importance of scale in assessing the role of ecological determinants of community structure and suggested that analyses at wider spatial scale could provide generalizations of heuristic value. This chapter, focused on the higher levels of parasite community organisation, component communities and regional faunas, appears to provide support to the prediction of Kennedy & Bush (1994) by depicting departures from randomness in the patterns of community richness, composition and structure in parasite communities in cod from the NE Atlantic.

7.4.1. Similarity patterns in parasite component communities

The results of the three multivariate techniques (MDS, cluster analysis and ANOSIM) applied in this study, exhibited an overall good agreement. An important result of the present assessment of similarity in parasite communities in cod from the NE Atlantic, is that the compositional patterns are common for both datasets examined (*i.e*. entire and restricted datasets) irrespective whether parasite abundance or prevalence data were used to generate the similarity matrices.

However, the observed patterns in total communities did not generalise to the component community clades (*i.e.* gastrointestinal and larval helminth assemblages and ectoparasite assemblages). Thus, ectoparasite assemblages did not show significant differences in composition between the five regions where ectoparasites were recorded (*i.e.* Celtic, Irish and North seas, Trondheimsfjord and Icelandic waters) in both analyses. Furthermore, although the regional differences in composition between gastrointestinal helminth assemblages contributed to the significant differentiation of total parasite communities, the ones in cod sampled from the open water locations exhibited a generally similar composition and structure. Finally, the larval helminth assemblages exhibited a lower degree of regional differences in their composition and structure.

Overall, the following general pattern emerges from the comparative analysis of community/assemblage similarity: (i) a distinct compositional segregation of communities in cod from the two low-salinity regions (Baltic Sea and Trondheimsfjord); (ii) an overall distinctive structure of communities in cod from Icelandic waters especially with respect to gastrointestinal and larval helminth assemblages; and (iii) higher homogenisation with respect to the composition and structure of parasite communities in cod from Celtic, Irish and North seas.

Therefore, although statistical tests indicated an overall significant regional differentiation of parasite communities/assemblages in cod, this appears to be a result of comparison of distinctly different and/or geographically isolated marine environments. On the other hand, the fact that no significant seasonal effects on composition of parasite communities within a given region were revealed, indicates that community predictability is relatively higher within regions. This feature can serve for discrimination of cod populations (a subject developed in Chapter 8).

7.4.2. Similarity-distance decay relationship: autocorrelation at the lower spatial scale

The present study appears to be the first attempt to test the similarity-distance decay hypothesis on a host-parasite system using original taxonomically consistent data at two nested spatial scales (*i.e.* parasite faunas and component communities). The results revealed a non-random pattern, namely that geographical distance affects the species composition only at the level of component communities.

This study represents the second marine example to show decline in compositional similarity with distance. Oliva & González (2005) using presence/absence parasite data found similarity-distance decay relationship in three of four fish species studied in the Eastern Pacific. These authors also reported a simple linear relationship between community similarity and geographical distance contrary to previous studies on both free-living (Nekola & White, 1999) and host-parasite systems (Poulin, 2003; Krasnov *et al.*, 2005; but see Fellis & Esch, 2005). Parasite communities in cod from the NE Atlantic, however, revealed substantially higher rates (*c.* 77-230 times higher) of decrease of community similarity with distance than those observed by Oliva & González (2005). Common features of the four marine hosts studied to date which exhibit spatial compositional autocorrelation, are their high vagility and migratory behaviour which presume substantial compositional homogenisation of local faunas and component communities of their parasites. This however, was not the case although the extent (*i.e.* distances covered) in both studies is large. Therefore, the data from parasite communities in marine fish confirm the suggestion that the extent and host vagility are not primary determinants of the similarity among parasite communities and its decay with distance in the marine environments (Poulin, 2003). Furthermore, the present data suggest that component communities in cod appear to be more strongly constrained by the spatial configuration of locations and perhaps the dispersal abilities of cod parasites.

Overall, the rates of similarity decay observed in the present study are much lower (*c.* 2-17 times) than those recorded by Poulin (2003) in helminth communities in freshwater fish (*Perca flavescens* and *Esox lucius*, respectively) and substantially greater (*c.* 77 times) than those reported by Fellis & Esch (2005) in bluegill sunfish (*Lepomis macrochirus*) parasite communities in Southeastern United States. This was unexpected considering the migratory behaviour of cod and the domination of generalist parasites in parasite communities with respect to both richness and abundance. Although these species are capable of infecting several coexisting host species which ensures their transmission and persistence on a large geographical range (Poulin, 2003) which was confirmed at the higher spatial scale in the present study, their composition in parasite communities in cod in the NE Atlantic departed from random spatial pattern at the lower scale.

7.4.3. Regional-local richness relationship: saturated parasite communities in cod

As Kennedy & Guégan (1996) have discussed, estimates of the number of niches available to, and occupied by, parasites can only be made by comparing one host species in a number of different localities or in one locality over time. The present dataset, which encompasses the spatial and temporal variation in parasite communities in cod in the NE Atlantic, offered the opportunity to combine both approaches. One important result of the study is the congruence of the observed relationship between regional and local richness at both spatial scales of analysis and its curvilinear nature. The latter, therefore, provided evidence to reject the null hypothesis of a proportional sampling between CCR - RR and ICR – CCR.

Both, the curvilinear relationship between CCR and RR and the lack of relationship when low-salinity regions were excluded from the analysis, indicate the little influence of patterns operating on large regional scales in determining community richness of parasite communities in cod. Component communities exhibited richness levels well below those of the parasite faunas and this was true for both poor and rich faunas. Similarly, at the lower scale, infracommunities reached saturation levels well below those of component communities and ICR exhibited increasing independence of CCR. It is also possible that lower spatial scales exist for parasite communities in cod whose consideration may deserve further studies.

Cornell & Lawton (1992) reviewed the theoretical evidence for saturation in various community models. They stated that interactive and non-interactive local assemblages should differ in their tendency to be saturated with species and proposed two theoretical extreme curves defining the continuum for the relationship between local and regional

richness. In Cornell & Lawton's 'Type I' communities, local species richness is independent of local biotic interactions and increases proportionally with regional richness (a pattern called by them 'proportional sampling' and used here as a null hypothesis). In 'Type II' communities, biotic interactions limit local richness, which then saturates and becomes independent of regional richness (Cornell & Lawton, 1992).

By definition, and this was followed in the present study, the regional pool of species is the sum of the species in local assemblages (Cornell & Lawton, 1992). This makes it difficult to define dependent and independent variable clearly. Thus, it can be assumed that if local richness is saturated then regional diversity may be limited by local processes. If all local habitats are basically uniform with the same set of species (hence low β-diversity) local and regional richness would converge (Cornell & Lawton, 1992). However, and this appears to be the case of the relationship in the present system, habitat heterogeneity (and therefore high β-diversity) would set the limits to regional richness and saturation would occur at a progressively smaller proportion of the regional pool. Therefore, the present data appear to agree with the pool-exhaustion hypothesis rather than 'niche saturation' model of community development (Aho, 1990).

It appears that studies on parasite communities have shown the existence of Type II communities (as opposed to studies on free-living organisms, see Guégan *et al.*, 2005), *e.g.* intestinal helminths of amphibians (Aho, 1990), freshwater fish in England and Ireland (Kennedy & Guégan, 1994; 1996), freshwater fish in North America (Aho & Bush, 1993). Poulin (1996; 1997a) on the opposite, reported a linear relationship between the maximum ICR and CCR for intestinal helminth communities using a dataset for 68 vertebrate hosts possessing species-rich communities (birds and mammals). Nevertheless, the latter results are based on a meta-analysis across hosts and it may appear that curvilinear relationships would be more common as more studies on different populations of the same host species are conducted (*e.g*. Kennedy & Guégan, 1996; Calvete *et al.*, 2003; present study).

Guégan *et al.* (2005) stressed the possible connection between community saturation and the density of parasites. Density compensation in species-poor communities, *i.e.* the population density of each species being greater in species-poor than in species-rich communities, is generally associated with competition for resources (MacArthur *et al.*, 1972; Tonn, 1985; Krasnov *et al.*, 2006). The present analyses appear somewhat inconclusive. Due to the lack of a significant linear relationship between the mean abundance and CCR, an indication of the occurrence of density compensation was observed in cod parasite communities from the open water regions (*i.e.* North, Irish and Celtic Seas

and Icelandic waters). On the other hand, the significant linear trend observed when the entire dataset was tested, suggests the lack of density dependence in the poorer parasite communities in cod sampled from Baltic Sea and Trondheimsfjord.

7.4.4. Are there compositional gradients in parasite communities in cod?

The results of the present study show that the non-random patterns of faunal composition generalise to the component communities (i.e. to the lower level of community spatial organisation). This indicates that the diversity patterns in parasite communities in cod in the NE Atlantic are quite general. Although the non-randomness in faunal composition appeared associated with a longitudinal gradient at first glance, it is clearly related to the salinity which represents a major obstacle to the distribution of marine organisms. Whereas ectoparasites are directly affected, internal parasites, which typically posses complex life-histories, also exhibit distributional trends related to salinity because of its effect on free-living larvae or the restricted distribution of at least one of the hosts in their life-cycles at low salinities (Zander, 2005). Therefore, the observation that poor faunas and communities from low-salinity regions (Baltic Sea and Trondheimsfjord) are nested in the richer faunas/communities from the high-salinity open water regions, was not unexpected.

However, the order of component communities with respect to the temporal series of sampling was unexpected. The initial hypothesis was that communities sampled in autumn would represent subsets of those sampled in spring due to the maximum in zooplankton abundance in this season (*i.e.* increased abundance of the intermediate and paratenic hosts for many cod parasites). Thus Strømnes & Andersen (2000) have shown that larval stages of *A. simplex* in cod from Norwegian waters exhibit a clear abundance peak in April. These authors suggested that the spring bloom of plankton constitute one of the most important factors governing the phenomenon of "spring rise" in *A. simplex* third-stage larvae in this area. However, this hypothesis was not supported because of the lack of correlation of the observed order of communities and season. Therefore, the present nested subsets analysis appears to indicate the possibility of temporal autocorrelation of parasite communities in cod thus adding an additional level of non-randomness (*i.e.* upgrades to the spatial autocorrelation revealed by the similarity-distance decay relationship). Time-series data on parasite communities, however, are needed to test this hypothesis. A possible explanation for this unexpected pattern is the fact that the summer of 2002 was unusually hot (ICES, 2003; 2005b). This might have sped up parasite transmission rates resulting in higher diversity in communities sampled in the autumn 2002. Most cod parasites with good

colonising abilities also possess long life-spans and accumulate in the hosts. It is therefore, plausible to suggest that communities observed in the following spring (2003, few months later) are a result of species addition to communities with generally higher background richness. Notably, this suggestion appears to be supported by two of the three exceptional cases (*i.e*. that did not 'fit' to the pattern): communities in cod sampled in the spring 2003 in Irish Sea and those in cod sampled in autumn in Icelandic waters (Figure 7.6). A closer inspection revealed that both samples had high representation of juvenile fish and this therefore, appeared to lower the background diversity. Overall, the species dominating both component and infracommunities in cod (Chapter 6) contributed strongly to the observed patterns; the best colonisers were also the most locally abundant species.

González & Poulin (2005a) recently stressed that the underlying theory of nested subset patterns (Patterson & Atmar, 1986) is more appropriate to patterns of species presence/absence in various host populations or localities than to patterns of presence/absence in individual hosts. However, among component community nestedness analyses for parasites have rarely been carried out (Poulin, 1997b; Valtonen *et al.*, 2001; Calvete *et al.*, 2004). Despite that component community level of organisation is more relevant for nestedness analyses, the study of González & Poulin (2005a) was the only one to search for nested patterns among component communities of the same host species (*Sebastes capensis*).

The present study is therefore, the first to attempt nested subset analyses at the level of local faunas and the second at the level of component communities of a single host species. González & Poulin (2005a) found that component communities of both ectoparasites and endoparasite assemblages in *S. capensis* exhibit significant but different nested subset patterns the differences in both cases being related to latitude. These authors recorded very low temperature (3.64º) for the packed matrix of ectoparasite communities and comparable to the present data temperature for the matrix of endoparasite communities (26.74º).

There appear no latitudinal gradient influence on the composition of parasite faunas and communities in cod in the NE Atlantic. This can be associated with the low latitudinal extent of the present study (range *c.* 15 *vs* 45º). On the other hand, although the longitudinal gradient was much greater (*c.* 41º), and this seemed to affect faunal non-random pattern, the hypothesis could not be tested due to the confounding effect of salinity. The two host species also differ substantially in vagility (greater in cod), community richness (substantially greater in cod) and perhaps the degree of host specificity of the parasites

[however, 29 out of the 39 forms found in *S. capensis* (74%) were not identified to species level]. The results of the present study revealed non-random structure of parasite faunas in cod in the NE Atlantic and suggest that large-scale processes are capable of influencing the composition of component parasite communities in this fish species.

In a recent review Timi & Poulin (2008) provided detailed comparison of the sensitivity of analytical methods used to detect nestedness and showed that NTC yields consistently more significant nested patterns and concluded that the probability of observing a nested pattern in a parasite community depends entirely on the metric and null model of the analysis. Clearly, the patterns observed in parasite faunas and component communities in cod from the NE Atlantic deserve an in depth study that would reveal underlying processes. Thus, although the positive correlation between component population size and parasite species rank indicate that the observed non-random subsets may be result of passive sampling, the null hypothesis applied by NTC does not allow test for the influence of this process. The metric T was used here for comparative purposes because it is the only nestedness metric that is independent of matrix size.

In conclusion, although species density distributions indicate neutral structure and independent acquisition of species in parasite communities in cod, the non-random patterns in species composition and structure detected in parasite faunas and component communities in the six regions of the NE Atlantic detected in the present study confirm the importance of scale in assessment of the ecological determinants of community structure.

8. Parasite communities for discrimination of cod populations: Random Forests, a novel multivariate statistical approach

8.1. Introduction

The "stock"- concept is perhaps one of the most controversial due to the marked difference in its perception and application between fishery biologists and fisheries managers. Perceived as biological entities by the former and as management units by the latter and both not necessarily matching (Waldman, 2005; Hammer& Zimmermann, 2005). The most robust, yet sufficiently specific to be useful, definition of stock is that of Ihssen *et al.* (1981) who proposed that stock is "... an intraspecific group of randomly mating individuals with temporal or spatial integrity" (see Waldman, 2005 for a review). In spite of the problems with operational definitions, stock identification (*i.e.* defining stock characteristics and boundaries) and discrimination (or separation, *i.e.* identification of members of different stocks in the catches of mixed aggregations) studies have developed rapidly in the last decade due to their importance for the development of sustainable harvest and monitoring strategies by fisheries management.

Fisheries management of cod is related to the future prospect for economically viable cod fisheries (ICES, 2006). Separate cod populations with little or no interbreeding (*i.e.* cod stocks, see also Chapter 1) are recognised in the NW (10 cod stocks) and NE Atlantic (14 cod stocks) (ICES, 2005a). Some of the stocks, *e.g.* those in the North Sea, the Baltic and in the Canadian waters, have declined to very low population levels (Hutchings & Myers, 1994; Cook *et al.*, 1997; O'Driscoll *et al.*, 2000; Bundy, 2001; Jonzen *et al.*, 2002; Hutchinson *et al.*, 2003). In order to re-establish these stocks to population levels that will safeguard fisheries in the future, they have been subject to either closure or significant reduction of fishing operations (ICES, 2006).

Several types of classifier tools have been used in fishery science for stock identification and discrimination, the most frequently employed being conventional discriminant analysis (reviewed in Pella & Masuda, 2005). Recently, Saila (2005) reviewed the advantages of using Neural Networks (NNs) for classification of fish populations. The most widely used biological traits in fisheries for stock identification have been genetic markers and morphometric characters; useful biological tags are otolith elemental composition, otolith shape and parasite assemblages (Cadrin *et al.*, 2005 and references therein).

Marine fish parasites have been used as biological markers of fish populations since Herrington *et al.* (1939). The pioneer studies included small numbers of parasite species fulfilling the criteria of Sindermann (1983) and reviewed by Williams *et al.* (1992), MacKenzie & Abaunza (1998; 2005) (*i.e.* Margolis, 1963; Chenoweth *et al.*, 1986; Leaman

& Kabata, 1987; Kabata *et al.*, 1988; MacKenzie, 1990; Hemmingsen *et al.*, 1991; Moser & Hsieh, 1992; Somdal & Scram, 1992; Stanley *et al.*, 1992). MacKenzie & Abaunza (1998; 2005) stressed the utility of multivariate approaches which include entire parasite assemblages and Timi (2007) provided a recent review on studies in SW Atlantic justifying the application of these approaches. Indeed, the increased application of more sophisticated statistical techniques has allowed consideration of almost the entire parasite assemblages in the stock identification methods and a subsequent selection of the most discriminating parasite species. The most commonly used technique in parasite tag studies is linear discriminant analysis (*e.g.* Arthur & Arai, 1980; Arthur, 1983; Arthur & Albert, 1993; Boje *et al.*, 1997; Hoff *et al.*, 1997; Blaylock *et al.*, 2003, Sardella & Timi, 2004; Melendy *et al.*, 2005; Timi *et al.*, 2005; Chavez *et al.*, 2007; Ferrer-Castelló *et al.*, 2007), canonical discriminant analysis (*e.g.* Oliva & Ballón, 2002; Oliva *et al.*, 2004; Oliva & Sánchez, 2005) or correspondence analysis (Valdivia *et al.*, 2007). Power *et al.* (2005) used LDA, quadratic DA and NN to classify individual bogue (*Boops boops*) samples to their harvest locations.

Studies attempting stock discrimination of cod using parasites as biological markers are relatively few the most recent dating from 1998: (i) eight in the NW Atlantic (Sherman & Wise, 1961; Templeman & Fleming, 1963; Templeman *et al.*, 1976; Khan *et al.*, 1980; Bishop *et al.*, 1988; McClelland & Marcogliese, 1994; Khan & Tuck, 1995; Jones & Taggart, 1998); and (ii) nine in the NE Atlantic (Polyansky & Kulemina, 1963; Reimer, 1970; Platt, 1976; Buchman, 1986; Boje, 1987; Hemmingsen *et al.*, 1991; Larsen *et al.*, 1997; Karasev, 1994; 1998, see Chapter 1 for details of these studies). These studies are typically focused on a single or small number of parasite species and have applied mainly univariate techniques to compare the infection parameters between regions.

The present study applies for the first time an ensemble classification approach using Random Forests (RF) (Breiman, 2001) to the application of parasite community data as biological tags for fish population discrimination. Random Forests are ensembles of tree-type classifiers that use the method of bagging, an improved method of bootstrapping. The following advantages of the Random Forest approach for multisource classification may prove to be useful in solving the task of population assignment: it is non-parametric (*i.e.* no assumptions of normality or independence required concerning the data) and provides means for estimating the importance of individual variables in classification. In contrast to other machine learning methods RF are not prone to overtraining and develop models from

data which is both noisy and complex. Misclassified cases are easily identified and the evolved models can be readily applied to new data.

The aim of the study was two-fold. First, using the same version of the parasite community data derived from sampling of cod populations in the five areas in the NE Atlantic, the learning behaviour of RF was compared with two other algorithms, one traditionally applied (LDA) and one recently used (NN) in studies using parasites as biological tags. Secondly, the RF analysis was scrutinized in order to evaluate the effect of variable/data reduction on efficiency and consistency in class assignment and to examine the importance of the annual and seasonal variation in parasite community composition and structure for discrimination of fish populations.

8.2. Materials and methods

8.2.1. Parasite community dataset

Parasites in cod populations sampled at five spring (spawning) and autumn (feeding) areas in the NE Atlantic (Baltic, Celtic, Irish and North Seas, and Icelandic waters, see Figure 8.1 for sampling locations and Table 8.1 for sample sizes) served as material for the present study. Analyses were carried out on the data on parasite communities in individual fish (*i.e.* infracommunities, see Bush *et al.*, 1997). The entire dataset comprised parasite infracommunities in 763 fish collected in the five regions of study (see Chapter 3 for details on samples and parasite recovery). All fish were infected with 1-17 parasite species. Species with occurrence < 1% in the total sample were excluded from analyses. Thus, the distributions of 31 parasite species in the total sample of 763 fish were used as independent variables and the sampling region (*i.e.* putative stock class) was used as the dependent variable (see Table 8.2 for size of the sampling series and experimental design). A 'blind' mixed sample of 50 fish used in the model validation was collected in Spring 2003 and comprised of 10 (20%) individuals from each region.

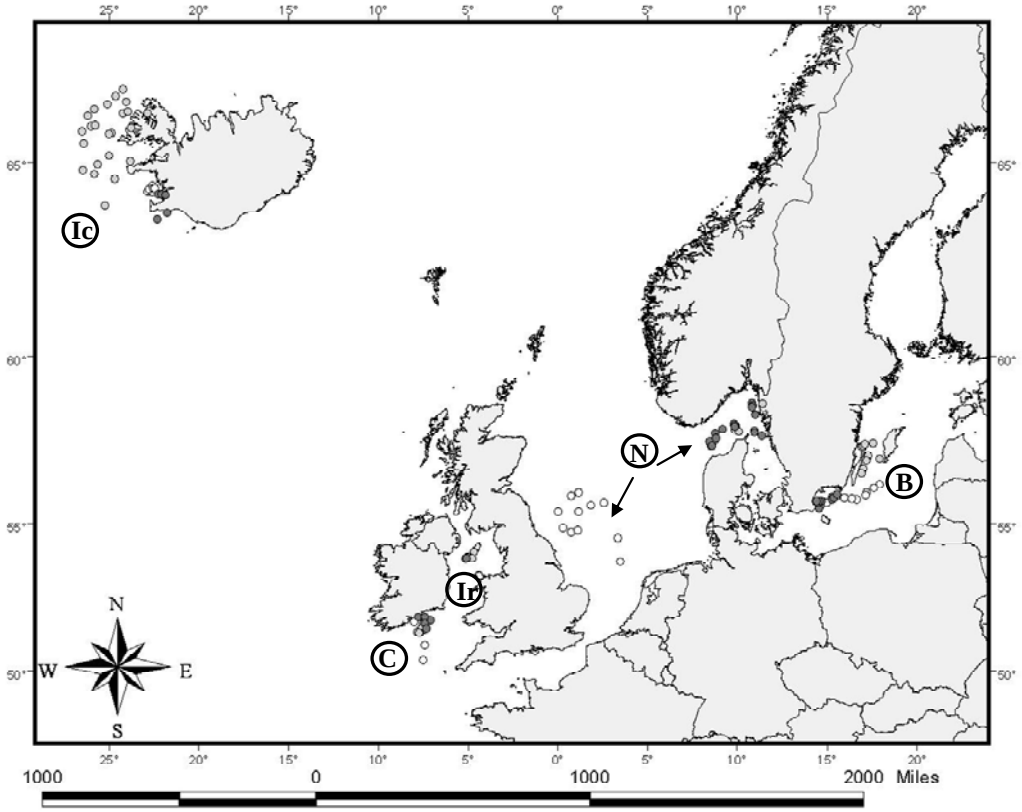

Figure 8.1. Locations at which fish were sampled. B, Baltic Sea; C, Celtic Sea; Ic, Icelandic waters; Ir, Irish Sea; N, North Sea. FSS, white circles; AS, light grey; SSS, dark grey.

Table 8.1. Sample size for the data used from the five NE Atlantic regions by sampling seasons and the 'blind' sample.

Region	Baltic Sea	Celtic Sea	Icelandic waters	Irish Sea	North Sea	Total
Spring 2002	59	23	45	60	27	214
Autumn 2002	61	56	62	52	60	291
Spring 2003	60	59	58	24	60	261
Total	180	138	165	136	147	766
'Blind' sample	10	10	10	10	10	50

8.2.2. Classification algorithms

8.2.2.1. Random Forest

Random Forests is an ensemble of random classifiers (trees) that combines the decisions by majority voting (*i.e.* 'votes' for the most popular class) of a large number of classifiers in order to obtain more accurate predictions than any individual classifier. RF uses bootstrap aggregating (bagging, *i.e.* each new training set is drawn, with replacement, from the original training set, leaving out about one-third of the cases). Then a tree is grown on the

new training set using random feature selection without prunning. Breiman (2001) provided empirical evidence that the out-of-bag error estimate is as accurate as using a test set of the same size as the training set and concluded that out-of-bag error estimate removes the need for a set aside test set. Both bagging and random feature selection inject randomness in the algorithm of RF which results in the generation of diverse low-correlated trees thus increasing the predictive performance of RF.

The learning performance of the RF was examined prior to experiment through a series of runs in which the number of variables used at each branch varied between 2 and 8. The following configuration was found to be optimal: 2000 trees and 5 variables (3 in Experiment 3). For random forest model development, the randomForest package of the statistical software R.2.5.1. was used (R-windows@r-project.org).

8.2.2.2. Algorithms used for comparison

To assess the consistency and effectiveness of RF to the problem of class assignment examined here, its performance was compared to one widely applied classification tool (LDA) and one recently used (NN).

8.2.2.2.1. Linear discriminant analysis

Linear discriminant analysis (LDA) is a popular tool that has proved useful for detecting the variables that allow discrimination between two or more naturally occurring groups, and for classifying cases into different groups with a better than chance accuracy. Once a model is finalized and the discriminant functions derived, the algorithm automatically computes the classification functions. The latter are then used for the predictive classification of cases *i.e.* using posterior probabilities derived from Mahalanobis distance for each case to determine its group membership. However, a number of underlying assumptions of the algorithm represent a threat to the validity of the classification results: (i) the data (for the variables) represent a sample from a multivariate normal distribution; (ii) the variance/covariance matrices of variables are homogeneous across groups; (iii) the variables that are used to discriminate between groups are not completely redundant; and (iv) the means for the variables across groups are not correlated with the variances.

LDA model development was built using the lda (MASS package) package in R.2.5.1 statistical software after a log (x+1) transformation of parasite abundance variables (although no complete linearization of the data was attained). Prior probabilities for classes

approximated 0.20 (Baltic Sea, 0.23; Celtic Sea 0.18; Icelandic waters, 0.21; Irish Sea, 0.18; and North Sea, 0.19) in all experiments (see below).

8.2.2.2.2. Neural Networks

Artificial neural networks (NNs) imitate the learning process of the animal brain in that they can identify and learn correlated patterns between input data sets and corresponding target values. After learning, NNs can be used to predict the output of new data. NNs appear well suited for modelling class assignment problems using parasite data since they are not constrained by assumptions about the type of relation between the variables and can process non-linear, complex and noisy data (Rumelhart *et al.*, 1986). The network architecture which is most commonly used with the back-propagation algorithm, *i.e.* a feed-forward supervised neural network with a single hidden layer, was chosen for the present experiments. In the back-propagation networks the neurons are arranged in successive layers, and the information flows unidirectionally, from the input layer, through the hidden layer to the output layer. In each successive layer, every neuron sums its inputs and then applies a transfer function to compute its output. The output layer of the network then produces the final response, *i.e.* the estimated category or value (see Lek & Guégan, 1999; Lek & Guégan, 2000 for details).

The input layer is connected with the variables used for discrimination. The number of neurones in the output layer corresponds to the number of categories in which individuals should be classified. Each connection is weighted according to the signal intensity. Each neurone is connected with the neurones of the neighbouring layers; it receives and sends signals through these connections and always from input to output. Each neurone from the hidden layer integrates the signals received from the former neurones and sends signal to the next ones. This signal is delivered according to a non-linear transfer function applied to the sum of the weighted signals of the former neurones (Lek & Guégan, 2000). If w_i and x_i are the weight and the signal outgoing from the former neurone i (layer n), the incoming signal for one neurone in the layer n + 1 will be:

$$I = \Sigma\, w_i * x_i$$

The outgoing signal for this neurone in layer n + 1 will then be:

$$f(I) = [1 + \exp(-I)]^{-1}$$

In each successive layer, every neuron sums its inputs and then applies a transfer function to compute its output. The output layer of the network then produces the final

response, *i.e.* the estimated category or value. The network must be trained in order to classify individuals correctly. For the input layer, incoming signals corresponded to the variables (parasite species abundances) used to classify the 763 cod in this study. The outgoing signals of the output layer designated the category (1 of the 5 fishing grounds) where the studied individual will be assigned by the network.

The present study used an NN of one hidden layer of five neurons with 12-31 independent variables (non-transformed parasite abundance data) depending on the experimental setup as described below. The dependent nominal variable was recoded (one-of-N encoding) to adapt it to the demands of the transfer function used (sigmoid function). Learning performance of the NN was examined prior to experiment through a series of runs in which the number of neurones in the hidden layer varied between 2 and 10 and the number of iterations varied (200-2000 with an increment of 200); various configurations were examined. What appeared an optimal model was a five-unit hidden layer with a weight decay term of 0.25 and maximum number of 1000 iterations. The connection weights were taken randomly in the range [-0.1, 0.1]. All models were developed with nnet package in R.2.5.1 software (Venables & Ripley, 2002).

8.2.3. Experimental design

A series of experiments (252 runs in total) was carried out. The experiments were configured to both assess RF effectiveness and allow comparative evaluation of the results obtained with the LDA and NN. Therefore, all three algorithms were tested using the same version of the datasets (see Table 8.2 for details). Experiment 1 comprised 50 runs performed on the entire dataset (763 fish). Each time the dataset was randomly and uniformly (*i.e.* maintaining the same proportion of classes as in the entire dataset) split into a training set (610 fish, 80%) and a validation set (153 fish, 20%). This subdivision followed the practical consideration that if an efficient classification rule is derived, its evaluation should be applied on a limited number of fish, thus reducing the sampling effort in subsequent studies. The results were averaged over these 50 independent models.

A 10-fold stratified cross-validation technique was performed in Experiment 2 on the entire dataset (763 fish). The dataset was randomly split into 10 non-overlapping segments of approximately equal size and conserving the class proportions of the entire dataset. Ten models were built each time using a version of the data in which one of the segments is omitted (training set). Each model was then tested on the data from the segment

not used during training (test set) and the results were averaged over the 10 models to obtain an overall error estimate.

Table 8.2. Details of the experimental data sets.

	No. of cases in the training set	No. of cases in the test set	No. of variables	No. of models
Experiment 1	610	153	31	50
Experiment 2	687	76	31	10
Experiment 3	687	76	12	10
Experiment 4	397	44	29	10
Experiment 5				
(i) Spring 2002 *vs* Autumn 2002	212 (Spring 2002)	290 (Autumn 2002)	31	1
(ii) Spring 2002 *vs* Spring 2003	212 (Spring 2002)	261 (Spring 2003)	31	1
(iii) 2002 *vs* Spring 2003	502 (year 2002)	212 (year 2003)	31	1
(iv) 'Blind' experiment	763	50	31	1

The 10-fold stratified cross-validation technique was used in Experiment 3 on the entire dataset (763 fish) to assess the effect of variable reduction. The variables for this experiment were selected on the basis of variable importance in RF in Experiment 1 (these also exhibited the highest partial b values in LDA). Experiment 4 was carried out on a reduced dataset including only fish within the standard length range 40-70 cm (441 fish, 10-fold stratified cross-validation technique).

In order to assess the effect of seasonal and annual variations in parasite abundance on fish class assignment three single models were developed in Experiment 5 with different training and test sets: (i) Spring 2002 samples (training set) *vs* Autumn 2002 samples (test set); (ii) Spring 2002 samples (training set) *vs* Spring 2003 samples (test set); and (iii) 2002 samples (training set) *vs* 2003 samples (test set) (see Table 8.2 for sample sizes). Finally, a model developed on the entire dataset was validated with the use of a 'blind' sample (50 fish). The latter was used for comparative model evaluation since all three algorithms were applied to the same fish sample.

8.3. Experimental Results

An inspection of the MDS plot obtained in RF on the entire dataset revealed the difficult structure of the cod parasite data (Figure 8.2). The 'arms' indicating two long gradients (based on proximity measure) between cases represented the samples from Baltic Sea and Icelandic waters whereas those from Irish, Celtic and North Sea appeared tightly clustered together. Figure 8.3 presents a plot of the entire dataset with respect to the measure of 'outlyingness' for each case computed in RF. Nine outliers (Figure 8.3) were identified: 7 fish from Baltic Sea (4 sampled in Autumn 2002 and 3 sampled in Spring 2003) and 2 fish

from Icelandic waters (1 sampled in Autumn 2002 and 1 sampled in Spring 2003). These were left in the analysis assuming that they represent natural variation rather than noise.

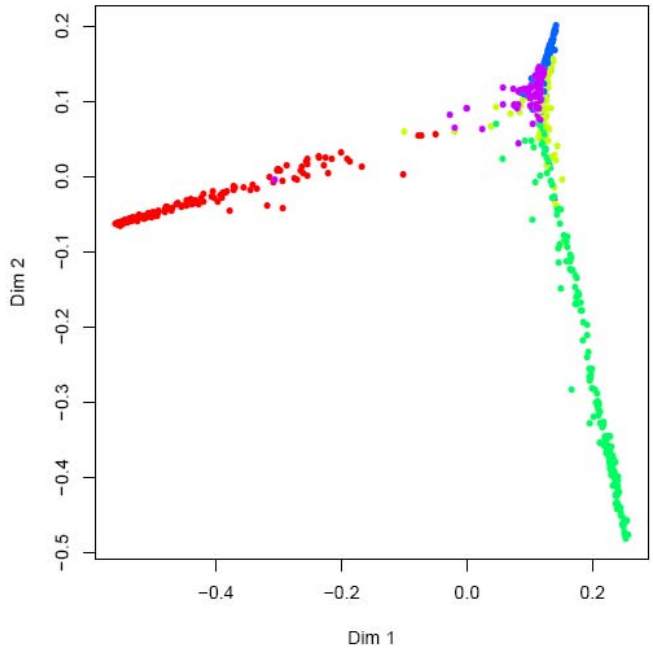

Figure 8.2. MDS plot of the entire dataset, *i.e.* 763 infracommunities from the five regions in NE Atlantic. Baltic Sea, red; Celtic Sea, blue; Icelandic waters, green; Irish Sea, violet; North Sea, orange.

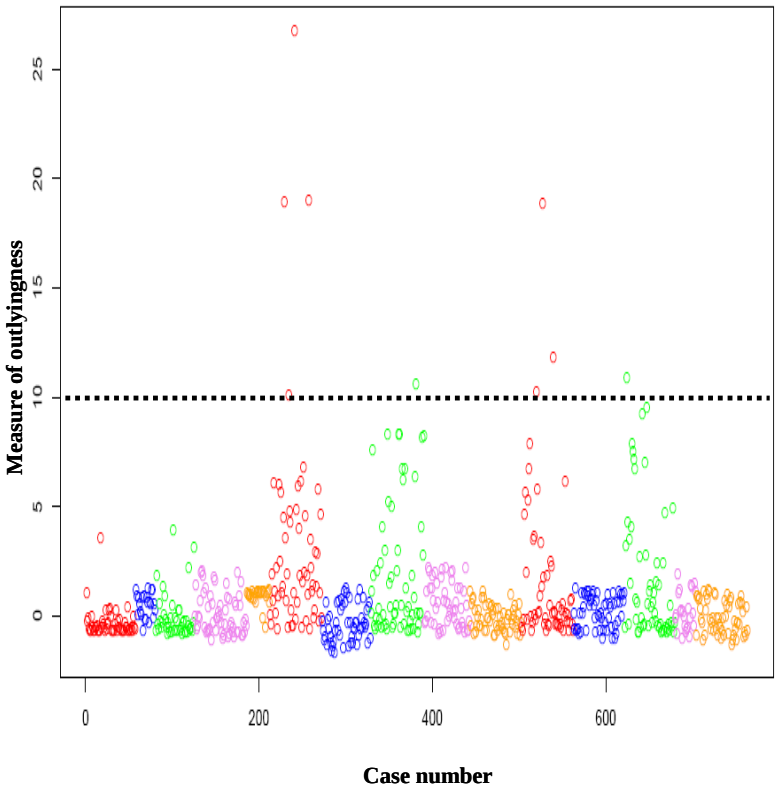

Figure 8.3. Plot indicating outliers (cases above the dotted line) in the entire dataset. Baltic Sea, red; Celtic Sea, blue; Icelandic waters, green; Irish Sea, violet; North Sea, orange.

Table 8.3 presents a summary of the performance in terms of the classification error (averaged over runs with the related SD where available) of the three algorithms in the experiments conducted on the cod parasite dataset. The average error rates in experiments 1-4 were substantially lower than those obtained in the four specifically designed 'real world' validation experiments. Although RF performed better in all experiments, building more models with low test set error (<10%, data not shown), the overall error means in Experiments 1, 2 and 4 were similar to those obtained with LDA.

Table 8.3. Summary of the experimental performance (test set errors, %) of the three algorithms evaluated using cod parasite dataset. Means±SD are given for the experiments where error rates were averaged over the independent models.

	RF	LDA	NN
Experiment 1	14.35 ± 2.57	16.35 ± 2.56	18.73 ± 3.26
Experiment 2	14.29 ± 3.49	16.53 ± 3.66	17.83 ± 5.45
Experiment 3	14.95 ± 3.14	22.15 ± 4.31	18.11 ± 2.38
Experiment 4	11.79 ± 3.42	12.46 ± 3.39	19.04 ± 5.14
Spring 2002 *vs* Autumn 2002	41.38	52.76	48.28
Spring 2002 *vs* Spring 2003	39.85	42.53	49.81
2002 *vs* Spring 2003	24.90	34.87	31.42
'Blind' experiment	24.00	42.00	48.00

It is worth noting that the test set errors were very similar to the out-of-bag error estimates in RF (means 14.85 *vs* 14.35% in Experiment 1; 14.58 *vs* 14.29% in Experiment 2; 15.96 *vs* 14.95% in Experiment 3; and 12.52 *vs* 11.79% in Experiment 4). This fact indicates that the training sets in the present experimental setup were large enough to develop adequate classifiers and supports the view that RF do not overfit (Breiman, 2001).

A comparison between test error rates in the first two experiments suggests that the different approaches in selecting the test sets do not affect the models developed by all three algorithms. Therefore, only 10-fold cross validation sets were used to evaluate the effect of variable and data reduction on model discriminating efficiency. Reducing the number of variables (Experiment 3) did not improve accuracy of RF which performed marginally better with all variables even if the restriction was limited to the variables identified as most important in previous experiments. However, the performance of LDA worsened notably.

On the other hand, 'trimming' the dataset by removing parasite community data in fish outside the range 40-70 cm (SL, *i.e.* using only communities present in adult 2-7 year-old fish) noticeably improved the performance of RF and LDA (Experiment 4, see Table 8.3). RF outperformed LDA in 5 and NN in 9 of the 10 models. A total of 8 best models were developed in this experiment: 3 with RF, 4 with LDA and 1 with NN algorithm (test

set errors 6.9-9.1%; 9.1%; and 6.8%, respectively). Although weighting the input data resulted in a marginal increase of performance of RF in Experiment 4 (mean test set error 11.54 *vs* 11.79%) the number of best models increased twice.

A close examination of the error rates in RF models developed in Experiment 4 revealed a significant variation between classes (*i.e.* putative stocks in the studied areas) over the 10 models with some classes more often misclassified. These misclassifications were not very common (SD> means in all cases) except for North Sea cod which were misclassified as Celtic (test set mean error 39.33%). Overall, RF provided a very good prediction for Icelandic, Baltic and Celtic fish (Table 8.4). However, the predictions for North and Irish Sea cod were poorer (the former notably so, see Table 8.4). A closer examination of the training sets revealed highest error rates for the sample collected in Spring 2002 at Dogger Bank (North Sea) probably due to the low representation of this apparently different sample in the total cod sample from the North Sea (27 out of 147). Notably, fish from this sample were most heavily misclassified in the 'blind' experiment (81.5% of the fish from this sample *vs* 6.7% and 25.0% of the fish from the autumn and second spring sample from Skagerrak, respectively).

Table 8.4. Confusion matrix for the models developed in Experiment 4 [test set, mean correct assignment ±SD (%)]

Original/Predicted	Baltic Sea	Celtic Sea	Icelandic waters	Irish Sea	North Sea
RF					
Baltic Sea	100	0	0	0	0
Celtic Sea	0.83 ± 2.63	91.37 ± 7.03	2.65 ± 4.27	5.15 ± 5.93	0
Icelandic waters	0	9.28 ± 13.83	90.72 ± 13.83	0	0
Irish Sea	0	8.92 ± 10.38	0	88.57 ± 10.98	2.50 ± 7.91
North Sea	4.00 ± 8.00	39.33 ± 18.97	3.66 ± 7.77	2.00 ± 6.32	51.00 ± 18.19
LDA					
Baltic Sea	99.17 ± 2.63	0	0	1.04 ± 2.95	0
Celtic Sea	0	86.68 ± 12.07	7.80 ± 7.34	8.02 ± 9.84	0
Icelandic waters	0	9.46 ± 13.88	90.54 ± 13.88	0	0
Irish Sea	0	6.43 ± 9.27	1.25 ± 3.95	88.57 ± 9.27	3.75 ± 8.44
North Sea	2.00 ± 6	34.67 ± 12.49	0	2.00 ± 6.32	61.33 ± 13.62
NN					
Baltic Sea	97.50 ± 5.62	0.83 ± 2.63	0.83 ± 2.63	0.83 ± 2.63	0
Celtic Sea	3.49 ± 7.36	85.53 ± 13.14	6.21 ± 11.3	6.82 ± 8.64	8.86 ± 10.36
Icelandic waters	3.93 ± 6.35	8.22 ± 14.87	80.89 ± 13.47	4.11 ± 9.45	2.86 ± 9.04
Irish Sea	0	10.00 ± 12.91	0	83.75 ± 15.65	10.00 ± 9.86
North Sea	3.00 ± 7.00	41.00 ± 12.38	0	6.00 ± 9.66	49.67 ± 50.33

'Real world' situations were mimicked in the single experiments in order to evaluate the generalisation abilities of the models developed by RF approach in comparison to LDA and NN. The main assumption was related to the possibility to build good predictive models with already existing data and assess the possibility of seasonal/annual effects on parasite community variation. In the first experiment the samples collected in spring 2002 were used for training and the ones collected in autumn 2002 for model evaluation. All three algorithms exhibited a substantially worse error rate compared to previous experiments (see Table 8.3). The models developed in the second experiment using the samples collected in spring 2002 for training and those collected the following spring for the test set performed similarly whereas increasing the sample size of the training set (by including all samples of 2002) resulted in a notable decrease of the error rates obtained with a test set comprising samples of spring 2003 (Table 8.3). RF outperformed the two other algorithms in all three experiments. Finally, the accuracy of RF prediction in the validation experiment with the 'blind' sample although generally low was twice as high (Table 8.3).

One of the advantages of RF is that it provides a measure (expressed in both numerical and graphical form) for the variable importance in each model (*e.g.* see Figure 8.4 which shows the graphical output of the program for the 'blind' sample experiment). Table 8.5 presents lists of the 'top ten' variables (*i.e.* parasite species) with respect to their importance for model development in the experiments. The lists largely overlapped between models and included invariably the anisakid nematodes and *C. cirratus*, the trematodes *D. varicus* and *H. communis*, the acanthocephalan *E. gadi* and the copepode *C. adunca*.

Table 8.5. Top ten variables listed in order of their importance in different RF models.

Experiment 2	'Blind' experiment	Spring 2002 *vs* Autumn 2002/Spring 2003	2002 *vs* Spring 2003
D. varicus	*D. varicus*	*A. simplex*	*A. simplex*
A. simplex	*A. simplex*	*D. varicus*	*D. varicus*
C. osculatum	*C. osculatum*	*H. aduncum*	*H. aduncum*
H. aduncum	*H. aduncum*	*C. osculatum*	*C. osculatum*
H. communis	*E. gadi*	*H. communis*	*H. communis*
E. gadi	*H. communis*	*E. gadi*	*A. morrhuae*
A. morrhuae	*A. morrhuae*	*C. cirratus*	*H. rigidum*
C. adunca	*C. adunca*	*C. adunca*	*E. gadi*
C. cirratus	*C. cirratus*	*A. morrhuae*	*C. cirratus*
H. rigidum	*H. rigidum*	*Stephanostomum* spp.	*C. adunca*

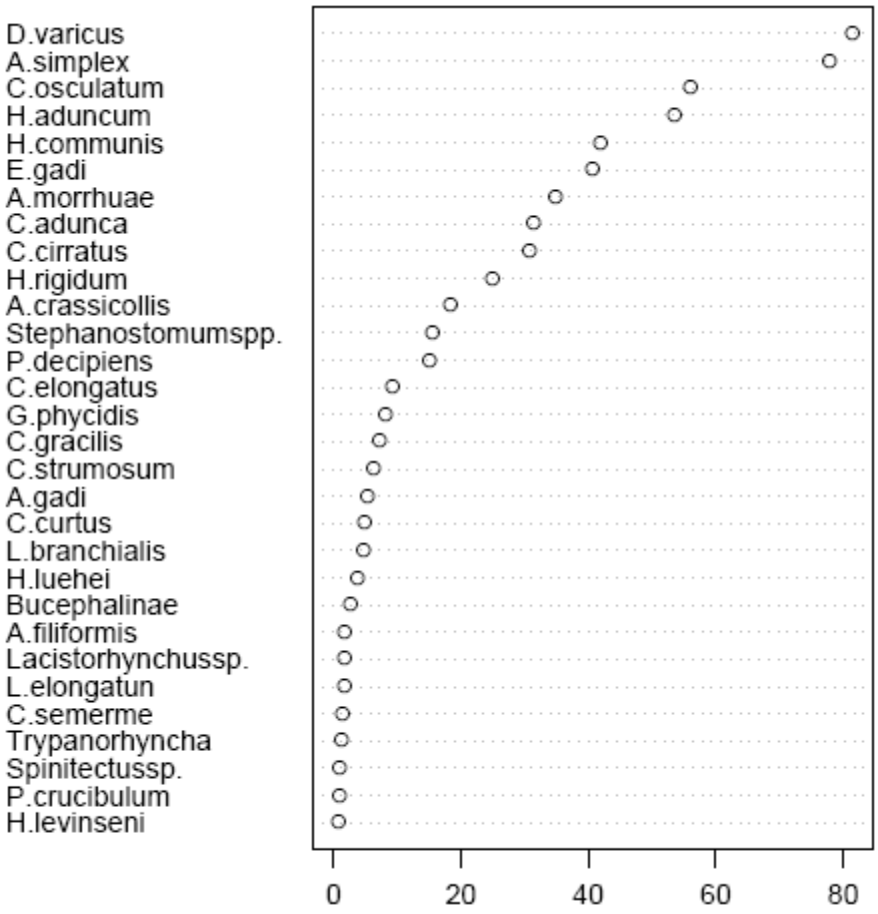

Figure 8.4. Variable importance plot. 'Blind' experiment.

8.4. Model evaluation

The performance of the three algorithms, RF, LDA and NN was compared based on the predictions made in the validation 'blind' experiment by means of McNemar test and evaluation of the performance measures of the three algorithms for each class separately.

8.4.1. McNemar test

Overall, 39 correct predictions for the class assignment of the 'blind' validation sample were made by RF (*vs* 30 and 28 for LDA and NN, respectively). McNemar test was selected and carried out as described in detail in Peters *et al.* (2007). RF exhibited a significantly lower error rate than either LDA or NN algorithms (χ^2=4.9231, p=0.027 and χ^2=5.5, p=0.019, respectively).

8.4.2. Performance measures for separate classes

The model validated on the 'blind' sample was used in order to assess and compare the performance of the three algorithms for each class. Four test statistics were calculated using confusion matrices arranged as contingency tables for binary classifier (*e.g.* Fielding & Bell, 1997; Kohavi & Provost, 1998; Peters *et al.*, 2007) (see Table 8.6):

Table 8.6. Contingency table for a binary classifier.

Original/Predicted class	**Assigned to class X**	**Not assigned to class X**
From class X	true positives (**tp**)	false negatives (**fn**)
Not from class X	false positives (**fp**)	true negatives (**tn**)

(i) *Accuracy* (A);

$$A = \frac{tp + tn}{tp + tn + fp + fn}$$

(ii) *Precision* (P, *=specificity, =positive predictive power*);

$$P = \frac{tp}{tp + fp}$$

(iii)*Recall* (R, *=sensitivity*, *=true positive rate*).

$$R = \frac{tp}{tp + fn}$$

Precision and recall were combined by means of the 'F-measure (Van Rijsbergen, 1979):

$$F = \frac{2PR}{P + R}$$

A balanced variant of the F-measure was used, *i.e.* P and R were given equal importance (see for details Peters *et al.*, 2007).

Table 8.7 presents a summary of the four test statistics. Overall RF appears as the best classifier which outperformed the other algorithms. It exhibited both the highest scores for the lower ranges and the means (across classes) for all statistics. The second best classifier was LDA whereas the worst classifier was NN which performed marginally better

in the prediction of the Baltic fish (all statistics) and best with respect to A, P and F statistics in the prediction of North Sea fish only.

Table 8.7. Accuracy, precision, recall and F for RF, LDA and NN of the models validated on the 'blind' sample.

		Baltic Sea	Celtic Sea	Icelandic waters	Irish Sea	North Sea	Mean across classes
Accuracy	RF	0.96	0.86	0.96	0.88	0.86	0.90
	LDA	0.90	0.86	0.78	0.70	0.86	0.82
	ANN	0.98	0.78	0.68	0.68	0.94	0.81
Precision	RF	1.00	0.80	0.90	0.64	0.62	0.79
	LDA	0.86	0.80	0.47	0.27	0.62	0.60
	ANN	1.00	0.33	0.36	0.13	1.00	0.56
Recall	RF	0.80	0.40	0.90	0.90	0.80	0.76
	LDA	0.60	0.40	0.80	0.30	0.80	0.58
	ANN	0.90	0.10	0.80	0.10	0.70	0.52
F	RF	0.89	0.53	0.90	0.75	0.70	0.75
	LDA	0.71	0.53	0.59	0.29	0.70	0.56
	NN	0.95	0.15	0.50	0.11	0.82	0.51

All three algorithms discriminated the fish samples from the Baltic Sea well (which also appeared more differentiated in the MDS plot, see Figure 8.2) and to a lesser extent those from Icelandic waters (Table 8.6). Notably, considering the range of performance, all three algorithms exhibited overall low scores for the accuracy and precision of predicting the Irish Sea fish. This is probably related to the notably lower ranges for the true positive rate R and F with respect to the prediction of the Celtic Sea fish. Here, again, RF outperformed LDA and NN (except for the R-score for Celtic Sea which is equal to that obtained in LDA models).

8.5. Discussion

As delineated by the two-fold approach, the results of the present study fall into two areas: (i) those related to the application of the RF algorithm to complex ecological data, and in particular, its ability to predict multiclass assignment of fish stocks based on parasite community data; and (ii) those related to the intrinsic properties of the data analysed, *i.e.* the variability of parasite communities in individual fish within a wide geographical range of their host populations in the NE Atlantic.

8.5.1. RF as a useful novel approach for stock discrimination using parasite communities

One important outcome of this study is that the comparative approach to RF, LDA and NN algorithms applied on the same datasets demonstrated the potential of RF for developing predictive models using data that are both complex and noisy. Overall RF exhibited better prediction accuracy and outperformed the other two algorithms in assignment of fish using parasite community data. The main promise of the example presented here is that the models were developed on a host–parasite system with unrestricted noise. Thus, a wide size-range of fish was sampled from a wide geographical range in the NE Atlantic, seasonal data from two years were combined, and a large number of parasite species with variable distributions within the hosts were used as variables in the analyses.

Supervised methods are prone to overtraining – the phenomenon whereby improving predictive performance in terms of the training data is accompanied by increasingly poor performance on independent (test) datasets, resulting in poor generalization capacity. LDA tends to overfit the training data if there are too many correlated predictors and overtraining is one of the main problems in the application of NN which therefore require elaborate tuning. This disadvantage of the two algorithms observed in the experiments suggests that RF is a promising alternative in supervised classification tasks.

Granitto *et al.* (2007) observed that RF predictive power does not improve with a decreased number of input variables, behaviour similar to that recorded in the present study. These authors pointed out that this behaviour is opposite to that of other discriminant methods and has some relation with the increase in diversity between trees in the forest provided by the added variables in the RF procedure.

One important problem in class assignment tasks is that often there are many weak input variables with each one containing only a small amount of information so that no

single input or small group of inputs can distinguish between classes (Breiman, 2001). This type of data is difficult to interpret for the usual classifiers such as LDA and NN.

Advantages of RF additional to those mentioned in the Introduction and confirmed in the present study include: (i) input can be weighted if data is very unbalanced; (ii) handles well data with many zeros; (iii) models from replicate runs can be combined; (iv) a number of useful plots can be generated for exploratory data analysis; (iv) user friendly, with only two parameters to optimise (number of trees and number of dependent variables used at each split).

Although the algorithm is relatively recent and the applications are still few, the results of the present study agree with literature data, where performances of RF are becoming repeatedly reported to surpass those of other, better-known classifiers (*e.g.* LDA, see Granitto *et al.*, 2007; multiple logistic regression, see Peters *et al.*, 2007; ensemble classification methods such as bagging and boosting, see Gislason *et al.*, 2006; decision trees, support vector machines and naïve Bayes, see Koprinska *et al.*, 2007).

8.5.2. Parasite communities as biological indicators of fish populations (stocks)

Due to the complexity of the host–parasite relationship discrimination between fish populations using parasites as tags is a difficult classification task. Parasite communities in fish are shaped by processes associated with the behaviours, feeding habits, immunological responses of the fish hosts and by large-scale geographical processes influencing the hosts' environments (the latter includes all hosts in a parasite life-cycle). The latter processes, however, appear to be an advantage for the use of parasites as biological markers of fish populations, since local environmental factors can regulate the survival and transmission success of parasite infective stages, thus causing interpopulation variations of parasite burdens (Pietrock & Marcogliese, 2003; Timi, 2007).

Success in stock discrimination depends to a large degree on the migratory or sedentary behaviour of the host and the geographical distance between the populations (Ferrer-Castelló *et al.*, 2007). The importance of thermal gradients which influence the latitudinal distribution of parasites in identification of stocks in SW Atlantic was recently stressed by Timi (2007). MacKenzie *et al.* (2008) also reported that temperature could be one of the most probable environmental factors that determine the distribution of an effective biological tag.

The present study using RF models developed on parasite community data demonstrated an overall high accuracy (85-88%) in assignment of cod samples to their

putative stocks in the five regions sampled in the NE Atlantic, and therefore clearly suggests the high potential of this algorithm for parasite tagging studies.

A number of parasite species were selected as important for the model development in the various experiments, thus reinforcing the statement of Timi (2007) on the importance of local factors to parasite transmission. It is worth noting that anisakid nematodes which have been traditionally used for discrimination of cod stocks in the NW Atlantic (see Chapter 1) appear important in the development of the models in the present study. The latter group was also successfully applied to stock discrimination of fish populations in the SW Atlantic waters (see Timi, 2007 for a review) and a recent study using parasites for stock identification of *Trachurus trachurus* suggests that larval *Anisakis* spp. and *H. aduncum* served as the most effective population tags (MacKenzie *et al.*, 2008).

One of the main results of the present study is that it revealed differences in the accuracy of the solutions with respect to the populations (putative stocks) sampled. Thus, the differentiation between stocks from the Baltic Sea and Icelandic waters was easily achieved, whereas the remaining stocks exhibited greater variation.

The Baltic Sea is a brackish semi-enclosed sea with specific hydrological characteristics which determine a peculiar distribution of both hosts and parasites. On the other hand, Iceland is located at much higher latitude and cod populations in Icelandic waters are virtually disconnected from the NE Atlantic populations. The characteristics of parasite communities in cod from these areas illustrate the suggestion of Esch & Fernández (1993) that distribution patterns of marine parasites are mainly determined by temperature-salinity profiles and their association with specific masses of water. Therefore, the physical characteristics of the environment in these two regions appear the main determinants of the distinctiveness in the composition of parasite infracommunities observed in the present study. The high accuracy of the predictive models developed here indicate that the populations from both spawning and feeding localities of Baltic and Icelandic stocks can be confidently differentiated from those of the other stocks studied in the NE Atlantic using both RF and LDA.

As clearly indicated by the ordination based on proximities between cases, parasite communities in the spawning/feeding cod populations captured in the Celtic, Irish and North seas were most similar. Overall, RF provided a very good prediction for Celtic fish whereas the predictions for North and Irish Sea cod were poorer. The fact that the classification of the Celtic Sea fish exhibited a low value of recall in the 'blind' experiment is related to the lowest values of precision for the Irish and North Sea cod samples, *i.e.*

Celtic cod were correctly assigned but Irish and North Sea cod were erroneously assigned to the Celtic stock. MacKenzie & Abaunza (1998) pointed out that the use of parasites as biological tags of marine fish populations is based on the principle that a fish can become infected with a given parasite only when it is within the endemic area (*i.e.* geographical region possessing all suitable conditions for the completion of the life-cycle) of that parasite species. In the case of cod sampled in the above three NE Atlantic regions the geographical range of the major part of the parasite species present in communities overlapped with the areas of sampling, thus resulting in overall higher error rates which reflect higher levels of homogeneity of cod parasite infracommunities in all three regions.

Another explanation for the highest misclassification rates of the North Sea cod stock is the sampling design. Cod samples in the North Sea were obtained from two distant areas (see Figure 8.1) and this may have resulted in increased variation between parasite communities. The two sampling locations fall within the ICES areas of the North Sea stock but in two regional groupings, the Central North Sea (Dogger Bank) and Skagerrak cod, respectively (ICES, 2005a). These two locations have very dissimilar hydrographic conditions, one of the most remarkable being the depth (*c.* 50 m in Dogger Bank *vs* 700 m in Skagerrak). This influences the mixing of the water resulting in higher salinity variations along the vertical gradient in the latter location. The present results might, therefore, indicate that the two regional groupings of cod identified by ICES, *i.e.* Central North Sea and Skagerrak cod exhibit differing parasite community structure. This conclusion, however, should be treated with caution since it is also possible that sampling heterogeneity due to the low representation (*i.e.* 27 out of 147 fish) of the apparently different sample from Dogger Bank has influenced model development.

Two mutually non-exclusive hypotheses can be suggested for the somewhat lower discrimination between the Celtic and Irish stocks observed in the present study. One is related to the smaller geographical distance between the two populations sampled (compared to the other sampling locations). Poulin & Morand (1999) and a recent study on marine fish hosts (Oliva & González, 2005) have shown that geographical distance between host populations is a determinant of the probability of parasite exchange between these populations and therefore for the overall similarity. Furthermore, the populations of the intermediate hosts may be spatially autocorrelated thus resulting in similar transmission rates of parasites in closer locations. Recently the two regions were considered one eco-region, Celtic Seas (ICES, 2004), based on similarities between them and in order to manage more accurately the fishery. Finally, migration of cod stocks between Irish and

Celtic seas has been reported (ICES, 2005a and references therein) and this represents another possible explanation for the interchange in assignment between the Irish and Celtic samples in the present study.

Many studies using parasites as markers of spatial discrimination of fish populations, stock identification and prediction of harvest location of fish develop predictive models based on a single sampling in different localities (see for a discussion Ferrer-Castelló *et al.*, 2007). These authors stressed the problem of pseudoreplication due to the lack of replication, the error consists of assigning an exaggerated estimate of the statistical significance of a set of measurements where either sample is not replicated (another frequent type of pseudoreplication problem is when replicates are not statistically independent, see Hurlbert, 1984).

Ferrer-Castelló *et al.* (2007) obtained relatively good classification rates using the leave-one-out validation method for the pooled and yearly datasets (79-84%) and half random test set (73%) in LDA of parasites in the benthic fish, *Mullus surmuletus* (Teleostei: Mullidae) sampled in three localities off the Spanish Mediterranean. However, they found that predictive power drops drastically to 46% when an LDA model was developed on data from the first year and the data from the second year was used as a validation set. They recommended sampling replication on several spatial and temporal scales whenever possible (Ferrer-Castelló *et al.*, 2007). The present study, therefore, profited from the sampling design of the CODTRACE project, which allowed the validation of the models developed on temporal replicates. Moreover, pseudoreplication was avoided by differential points (coordinates) of capture in the same sampling location.

Although the predictions worsened in the Spring – Spring and Spring – Autumn models (59-60% accuracy) thus indicating substantial annual/seasonal variations in parasite communities in cod, a clear pattern of repeatability (75% accuracy) was found when both samples from year 2002 were used to predict the assignment of fish collected in the following Spring. The very similar result obtained in the prediction in the validation experiment with the 'blind' sample (76% accuracy) confirmed the initial expectation that RF models generalise better with a large and diverse training set and a large number of variables. Overall, the range observed in the present study on the difficult cod parasite dataset illustrates the good performance of RF (on average 85-88% accuracy).

Is it finally possible to predict cod populations/stocks from parasite community data? The conclusion of this study is that parasite community data can be used successfully to discriminate cod populations (putative stocks) of the NE Atlantic cod using RF. The fact

that good discrimination results were obtained for a migratory fish species with largely overlapping parasite faunas (see Chapters 4, 6, 7) and with unrestricted noise in the data indicates that RF is a promising tool for parasite tagging studies. The experiments performed clearly indicate that further studies should control more precisely for fish age/size and this will improve the accuracy of the predictions. RF can be used confidently in cod stock traceability in order to detect illegal fishing or avoid legal disputes between the countries managing a fishery, which is especially important for an endangered commercial fish species such as Atlantic cod.

9. Conclusions

9. Conclusions

The application in the present study of both descriptive and comparative approaches to the examination of large samples of *G. morhua* provided novel information on the current composition and structure of parasite faunas and communities of this host in a large area of its distributional range. The detailed descriptions of , and comparative analyses on, the composition and structure of parasite communities in cod in the regions of study helped shed more light on the levels of temporal and spatial community variability at different scales and permitted an evaluation of the usefulness of cod parasites as biological markers of spatial discrimination of cod populations. The following conclusions can be drawn from the five main chapters of the thesis:

1. The metazoan parasite fauna of *G. morhua* in the six NE Atlantic regions, described for the first time in the present study, is species rich and comprises 55 parasite taxa (1 monogenean, 19 trematodes, 8 cestodes, 13 nematodes, 3 acanthocephalans, 7 copepods, 2 hirudineans, 1 amphipod and 1 isopod). Seven parasite species, *Diclidophora merlangi*, *Rhipidocotyle* sp., *Fellodistomum* sp., *Steringotrema* sp., *Cucullanus* sp., *Spinitectus* sp and *Chondracanthus ornatus* represent new host records. Only three parasite species (*Contracaecum osculatum*, *Hysterothylacium aduncum* and *E. gadi*) were found to infect farmed cod *via* food ingestion of the intermediate host (copepods and amphipods) the latter probably introduced to the farm tanks through the water circulation.

2. Generalist parasites with Arctic-Boreal or worldwide distribution comprised the best represented group of the parasite fauna of *G. morhua* with respect to both richness and numerical dominance, thus supporting the suggestion of Hemmingsen & MacKenzie (2001) that cod acts as a distribution agent of generalist parasites in the North Atlantic because of its omnivorous diet, migratory behaviour and the mixture of stocks.

3. The regional parasite faunas exhibited lower richness (63-65% of the total list) with a notable decrease in the Baltic Sea and Trondheimsfjord (21 and 32% of the total list, respectively). Trematodes and nematodes were predominant groups in terms of richness whereas nematodes, and larval anisakids in particular, predominated numerically in the regional faunas. Parasite faunas in cod from Celtic, Irish and North

seas and Icelandic waters exhibited a higher structural similarity and were characterised by the predominance of generalist anisakid nematodes with an Arctic-Boreal distribution whereas those from the two low-salinity regions (Baltic Sea and Trondheimsfjord) showed notably different structure.

4. Eleven species were present in the parasite faunas of all six regions studied: the trematode *Lepidapedon elongatum*; the nematodes *Anisakis simplex*, *C. osculatum*, *H. aduncum*, *H. rigidum*, *Pseudoterranova decipiens*, *Ascarophis crassicollis* and *Capillaria gracilis*; and the acanthocephalans *Corynosoma semerme*, *C. strumosum* and *Echinorhynchus gadi*. This fact suggested substantial homogenisation at the lower scales of community organisation, a prediction further tested at the level of infracommunities and component communities.

5. The detailed morphological and morphometrical analyses of the monogenean *D. merlangi*, a new host record re-described in the present study (Perdiguero-Alonso *et al.*, 2006), suggest a flexible response in attachment on a non-specific host but unsuccessful development. The observations on reproductive structures suggested that the uterus also participates in the assembly of the egg capsule and that egg shape and size is genetically fixed.

6. The results of the comparative analyses carried out at the infracommunity and component community level agreed well with the predictions based on the higher level taxonomical structure of the regional parasite faunas. Parasite communities in cod from the low-salinity regions (Baltic Sea and Trondheimsfjord) were characterised by the lowest richness, abundance and diversity of total communities and both larval and ectoparasite assemblages and exhibited higher heterogeneity of infracommunity composition and structure. Communities in cod from the open water regions (Celtic, North and Irish seas and Icelandic waters) had higher richness and abundance but infracommunities exhibited wider compositional variations between regions, communities from Icelandic waters being more species rich, abundant and predictable due to the strong domination of the larval anisakids.

7. Component parasite communities in cod exhibited significant compositional homogenisation within each region whereas infracommunities showed a generally lower predictability. This is related to the fact that only a restricted set of the species contributing to the similarity between component communities showed high abundance and dominated infracommunities. Three species with a wide geographical distribution, *H. aduncum, A. simplex* and *Derogenes varicus*, were found to dominate consistently at both the component and infracommunity level.

8. The results of the three multivariate techniques applied (*i.e.* multidimensional scaling, cluster analysis and analysis of similarity) to the evaluation of the similarity patterns of component communities across regions exhibited an overall good agreement irrespective of the dataset used (entire *vs* restricted size/age range of the host). The detection of significant differences in community composition and structure between regions was also in agreement with the analyses based on parasite abundance and prevalence data.

9. The similarity patterns observed in total communities did not generalise to the component community clades. No significant regional differences were found in the composition of ectoparasite assemblages; larval helminth assemblages showed lower regional differentiation; and gastrointestinal helminth assemblages in cod from the open water regions exhibited overlapping composition.

10. There exists a distinct compositional segregation of component communities in cod from NE Atlantic differentiating the two low-salinity regions (Baltic Sea and Trondheimsfjord) from the other four regions. Communities in cod from Icelandic waters also exhibit a distinctive structure of total communities and gastrointestinal and larval helminth assemblages, whereas component communities in cod from Celtic, Irish and North seas show a higher degree of homogenisation with respect to the composition and structure. The overall statistically significant regional differentiation of component communities/assemblages in cod, therefore, may be due to the distinctive characteristics of the marine environments related to salinity and/or geographical isolation.

11. Geographical distance affects the similarity in species composition and structure between parasite component communities in cod but not between regional faunas. The higher homogenisation of regional parasite faunas can be related to the migratory behaviour of cod and the domination of generalist parasites which have a wide geographical distribution. The spatial compositional synchrony exhibited by component communities and the substantially higher rates of similarity decay compared to other marine fish parasite communities, however, indicate that component communities in cod are more strongly constrained by the spatial configuration of locations and the dispersal abilities of cod parasites.

12. The relationship between regional and local richness of cod parasites was congruent at the two spatial scales of analysis. Component communities in cod attained richness levels well below those of the regional faunas and similarly, infracommunities exhibited increasing independence of the richness of component communities. The curvilinear nature of the regional-local richness relationship provided evidence to reject the null hypothesis of proportional sampling as a mechanism leading to the observed pattern. The relationship between the mean parasite abundance and component community richness indicates density compensation in parasite communities from the open water regions and its absence in communities in cod sampled from low-salinity regions.

13. The present study is the first attempt to test for the existence of nested subsets at the level of local parasite faunas. The fact that the non-random patterns of faunal composition generalise to the component communities indicates that the diversity patterns in parasite communities in cod in the NE Atlantic are quite general. The non-randomness in the faunal/component community composition was clearly related to the salinity, with poor faunas/communities from low-salinity regions (Baltic Sea and Trondheimsfjord) nested within the richer faunas/communities from the high-salinity open water regions.

14. The comparison of the learning behaviour of a novel ensemble classification approach, Random Forests (RF), with two other algorithms, Linear Discriminant Analysis (LDA) and Artificial Neural Networks (NN), using the same version of the parasite community

data derived from sampling of cod populations in five regions in the NE Atlantic, revealed that RF appears as the best classifier. RF exhibited better prediction accuracy and outperformed the other two algorithms (LDA and NN) in assignment of cod samples to their putative stocks using parasite community data.

15. A number of parasite species were selected as important for RF model development, species lists being consistent between models. Invariably, the anisakid nematodes traditionally used for discrimination of cod stocks in the NW Atlantic, were identified as important in the development of the models. Additional species contributing to the successful classification were the nematode *Cucullanus cirratus*, the trematodes *D. varicus* and *Hemiurus communis*, the acanthocephalan *E. gadi*, and the copepod *Clavella adunca*.

16. There were differences in the accuracy of the solutions with respect to the populations (putative stocks) sampled. The high accuracy of the predictive models developed for the Baltic and Icelandic samples indicate that the populations from both spawning and feeding localities of these stocks can be confidently differentiated from those of the other stocks studied in the NE Atlantic using both RF and LDA.

17. The predictive power of all algorithms used decreased due to the similarities between infracommunities in the spawning/feeding cod populations captured in the Celtic, Irish and North seas. Overall, RF provided a very good prediction for Celtic fish whereas the predictions for North and Irish Sea cod were poorer. The lower discrimination between the Celtic and Irish stocks might be related to the geographical proximity and migration of cod stocks between Irish and Celtic seas whereas the highest misclassification rates of the North Sea sample might be due to the heterogeneity in the sampling design, especially the low representation in the datasets of the Dogger Bank regional grouping of the North Sea cod stock.

18. Although analyses indicated substantial annual/seasonal variations in parasite communities in cod, a clear pattern of repeatability was found when both samples from year 2002 were used to predict the assignment of fish collected in the following spring. This coupled with the results from the validation experiment with the ‘blind’ sample confirmed the initial expectation that RF models generalise better with a large and diverse training set and a large number of variables.

19. Parasite community data can be used successfully to discriminate cod populations (putative stocks) of the NE Atlantic cod using RF. The fact that good discrimination results were obtained for a migratory fish species with largely overlapping parasite communities reflects the high potential of RF for developing predictive models using data that are both complex and noisy and indicates that it is a promising tool for parasite tagging studies.

10. Appendix

Appendix I. References on parasite studies on *G. morhua* in specific geographic areas and three subjects.

NE Atlantic

Bray, R.A. & Gibson, D.I. (1995)
Bray, R.A. & Gibson, D.I. (1991)
Bray, R.A. & Des Clers, S.A. (1992)
Karlsbakk, E. (2004)
MacKenzie, K., Kalavati, C., Gaard, M. & Hemmingsen, W. (2005)
Perdiguero-Alonso, D., Montero, F. E., Raga, J.A. & Balbuena, J.A. (2006)
Petter, A.J. & Cabaret, J. (1995)

Baltic Sea

Buchmann, K. (1986)
Buchmann, K. (1995)
Mellergaard, S. & Lang, T. (1999)
Myjak, P., Szostakowska, B., Wojciechowski, J., Pietkiewicz, H. & Rokicki, J. (1994)
Pilecka-Rapacz, M. & Sobecka, E. (2004)
Reimer, L.W. & Walter, U. (1993)
Rokicki, J., Valter, E.D. & Myjak, P. (1993)
Szostakowska, B., Myjak, P., Kur, J. & Sywula, T. (2001)
Wawrzyniak, W. & Grawiński, E. (1991)

Barents Sea

Hemmingsen, W., Jansen, P. A. & MacKenzie, K. (2005)
Kornakova, E.E. (1989)
Kulachkova, V.G. & Timofeeva, T.A. (1987)
Mitenev, V.K., Shullman, B. S. & Karasev, A.B. (1991)

Off Denmark

Buchmann, K. (1988)
Køie, M. (1985)
Køie, M. (2000)

Off Finland

Valtonen, E. T. & Crompton, D.W.T. (1990)

Off Germany

Palm, H.W., Klimpel, S. & Bucher, C. (1999)

Off North Sea

Wayland, M.T., Gibson, D.I. & Sommerville, C. (2005)

Off Norway
Appleby, C. (1996)
Balbuena, J. A., Karlsbakk, E., Saksvik, M., Kvenseth, A.M. & Nylund, A. (1998)
Engen, F. & Folstad, I. (1999)
Hemmingsen, W., Halvorsen, O. & MacKenzie, K. (2000)
Hemmingsen, W., Lile, N. & Halvorsen, O. (1992)
Hemmingsen, W., Lile, N. & Halvorsen, O. (1995)
Hemmingsen, W., Lombardo, I. & MacKenzie, K. (1991)
Hemmingsen, W., Lysne, D.A., Eidnes, T. & Skorping, A. (1993)
Jensen, T. (1997)
Jensen, T. & Idås, K. (1992)
Karlsbakk, E., Haugen, E. & Nylund, A. (2005)
Larsen, G., Hemmingsen, W., MacKenzie, K. & Lysne, D.A. (1997)
Lysne, D.A., Hemmingsen, W. & Skorping, A. (1994)
Lysne, D.A. , Skorping, A. & Hemmingsen, W. (1998)
Lysne, D.A., Hemmingsen, W. & Skorping, A. (1997)
Stromnes, E. & Andersen, K. (1998)
Stromnes, E. & Andersen, K. (2000)
Stromnes, E. & Andersen, K. (2003)
Off Scotland
Bron, J., Pert, C., Sommerville, C., Hellberg, H. & Bricknell, I. (2006)
Des Clers, S. (1989)
Des Clers, S. (1991)
Des Clers, S.A. & Wootten, R. (1990)
MacKenzie, K. (1991)
NW Atlantic
Gaevskaya, A.V. (1996)
Canada (off Labrador)
Brattey, J. & Bishop, C.A. (1992)
Khan, R.A. & Chandra, C.V., (2006)
Lee, E.M. & Khan, R.A. (2000)
Canada (off St. Lawrence)
Boily, F. & Marcogliese, D.J. (1995)
McClelland, G. & Marcogliese, D. (1994)
Canada (off Newfoundland)
Khan, R.A. & Kiceniuk, J.W. (1988)
Khan, R.A. & Tuck, C. (1995)
Likely, C.G. & Burt, M.D.B. (1992)
Canada (off Nova Scotia)
Marcogliese, D.J. & McClelland, G. (1992)
Canadian waters
Brattey, J. & Davidson, W.S. (1996)
NW-NE Atlantic
MacKenzie, K. & Hemmingsen, W. (1996)
Hemmingsen, W. & MacKenzie, K. (1993)

Farmed cod diseases
Bricknell, I.R., Bron, J.E. & Bowden, T. J. (2006)
Karlsbakk, E. , Otterlei, E., Hoie, H. & Nylund, A. (2001)
Treves-Brown, K.M. (1999)
Experiemntal studies
Appleton, T.E. & Burt, M.D.B. (1991)
Brattey, J. (1995)
Burt, M.D.B., Campbell, J.D., Likely, C.G. & Smith, J. W. (1990)
Dixon, B., Kimmins, W. & Pohajdak, B. (1993)
Fagerholm, H.P. (1988)
Hafsteinsson, H., Parker, K., Chivers, R. & Rizvi, S.S.H. (1989)
Heia, K., Sivertsen, A. H., Stormo, S.K., Elvevoll, E., Wold, J.P. & Nilsen, H. (2007)
Køie, M. (2001b)
McClelland, G. (1995)
Ramakrishna, N.R. & Burt, M.D. B. (1991)
Smith, J.W. & Hemmingsen, W. (2003)
Stormo, S.K., Ernstsen, A., Nilsen, H., Heia, K., Sivertsen, A.H. & Elvevoll, E. (2004)
FOOD HYGIENE
Audicana, M., García, M., Pozo, M.D. del, Díez, J., Muñoz, D., Fernández, E., Echenagusia, M., Fernández de Corres, L., Ansotegui, I.J. & Moneo, I. (2000)
Bredal, W. (1999)
Gill, C.J. & Hamer, D.H. (2005)
Mellergaard, S. (1997)
Black Sea
Doğanay, A. (1994)
Belgium
Piccolo, G., Manfredi, M.T., Hoste, L. & Vercruysse, J. (1999)
Brazil
Prado, S. de P.T. & Capuano, D.M. (2006)
Pereira, A.D., Atui, M. B., Torres, D.M.A.G.V., Mangini, A.C.S. & Zamboni, C.Q. (2000)
France
Chord-Auger, S., Miegeville, M. & Pape, P. le. (1995)
Huang, W. (1990)
Japan
Mattiucci, S., Paggi, L., Nascetti, G., Ishikura, H., Kikuchi, K., Sato, N., Cianchi, R. & Bullini, L. (1998)
Abe, N., Ohya, N. & Yanagiguchi, R. (2005)
Russia
Appleby, C. (1994)
Utevsky, S. Yu. & Karasev, A.B. (2002)
Spain
López Giménez, R. & Castell Monsalve, J. (1994)

11. Resumen en castellano

11.1. Introducción

11.1.1. El bacalao del Atlántico Norte, *Gadus morhua*: importancia económica del bacalao

El bacalao del Atlántico, *Gadus morhua* L. es una de las principales especies comerciales del Atlántico Norte, en 2005 representó casi el 1,2% del total de pesca mundial de capturas de peces marinos (FAO). Este pez bentopelágico se consumía ya en el Neolítico, y ha sido objeto de explotación comercial desde la Edad Media (Flick *et al.*,1990; Kurlansky, 1998). La pesca del bacalao ha sido tan importante para la economía de los países a ambos lados del Atlántico, que a lo largo de los años se ha ido acumulando una enorme cantidad de conocimiento sobre la biología del bacalao y sobre su pesca (véase Kurlansky, 1998).

A principios de la década de 1960, los desembarques de bacalao en el Atlántico Norte en conjunto oscilaron en torno a 2,5 a 3 millones de Tm por año, con un pico en 1969 de 4 millones de Tm. La pesca se redujo a 1,8 millones de Tm en 1975 y disminuyó a 0,8 millones de Tm en 1992 (FAO). A principios de la década de 1990, muchas poblaciones de bacalao se colapsaron en las zonas donde la pesca comercial era intensa. El colapso fue atribuido a la pesca excesiva y, específicamente, a la pesca comercial de los ejemplares más grandes (maduros) de bacalao y a la captura de los peces jóvenes antes de que hubieran tenido la oportunidad de madurar y reproducirse, lo que disminuyó la población de hembras fértiles (ICES, 2005a). La explotación excesiva de bacalao del Atlántico provocó que esta especie se incluyera como especie vulnerable en la lista roja de la IUCN en 1996. Pese a los esfuerzos para intentar recuperar poblaciones de bacalao, en 2005 los desembarques fueron de aproximadamente 0,84 millones de Tm, y de ellas 0,04 millones de Tm en América del Norte y 0,80 millones de Tm en Europa (FAO). Las moratorias y regulaciones de la pesca que se realizaron en algunas regiones han sido infructuosas hasta la fecha, al no conseguir aumentar o incluso mantener los tamaños de las poblaciones ya que las poblaciones sobreexplotadas se recuperan muy lentamente (Hutchings, 2000).

El concepto de “stock” es fundamental en la práctica para la investigación de las pesquerías, ya que constituye la unidad básica sobre la que se desarrollan los estudios de dinámica de poblaciones de los organismos acuáticos explotados comercialmente y sobre la que se aplican las políticas de gestión pesquera. Sin embargo, a pesar de su importancia, no se ha logrado una definición unánime del concepto de stock. Una de las definiciones más aceptadas es la que propusieron Ihssen *et al.* (1981) en la que un stock es un grupo intraespecífico de individuos que se aparean de forma aleatoria y mantienen una integridad espacial o temporal. Este término sirve como unidad de gestión muy útil para la

administración de los recursos de bacalao. Las poblaciones de bacalao se intentan gestionar por separado porque el efecto de la pesca y el cambio de las condiciones ambientales en muchos de ellos es más acusado que en otros, como son los casos de la costa oriental de Canadá (Hutchings y Myers, 1994, O'Driscoll *et al.*, 2000; Bundy, 2001), el Mar Báltico (Jonzen *et al.,* 2002; Hutchinson *et al.,* 2003), y el Mar del Norte (Cook *et al.,* 1997). En el caso del bacalao, a pesar de que los "stocks" se definen como unidades reconocibles con características únicas con escasa mezcla entre poblaciones adyacentes, las poblaciones de bacalao en ocasiones son compartidas por diferentes unidades de gestión de pesca debido a los movimientos migratorios según la edad y la época de reproducción (Gulland, 1980; Robichaud y Rose, 2004). En la actualidad hay definidas 14 poblaciones de bacalao en el Atlántico nororiental (NE) (regulado por el ICES) y alrededor de 10 poblaciones de bacalao en el Atlántico noroccidental (NO) (regulado por la NAFO) (ICES, 2005a). Algunas de esas poblaciones son extensas en términos de abundancia o de biomasa, como los que caladeros de Noruega (bacalao Ártico – Boreal), Islandia, Groenlandia, Terranova y el Mar de Barents. Otros, sin embargo son bastante reducidos, como el caso de Rockall al oeste de Irlanda (ICES, 2005a).

La principal dificultad en la adecuada gestión de las poblaciones de bacalao es debida a la distribución geográfica del bacalao (Fahay et al., 1999; Robichaud y Rose, 2004; ICES, 2005a). El bacalao está presente en todo el Atlántico Norte y, dado que la mayor parte de su área de distribución se encuentra en aguas internacionales, se hace difícil establecer reglamentos internacionales en cualquier región. La Comisión Europea (CE) ha reconocido la importancia de la gestión y acción a nivel europeo para restablecer las poblaciones de bacalao. En la "Nueva Política Pesquera Común" de la Unión Europea, una parte importante se dedica a proporcionar un marco de actuación para la conservación, control y ejecución de la normativa sobre las poblaciones de peces (comisión de febrero de 2001 (CE) n. º 259/2001), además el bacalao tiene una legislación específica [26 de febrero de 2004 REGLAMENTO (CE) N ° 423/2004].

11.1.2. Marcadores biológicos de las poblaciones de bacalao

La idea de "stocks", o poblaciones, es fundamental para la gestión de la pesca. Si las poblaciones son en gran medida entidades biológicas independientes, la gestión pesquera puede asignar tasas y pautas de explotación a éstas, asumiendo un rendimiento de esta población de peces (Hammer y Zimmermann, 2005). Además, la identificación de las poblaciones de peces puede ayudar al reconocimiento y la protección de áreas de cría y de

desove y por tanto optimizar la vigilancia y las estrategias de conservación (Begg, 2005). Ésta es la razón por la que las técnicas de discriminación entre poblaciones, que muestran diferentes características de individuos de diferentes zonas o poblaciones de peces, se han desarrollado rápidamente en la investigación pesquera (Nielsen *et al.,* 2001; Thorrold *et al.,* 2001). El principio en el que se basa el proceso de discriminación es el de que individuos de diferentes áreas (es decir, poblaciones de peces) muestran características diferentes para un determinado aspecto biológico. Existen marcadores biológicos que se han utilizado para discriminar entre poblaciones de bacalao como son los marcadores genéticos (Bentzen *et al.* 1996, Jónsdóttir *et al.,* 1999; Ruzzante *et al.,* 1999; Hutchinson, 2001, Nielsen *et al.*, 2003), la composición química de los otolitos (Campana *et al.,* 1994; Campana *et al.*, 1999), la morfología del otolito (Campana y Casselman, 1993), la composición de la fauna parasitaria (Hemmingsen *et al.,* 1991; Larsen *et al.,* 1997) y los caracteres morfométricos (Pepin y Carr, 1993, Swain *et al.*, 2001).

Se ha observado que los marcadores genéticos son alternativas útiles para los patrones de distribución de bacalao a largo plazo (Ruzzante *et al.,* 1999; Nielsen *et al.,* 2001), sin embargo la composición química del otolito y la fauna parásita reflejan las condiciones a las que el individuo ha estado expuesto recientemente y, por tanto, los acontecimientos cercanos que se produjeron durante la vida del individuo (Williams *et al.* 1992, Campana *et al.,* 1999; Larsen *et al.*, 1997). A pesar de que, en general, se ha insistido en la utilidad del enfoque multidisciplinar, es decir, la utilización de múltiples técnicas discriminantes para detectar la sensibilidad de las diferentes técnicas y su utilización de manera conjunta (p. ej., Waldman, 1999; Cadrin *et al.*, 2005), existen pocos estudios que hayan utilizado un enfoque multidisciplinar con el objetivo de distinguir o caracterizar entre poblaciones de peces [por ejemplo, Larsen *et al.* (1997) utilizaron la morfología del otolito y los parásitos como marcadores del bacalao y el proyecto HOMSIR lleva a cabo un enfoque holístico para la discriminación de las poblaciones de jurel, *Trachurus trachurus*, utilizando parásitos y marcadores genéticos como marcadores biológicos (Abaunza *et al.*, 2008; Mattiucci *et al.*, 2008)].

11.1.3. Estudios sobre los parásitos de bacalao. Los parásitos del bacalao como marcadores biológicos

Se han llevado a cabo numerosos estudios sobre los parásitos del bacalao y las interacciones hospedador-parásito a ambos lados del Atlántico Norte (ver revisión por Hemmingsen y MacKenzie, 2001). Una gran parte de estos estudios se centra en diversos aspectos de la variabilidad poblacional (diferencias geográficas, de temporada, genéticas) de nematodos

aniséquidos del bacalao (Des Clers, 1989; 1991; Jensen y Idas, 1992; Rokicki *et al.*, 1993; McClelland y Marcogliese, 1994; Myjak *et al.*, 1994; Boily y Marcogliese, 1995; Hemmingsen *et al.*, 1995; Brattey y Bishop, 1992; Petter y Cabaret, 1995; Brattey y Davidson, 1996; Jensen, 1997; Balbuena *et al.*., 1998 ; Stromnes y Andersen, 1998, 2000, 2003).

La infección de aniséquidos en el bacalao ha tenido un especial interés ya que algunas especies parásitas son de gran importancia económica y médica (por ejemplo, *Anisakis simplex* y *Pseudoterranova decipiens*). Las larvas de aniséquidos se pueden encontrar en la carne del pescado, lo que hace que el producto sea poco apetecible a los consumidores, además de que puede infectar a los seres humanos si se consume pescado crudo o poco cocinado.

Otros grupos de parásitos se han estudiado debido a sus efectos patológicos sobre el bacalao como: copépodos (Khan y Lee, 1989; Khan *et al.*., 1993), monogeneos (Kulachkova, 1987; Appleby, 1996), mixozoos (MacKenzie *et al.*, 2005) y protozoos (Karlsbakk *et al.*, 2005). Recientemente, también se han llevado a cabo estudios sobre aspectos veterinarios relacionados con la infección de parásitos problemáticos en la acuicultura (Karlsbakk *et al.* 2001; Bricknell *et al.* 2006). Otro grupo de estudios se asocia con aspectos taxonómico/faunísticos de algunos grupos de parásitos: trematodos (Køie, 1985; MacKenzie, 1991; Bray y Des Clers, 1992; Bray y Gibson, 1991; 1995; Gaevskaya, 1996; Lysne *et al.* 1994; 1997); monogeneos (Kulachkova y Timofeeva, 1987; Perdiguero - Alonso *et al.*., 2006), y acantocéfalos (Valtonen y Crompton, 1990; Buchmann, 1986, 1988, 1995; Wayland *et al.*., 2005). Reimer (1995), Zander (1998) y Zander y Reimer (2002) estudiaron las alteraciones a largo plazo en la fauna parasitaria en relación con la eutrofización del Mar Báltico. Algunos de los parásitos estudiados por estos autores son frecuentes bacalao. Khan y Chandra (2006) observaron una disminución general de los parásitos del bacalao en algunas zonas del Atlántico NO en el período 2000-2003 en comparación con los niveles de infección parasitaria en el bacalao antes del colapso de las pesquerías comerciales en 1990. Según estos autores los posibles responsables del colapso serían el cambio climático, asociado a la disminución de la principal fuente de alimento del bacalao y la baja densidad de la población de bacalao.

En general, la gran cantidad de estudios existentes sobre la fauna parásita del bacalao revelan un esfuerzo desigual en los aspectos mencionados anteriormente, así como una serie de lagunas en la cobertura geográfica, ya que existen regiones que han sido muy poco estudiadas. Los estudios comparativos faunísticos y/o ecológicos sobre los parásitos del

bacalao son prácticamente nulos en el Atlántico NE, aunque una notable excepción serían una serie de estudios llevados a cabo por Hemmingsen y colaboradores en el norte de Noruega. Hemmingsen *et al.* (1992) observó un empobrecimiento de la fauna parásita de Balsfjord (un fiordo noruego) y un predominio de parásitos con distribución boreal en comparación con la fauna parásita del bacalao del Mar de Barents. Estas diferencias fueron relacionadas con la edad y el tamaño de los bacalaos y el aislamiento de Balsfjord. En un estudio posterior, Hemmingsen *et al.* (1995) examinaron las variaciones estacionales en la fauna de parásitos del bacalao en Balsfjord y no encontraron ningún efecto temporal significativo en los parámetros de infección de las 13 especies de parásitos que estudiaron. También estudiaron la incidencia de los parásitos metazoos del bacalao en Balsfjord en relación con la edad y el sexo de los peces y sugirieron que pueden existir diferencias en la alimentación y el comportamiento entre machos y hembras de bacalao en este fiordo (Hemmingsen *et al.*, 2000).

Otro aspecto tratado en los estudios ecológicos sobre los parásitos de bacalao, en el Atlántico NE y NO, es su utilización como marcadores biológicos. Normalmente se selecciona un número determinado de parásitos de bacalao y se utilizan como marcadores, estas especies se seleccionan de acuerdo con los criterios sugeridos por Kabata (1963) y actualizados por MacKenzie y Abaunza (1998).

En el Atlántico NO la variación regional de las infecciones de los nematodos aniséquidos y el copépodo *Lernaeocera branchialis* fueron la base de la mayoría de estudios de poblaciones de bacalao que utilizan a los parásitos como marcadores biológicos. El primer estudio utilizó la prevalencia de *L. branchialis* para identificar 4 grupos generales de bacalaos desde las 13 subzonas situadas frente a las costas de Nueva Inglaterra (Sherman y Wise, 1961). Un estudio similar llevado a cabo por Templeman y Fleming (1963), en torno a Terranova, confirmó la interrelación entre las poblaciones de bacalao. Esta observación confirmó lo sugerido previamente en estudios morfológicos y de marcaje de individuos. Templeman *et al.* (1976) demostraron la utilidad de las diferencias en la presencia de *L. branchialis* para detectar las migraciones de bacalao desde la costa de Terranova hacia aguas más alejadas. Bishop *et al.* (1988) combinaron los datos parasitológicos de dos nematodos aniséquidos (*A. simplex* y *P. decipiens*) con datos de caracteres morfológicos, llegando a la conclusión de que se produce una mezcla de las poblaciones de bacalao en el Golfo de San Lorenzo. McClelland y Marcogliese (1994) utilizaron el análisis multivariante para estudiar los niveles de infección de 3 larvas de aniséquidos (*A. simple, Contracaecum osculatum* y *P. decipiens*) en el bacalao para distinguir entre las poblaciones residentes y los peces

inmigrantes en la zona de Breton, al sur del Golfo de San Lorenzo. Otra especie parásita utilizada como marcador biológico en el Atlántico NO es *Trypanosoma murmanensis*: Khan *et al.* (1980) sugirieron la existencia de seis poblaciones en el Golfo de San Lorenzo basándose en las diferentes tasas de infección parasitaria de este protozoo flagelado. En un estudio posterior Khan y Tuck (1995) utilizaron más especies de parásitos como marcadores (*P. decipiens, L. branchialis, Echinorhynchus gadi*, diversos nematodos gastrointestinales y el protozoo microsporídeo *Loma branchialis*) y corroboraron la existencia de al menos seis poblaciones de bacalao con cierto grado de mezcla en la citada zona.

Sólo dos estudios de parásitos de bacalao con marcadores biológicos se han llevado a cabo en Groenlandia e Islandia. Platt (1976) diferenció entre las dos zonas debido a la ausencia de *P. decipiens* en las poblaciones de bacalao de Groenlandia y la relativa elevada frecuencia en la zona de desove de bacalao situada al oeste de Islandia. Boje (1987) observó que sólo dos especies (*Hemiurus levinseni* y *Hysterothylacium aduncum*) de las 14 especies de parásitos encontradas en el bacalao, tenían tasas de infección significativamente diferentes entre las localidades de la costa oeste y la costa este de Groenlandia. A pesar de que los resultados de Boje (1987) sugieren una buena discriminación de estas zonas, el pequeño tamaño muestral del estudio (86 bacalaos examinados) no proporcionan suficiente confianza sobre la discriminación entre los grupos.

En los estudios del Atlántico NE se han empleado una mayor variedad de especies de parásitos como marcadores biológicos. En diversos estudios en el Mar Báltico, Reimer (1970) y Buchman (1986), discriminan entre una población residente y la población inmigrante de bacalaos que se mezclan en el área de desove de Borholm. Estas poblaciones se diferenciaron debido a la existencia de un gradiente de salinidad que aumenta de este a oeste, por lo que en la parte occidental del Mar Báltico aparecen especies de parásitos que serían marinas y que estaban ausentes en las zonas de baja salinidad. Polyansky y Kulemina (1963) utilizaron la fauna parásita del bacalao para discriminar entre adultos y jóvenes de diferentes zonas del Mar de Barents y sólo encontraron diferencias significativas en las tasas de infección de los bacalaos jóvenes, sugiriendo que sólo los juveniles de bacalao forman poblaciones locales con escasa migración entre las zonas. Hemmingsen *et al.* (1991) se centraron en las diferencias entre siete especies de parásitos para discriminar entre dos fiordos (Balsfjord y Ullsfjord) y una zona del Mar de Barents, concluyendo que el bacalao en Balsfjord puede representar una población aislada. Sin embargo, en un posterior estudio multidisciplinar en el que utilizaron la morfología del otolito en combinación con cuatro especies de parásitos (Larsen *et al.*, 1997), identificaron poblaciones mixtas en las zonas estudiadas (es decir, en alta mar y en los dos

fiordos), y que sólo el bacalao costero migra entre el mar y los fiordos, mientras que las poblaciones residentes de bacalao ártico-noruego se encuentran principalmente en los fiordos. Karasev (1994) identificó las especies que podrían utilizarse como marcadores biológicos de la población de bacalao utilizando la información proveniente de estudios previos sobre los parásitos de bacalao en el Mar de Barents. Sin embargo, este autor no encontró marcadores biológicos útiles para la discriminación entre las poblaciones locales del norte de Noruega y el norte de Rusia (Karasev, 1998).

11.1.4. Este estudio

Este estudio se ha llevado a cabo en el marco de un proyecto multidisciplinar "CODTRACE: Establishing traceability for cod (*Gadus morhua*): determining location of spawning and harvest", financiado por el 5 º Programa Marco "Calidad de vida y gestión de los recursos vivos" (Acción 5.4.3 Política Común de Pesca) de la Comisión Europea. El principal objetivo del proyecto era combinar diferentes técnicas de trazabilidad: morfológicas, bioquímicas, bacterianas, genéticas y parasitológicas. Se elaboró conjuntamente por seis grupos de investigación pertenecientes a universidades europeas u organismos de investigación (véase web codtrace). La Unidad de Zoología Marina del Instituto Cavanilles de la Universidad de Valencia fue responsable del estudio de las muestras de parásitos.

Para desarrollar el presente estudio se examinaron numerosas muestras de bacalao procedente de 6 regiones del Atlántico NE, lo que proporcionó una abundante información sobre las comunidades parásitas de éste hospedador. Gracias a la consecución de una amplia base datos, taxonómicamente consistente, se pudo realizar un estudio comparativo de la estructura de las comunidades parásitas del bacalao a diversas escalas de agrupación de comunidades (infracomunidades, comunidades componentes y faunas). Además, la información obtenida fue utilizada para buscar patrones no-aleatorios de la riqueza, composición y estructura de las comunidades prestando atención a los aspectos más globales de la organización de comunidades de parásitos que pueden revelar la posible influencia de los procesos biogeográficos a gran escala sobre las comunidades de parásitos del bacalao del Atlántico NE. Finalmente se utilizó una nueva técnica, "Random Forests", utilizada para predecir los posibles stocks de procedencia de las muestras de bacalao. Para ellos se tuvieron en cuenta los datos a nivel de infracomunidad, recolectados para los peces muestreados en las 5 áreas de este estudio. Utilizando "Random Forests" se pudo realizar un estudio sobre la utilidad de los parásitos del bacalao como marcadores biológicos para la discriminación espacial de las poblaciones y/o stocks de los hospedadores.

Este estudio pretende, por tanto, aportar nueva información al conocimiento actual de las comunidades parásitas del bacalao del Atlántico NE, intentando responder a las siguientes preguntas sobre la estructura de las comunidades parásitas de este hospedador:

(i) ¿Qué elementos contiene la fauna actual de parásitos en el bacalao del Atlántico NE? ¿Existe una estructura común en la composición de las faunas parásitas regionales?

(ii) ¿Existen patrones macroecológicos en la composición y estructura de las parasitofaunas y de las comunidades componentes de parásitos del bacalao?

(iii) ¿Cuáles son las características de las comunidades parásitas del bacalao? ¿Existen diferencias regionales en la complejidad, abundancia y predecibilidad de las infracomunidades y comunidades componentes?

(iv) ¿Es posible predecir las poblaciones/stocks de origen de los bacalaos utilizando datos procedentes de sus comunidades parásitas?

11.2. Interés y objetivos

Interés

El presente estudio está dedicado a proporcionar nueva información sobre el estado actual de la composición y estructura de las comunidades parásitas de *G. morhua* en el Atlántico nororiental, y aplica este conocimiento a dos niveles: el estudio comparativo de los patrones de organización de comunidades a diversas escalas y el estudio de la utilidad de los parásitos del bacalao como marcadores biológicos para discriminar espacialmente las poblaciones de bacalao.

Objetivos

La investigacion está enfocada a desarrollar los siguientes objetivos:

(i) Descripción de la composición y estructura de los parásitos metazoos de *G. morhua* en seis regiones del Atlántico nororiental**:** mares Báltico, Celta, de Irlanda y Norte, las aguas de Islandia y el fiordo de Trondheim (Noruega).

- Identificación de los metazoos parásitos y caracterización cuantitativa de las poblaciones de parásitos de cada región**.**
- Descripción de la composición y análisis comparativo de la estructura de las parasitofaunas con respecto a las agrupaciones de taxonómicas de nivel superior, especificidad de hospedador y distribución geográfica de los parásitos.

(ii) Redescripción de *Diclidophora merlangi* (Kuhn, en Nordmann, 1832) (Monogenea: Diclidophoridae), una nueva cita de hospedador en *G. morhua*.

(iii) Descripción de la composición y estructura de las comunidades parásitas de *G. morhua* en las regiones de estudio y análisis de las variaciones espaciales y temporales de la riqueza, abundancia y predecibilidad de las infracomunidades y las comunidades componentes.

(iv) Búsqueda de patrones macroecológicos no aleatorios en la composición y estructura de las parasitofaunas y comunidades componentes de *G. morhua*.

(v) Evaluación de la aplicabilidad y del poder predictivo de una nueva metodología de clasificación de grupos, "Random Forests" (Breiman, 2001), para discriminar poblaciones de hospedadores usando comunidades parásitas como indicadores biológicos.

- Comparación de los comportamientos de aprendizaje de "Random Forests" y otros dos algoritmos (Análisis Discriminante Linear y Redes Neurales Artificiales) aplicados previamente en estudios que utilizaron parásitos como marcadores biológicos de poblaciones.
- Evaluación de la importancia de la variación anual y estacional en la composición y estructura de las comunidades parásitas para la discriminación de las poblaciones de bacalao usando información sobre las mismas comunidades parásitas.

11.3. Material y métodos

La presente tesis doctoral está dedicada al estudio de la composición y estructura de la fauna de parásitos metazoos del bacalao atlántico, *Gadus morhua*, procedente de seis áreas de pesca del Atlántico Nororiental [mares Báltico, Celta, de Irlanda y del Norte, área de Islandia y un fiordo noruego (el fiordo de Trondheim)], así como 2 granjas marinas situadas en Islandia y Escocia. El presente trabajo es parte de un proyecto europeo multidisciplinar, CODTRACE,

dedicado al estudio de la trazabilidad de los stocks del Atlántico nororiental utilizando biomarcadores genéticos, morfológicos, bioquímicos, microbiológicos o parasitológicos. Los resultados obtenidos permitieron comprobar la utilidad de "Random Forests" (Breiman, 2001), un método novedoso de clasificación de conjuntos, para discriminar poblaciones de peces utilizando a las comunidades de parásitos como indicadores biológicos.

Se recolectaron 1254 peces siguiendo el diseño de muestreo planteado para el proyecto CODTRACE. Los muestreos habían sido diseñados para recolectar todos los tipos de muestras de cada pez para poder así testar diferentes técnicas de trazabilidad para discriminar el origen del bacalao atlántico. Cada pez fue medido, pesado y se le asignó un código individual de identificación, lo que aseguró que las muestras biológicas de cada individuo fueran siempre distinguibles. Los parásitos externos e internos visibles durante la disección fueron recogidos y fijados en etanol 70%, y las vísceras, incluyendo a las branquias, fueron separadas y conservadas congeladas (-20ºC). Las vísceras fueron enviadas congeladas a la Universidad de Valencia para su posterior examen parasitológico. La edad se determinó a través de los otolitos analizados por el grupo de investigación de la Universidad de Goteborg, Suecia, parte del proyecto CODTRACE. El examen parasitológico fue llevado a cabo siguiendo un protocolo estándar y los parásitos fueron identificados hasta el taxón de menor nivel posible. En general, los análisis estadísticos con datos no transformados se realizaron con tests no-paramétricos debido a que sus distribuciones eran agregadas (p. ej. test de la U de Mann–Whitney para comparaciones pareadas, test de Kruskal-Wallis para comparaciones múltiples y correlaciones de rango de Spearman). Cuando se necesitó realizar análisis paramétricos los datos fueron transformados logarítmicamente (p. ej. Análisis Cluster, Escalado Multidimensional, Análisis de Similitudes, Análisis Discriminante Linear, Modelos Lineales Mixtos, Regresión Linear Múltiple]. Las clasificaciones con "Random Forests" y Redes Neuronales Artificiales se realizaron utilizando datos no transformados.

11.4. La fauna parásita del bacalao en el Atlántico nororiental

Se recolectaron un total de 57 formas parásitas diferentes en los 1254 bacalaos examinados. Los grupos parásitos predominantes fueron los trematodos (19 especies) y los nematodos (13 especies). Nueve de las especies de parásitos encontradas en este estudio son citas nuevas en este hospedador (*Diclidophora merlangi*, *Rhipidocotyle* sp., *Fellodistomum* sp., *Steringotrema* sp., *Schistocephalus gasterostei*, *Cucullanus* sp., *Spinitectus* sp., *Acanthochondria soleae* and *Chondracanthus ornatus*). Dos de estas especies fueron consideradas como parte de la dieta de los peces: el copépodo *A. soleae* y el cestodo *S.*

gasterostei. Once especies estuvieron presentes en todas las regiones (el trematodo *L. elongatum*; los nematodos *A. simplex*, *C. osculatum*, *H. aduncum*, *H. rigidum*, *P. decipiens*, *A. crassicollis* y *C. gracilis*; y los acantocéfalos *C. semerme*, *C. strumosum* y *E. gadi*). La representación de especies parásitas fue muy similar en todas las regiones excepto en el mar Báltico y en el fiordo de Trondheim que tuvieron las faunas más pobres. Las faunas de estas dos áreas también mostraron marcadas diferencias respecto a la abundancia relativa de grupos taxonómicos superiores. Aunque los nematodos fueron el taxón con mayor riqueza en las muestras del báltico, la elevada dominancia numérica de los acantocéfalos fue el rasgo más distintivo de la fauna de esta región. La fauna del fiordo de Trondheim se diferenció por la excepcionalmente elevada abundancia de trematodos. Las faunas del mar Celta e Islandia exhibieron números sustancialmente elevados de especimenes de nematodo; las faunas de los mares de Irlanda y del Norte tuvieron mayores proporciones de especimenes de trematodo. Las faunas más diferenciadas fueron las del mar Báltico y las del fiordo de Trondheim, mientras que las de las otras cuatro regiones formaron un cluster de elevados niveles de similitud. Los parásitos generalistas formaron la mayoría de las faunas parásitas de bacalao de todas las regiones menos en el fiordo de Trondheim con la mayor representación de parásitos específicos de peces gádidos, especialmente en lo que respecta a la abundancia. La abundancia relativa de las especies de distribución Ártico-Boreal fue notablemente mayor en las faunas del Báltico, fiordo de Trondheim e Islandia. Además, la abundancia relativa de especies parásitas Boreales fue mayor en el fiordo de Trondheim que en el resto de regiones. La parasitofauna del bacalao de Islandia mostró una proporción insignificante de parásitos de esta categoría. El resto de regiones tuvo una mejor representación de parásitos de distribución mundial. *H. aduncum*, *C. osculatum* y *E. gadi* fueron las únicas especies de parásitos que sobrevivieron a las condiciones de cultivo. La transmisión de estas especies tuvo que ser por vía alimentaria, ya que requieren crustáceos planctónicos (copépodos, anfípodos y mísidos) como hospedadores intermediarios.

11.5. Redescripción de *Diclidophora merlangi* (Kuhn, en Nordmann, 1832) (Monogenea: Diclidophoridae), una nueva cita en *G. morhua*

El tamaño de los dos especimenes de *D. merlangi*, citados por primera vez en bacalao fue considerablemente menor que el de *D. merlangi* en el merlán, *Merlangius merlangus*, su hospedador tipo. El Análisis de Componentes Principales mostró que la morfología de los especimenes de bacalao fue más similar a la de *D. merlangi* de merlán que a la del resto de especies congenéricas del Atlántico Norte, lo que apoyó su asignación a la especie *D.*

merlangi. Los datos cuantitativos documentaron los potenciales efectos negativos en la reproducción de *D. merlangi* parasitando al bacalao. Los testículos y el germario de los especimenes de bacalao fueron notablemente menores que los de *D. merlangi* en merlán, sin embargo el número de testículos fue similar y se observó esperma en el espermiducto. En contraste, el aspecto y menor tamaño de los ovocitos sugirió que *D. merlangi* de bacalao no puede producir huevos viables, aunque un espécimen presentaba un huevo de cáscara con tamaño y forma normal.

11.6. Composición y estructura de las comunidades parásitas de *G. morhua* en el Atlántico nororiental

Las infracomunidades y comunidades componentes de parásitos de bacalao de las 6 regiones fueron estudiadas en profundidad con el fin de evaluar las variaciones temporales dentro de cada región. La composición de la parasitofauna fue enumerada y se compararon los parámetros de infección de las especies parásitas más prevalentes en cada muestra. La estructura de la infracomunidad y la comunidad componente se describió utilizando los descriptores ecológicos principales (riqueza de especies y abundancia, y los índices de dominancia y diversidad). Para completar el estudio, las mismas comparaciones fueron repetidas para helmintos larvarios, helmintos gastrointestinales y ectoparásitos en los dos niveles de comunidades. Para valorar la predecibilidad dentro de cada región se calculó un índice de similitud de las comunidades componentes entre muestras. A nivel de infracomunidad la diferencia en la estructura de las comunidades parásitas fue evaluada usando matrices de similitud. El mismo proceso se repitió con helmintos larvales y gastrointestinales y con ectoparásitos. Además se determinaron las especies que más contribuían a la similitud entre y dentro de las muestras. En todas las regiones las infracomunidades de parásitos mostraron más variabilidad y consecuentemente menos predecibilidad que las comunidades componentes, aunque las especies de parásitos que más influían a los dos niveles de comunidad fueron las mismas.

11.7. Patrones en la estructura de las comunidades parásitas de *G. morhua* en el Atlántico nororiental

Se encontró una clara segregación de composición de las comunidades en el bacalao del Atlántico nororiental diferenciando las dos regiones de baja salinidad (mar Báltico y fiordo de Trondheim) de las otras cuatro regiones. La mayor homogeneidad con respecto a la composición y estructura de las comunidades de parásitos de bacalao se observó en los mares

Celta, de Irlanda y del Norte. El bacalao de las aguas islandesas mostró una estructura general de comunidades única con respecto a los helmintos gastrointestinales y larvarios. Los ectoparásitos no mostraron diferencias significativas en la composición entre las regiones en las que éstos fueron registrados.

Se observó un declive de la similitud con la distancia geográfica existente entre las comunidades de parásitos de bacalao del Atlántico a pesar del comportamiento migratorio de este hospedador y el dominio de los parásitos generalistas con respecto a la riqueza y la abundancia. Sin embargo, la variación explicada por la distancia fue baja lo que sugiere que las comunidades componentes del bacalao parecen estar más fuertemente limitadas por la configuración espacial de las regiones y, tal vez, por la capacidad de dispersión de los parásitos del bacalao.

La relación observada entre la riqueza regional y local aportó pruebas para rechazar la hipótesis nula de proporcionalidad en las dos escalas espaciales de análisis (entre riqueza de la comunidad componente y riqueza regional, y riqueza máxima de la infracommunidad y riqueza de la comunidad componente). Por lo tanto, existe poca influencia de las pautas que operan a gran escala, a nivel regional, en la determinación de la riqueza de la comunidad parásita del bacalao y a menor escala, las infracomunidades exhiben una mayor independencia respecto a la riqueza de las comunidades componentes.

El hecho de que la composición faunística siga patrones no aleatorios es generalizable a las comunidades componentes, lo que indica que los patrones de diversidad de parásitos en las comunidades bacalao en el Atlántico nororiental son bastante similares. Por lo tanto, las faunas y/o comunidades parásitas empobrecidas de las regiones de baja salinidad (mar Báltico y fiordo de Trondheim) están anidadas, es decir son subconjuntos de las faunas y comunidades más ricas de las regiones de alta salinidad y aguas abiertas. Por otra parte, se observa que los procesos influidos por el aumento de la temperatura del agua son capaces de afectar la composición de las comunidades componentes de parásitos en esta especie de pez.

11.8. Comunidades parásitas para la discriminación de las poblaciones de bacalao: Random Forests, una nueva aproximación de estadística multivariante

La aplicación de una nueva técnica estadística, “Random Forests”, empleada para la discriminación del origen de la captura de bacalao del Atlántico utilizando a los parásitos como biomarcadores permitió poder predecir con éxito el área de alimentación de la que procedían los bacalaos de las cinco áreas de pesca muestreadas en este estudio: mar Báltico, Celta, Norte, Irlanda e Islandia. Las cinco áreas de pesca tuvieron tres réplicas temporales

para evaluar la variación en la composición de la fauna. Esta técnica predice, en general, mejor que las otras dos técnicas de estadística discriminante utilizadas previamente en la discriminación de poblaciones de peces: Análisis Discriminante Linear y Redes Neuronales Artificiales.

11.9. Conclusiones

A través de una aproximación descriptiva y ecológica, este estudio ha investigado la parasitofauna de cuantiosas muestras de bacalao, *Gadus morhua*, consiguiendo recopilar nueva información sobre la composición y estructura de la parasitofauna y las comunidades de este hospedador en una amplia área de distribución. Las detalladas descripciones y los análisis comparativos sobre la composición y estructura de las comunidades parásitas del bacalao en las regiones de estudio han aportado nueva información sobre los niveles de variación temporal y espacial a diferentes escalas y, asimismo, ha permitido evaluar la utilidad de los parásitos de bacalao como biomarcadores para la discriminación de las poblaciones de bacalao. A continuación se enumeran las conclusiones como síntesis de este estudio:

1. La parasitofauna de metazoos de bacalao de 6 regiones distintas del Atlántico nororiental se describen detalladamente por primera vez. Se trata de una fauna rica formada por 55 taxones parásitos diferentes: 1 monogeneo, 19 trematodos, 8 cestodos, 13 nematodos, 3 acantocéfalos, 7 copépodos, 2 hirudíneos, 1 anfípodo y 1 isópodo. Siete especies, *Diclidophora merlangi*, *Rhipidocotyle* sp., *Fellodistomum* sp., *Steringotrema* sp., *Cucullanus* sp., *Spinitectus* sp. y *Chondracanthus ornatus* son primeras citas en este hospedador. Sólo 3 especies parásitas (*Contracaecum osculatum*, *Hysterothylacium aduncum* y *Echynorhynchus gadi*) infectaron a bacalaos de cultivo acuícola a través de la ingestión de crustáceos planctónicos como hospedadores intermediarios, probablemente introducidos en los tanques a través de la circulación del agua.

2. Los parásitos generalistas de distribución ártico-boreal o mundial son los grupos más representativos con respecto a la riqueza y dominancia numérica en la parasitofauna del *G. morhua*, lo que apoya las sugerencias de Hemmingsen & MacKenzie (2001) sobre que el bacalao actúa como agente distribuidor de parásitos generalistas en el Atlántico norte debido a su dieta omnívora, su comportamiento migratorio y la mezcla de poblaciones.

3. Las parasitofaunas regionales exhibieron riquezas menores (63-65% de la lista total) con un notable descenso en el mar Báltico y el fiordo de Trondheim (21 y 32% de la lista total, respectivamente). Trematodos y nematodos son los grupos predominantes en términos de riqueza, mientras que los nematodos, y las larvas de anisáquidos en particular, predominaron numéricamente en las faunas regionales. Las faunas parásitas de bacalaos de los mares Celta, de Irlanda y Norte, así como los de Islandia, exhibieron una mayor similitud estructural y se caracterizaron por la predominancia de nematodos anisáquidos generalistas de distribución ártico-boreal, mientras que las dos regiones de baja salinidad (mar Báltico y el fiordo de Trondheim) mostraron una estructura notablemente distinta.

4. Once especies estuvieron presentes en las parasitofaunas de las 6 regiones naturales estudiadas: el trematodo *Lepidapedon elongatum*; los nematodos *Anisakis simplex*, *C. osculatum*, *H. aduncum*, *H. rigidum*, *Pseudoterranova decipiens*, *Ascarophis crassicollis* y *Capillaria gracilis*; y los acantocéfalos *Corynosoma semerme*, *C. strumosum* y *Echinorhynchus gadi*. Este hecho sugiere la existencia de una notable homogeneidad en las escalas de organización de comunidades, lo que fue posteriormente comprobado a nivel de infracomunidad y comunidad componente.

5. Los detallados análisis morfológicos y morfométricos del monogeneo *D. merlangi*, citado por primera vez en bacalao y redescrito en el presente estudio (Perdiguero-Alonso *et al.*, 2006), sugiere una respuesta flexible al anclaje de un hospedador no específico, aunque con un desarrollo no exitoso. Las observaciones en las estructuras reproductivas sugirieron que el útero también participa en la producción de la cápsula del huevo y que la forma y tamaño del huevo está fijada genéticamente.

6. Los resultados de los análisis comparativos llevados a cabo a nivel de infracomunidad y comunidad componente están de acuerdo con las predicciones basadas en la estructura, a mayor nivel taxonómico, de las faunas parásitas regionales. Las comunidades parásitas de bacalao de las regiones de baja salinidad (mar Báltico y fiordo de Trondheim) estuvieron caracterizadas por las más bajas riquezas, abundancias y diversidades totales de todas las comunidades, así como de los parásitos en fase larvaria y los ectoparásitos, exhibiendo la mayor heterogeneidad en la

composición y estructura de las infracomunidades. Las comunidades de bacalao en las regiones de mar abierto (mares Celta, del Norte y de Irlanda e Islandia) tuvieron mayor riqueza y abundancia aunque las infracomunidades exhibieron variaciones de composición más acusadas entre regiones, siendo las comunidades de Islandia las de mayor riqueza, abundancia y predecibilidad de especies debido a la fuerte dominancia de las larvas de anisáquidos.

7. Las comunidades componentes del bacalao exhibieron una homogeneidad significativa en la composición dentro de cada región, mientras que las infracomunidades mostraron, generalmente, una menor predecibilidad. Este hecho está relacionado con que sólo un grupo restringido de las especies que contribuyen a la similitud entre comunidades componentes mostraban una elevada abundancia y dominaban las infracomunidades. Se encontraron tres especies de amplia distribución geográfica, *H. aduncum*, *A. simplex* y *Derogenes varicus*, que dominaban de forma evidente tanto a nivel de comunidad componente como de infracomunidad.

8. Los resultados de las 3 técnicas multivariantes aplicadas para la valoración de los patrones de similitud de las comunidades componentes entre las regiones (p. ej. escalado multidimensional, análisis clúster, y análisis de similitud) exhibieron, en general, resultados similares independientemente de la base de datos empleada (completa o restringida según el tamaño del hospedador). La detección de diferencias significativas entre regiones en la composición y estructura de la comunidad estuvo también en concordancia con los resultados obtenidos en los análisis basados en los valores de abundancia y prevalencia de parásitos.

9. Los patrones de similitud observados en las comunidades totales (*i.e.* faunas) no fue generalizable con los clados de las comunidades componentes. No se encontraron diferencias regionales significativas en la composición de ectoparásitos. Los helmintos larvales mostraron menor diferenciación regional y los helmintos gastrointestinales en los bacalaos de regiones de mar abierto mostraron un solapamiento en su composición.

10. La segregación entre las comunidades componentes del bacalao del Atlántico nororiental es diferente entre las dos regiones de baja salinidad (mar Báltico y

Trondheim) y las otras 4 regiones. Las comunidades del bacalao de Islandia también exhibieron una estructura diferente entre las comunidades totales y las de helmintos gastrointestinales y larvales, mientras que las comunidades de bacalaos de los mares Celta, de Irlanda y Norte muestran un mayor grado de homogeneidad en composición y estructura. La diferenciación estadísticamente significativa observada, a nivel global, en las comunidades componentes y la parasitofauna del bacalao podría ser debida, por tanto, a las diferentes características de los ambientes marinos relacionadas con la salinidad y/o aislamiento geográfico.

11. La distancia geográfica afecta a la similitud en la composición y estructura de las comunidades componentes de parásitos del bacalao pero no a las faunas regionales. La mayor homogeneidad de las parasitofaunas regionales puede estar relacionado con el comportamiento migratorio del bacalao y el dominio de los parásitos generalistas que tienen una amplia distribución geográfica. La sincronización espacial de la composición de las comunidades componentes y las substancialmente mayores tasas de declive de similitud exhibidas en comparación con las comunidades parásitas de otros peces, indican que las comunidades componentes de bacalao están fuertemente comprometidas por la configuración espacial de las regiones y la facilidad de dispersión de los parásitos de bacalao.

12. La relación existente entre la riqueza regional y local de las comunidades de bacalao fue congruente en las dos escalas espaciales del análisis. Las comunidades componentes de bacalao alcanzaron menores valores de riqueza que las faunas regionales, y de manera similar, las infracomunidades mostraron una mayor independencia de la riqueza respecto de las comunidades componentes. La naturaleza curvilínea de la relación entre la riqueza regional y local aportaron evidencias para rechazar la hipótesis nula de proporcionalidad del muestreo como mecanismo que explique los patrones observados. La relación entre la abundancia media de los parásitos y la riqueza de las comunidades componentes apunta hacia una compensación de la densidad en comunidades parásitas de regiones de mar abierto y su ausencia en las comunidades de bacalao muestreadas en regiones de baja salinidad.

13. El presente estudio es la primera aproximación para testar la existencia de subgrupos anidados al nivel de las parasitofaunas locales. El hecho de que lo patrones no

aleatorios de la composición de la fauna puedan generalizarse a las comunidades componentes indica que los patrones de diversidad en las comunidades parásitas del bacalao del Atlántico nororiental muestran pautas bastante generales. La ausencia de aleatoriedad en la composición de las faunas y comunidades componentes estuvo claramente relacionada con la salinidad, las faunas y comunidades empobrecidas de las regiones de baja salinidad (Báltico y Trondheim) estaban anidadas dentro de las faunas y comunidades más ricas de las regiones de mayor salinidad en mar abierto.

14. La comparación del comportamiento de aprendizaje de una novedosa metodología de clasificación de grupos, “Random Forests” (RF), con otros algoritmos, Análisis Discriminante Linear (ADL) y las Redes Neurales Artificiales (NN), utilizando la mima versión de datos de comunidades parásitas derivados del muestreo de poblaciones de bacalao de cinco regiones del Atlántico nororiental, reveló que RF era la mejor herramienta de clasificación. RF mostró una mayor predicción que los otros dos algoritmos (ADL y NN) en la asignación de las muestras de bacalao a sus stocks/poblaciones de procedencia, usando datos de comunidades parásitas.

15. Algunas especies parásitas fueron seleccionadas como “importantes” para desarrollar el modelo de RF, los listados de especies entre los diferentes modelos utilizados fueron consistentes. Invariablemente, los nematodos anisáquidos, tradicionalmente utilizados para la discriminación de stocks en el Atlántico noroccidental, fueron identificados como “importantes” para desarrollar los modelos. Otras especies que contribuyeron para el acierto en la clasificación fueron el nematodo *Cucullanus cirratus*, los trematodos *D. varicus* y *Hemiurus communis*, el acantocéfalo *E. gadi* y el copépodo *Clavella adunca*.

16. Se hallaron diferencias en la precisión de las predicciones con respecto a las poblaciones/stocks de origen muestreados. La mayor precisión en los modelos predictivos fue exhibida por las muestras bálticas e islandesas, lo que indica que las poblaciones de las localidades de freza y forrajeo de estos stocks pueden ser diferenciadas con certeza de aquellas del resto stocks estudiados en el Atlántico nororiental usando RF y ADL.

17. El poder de predicción de todos los algoritmos disminuyó debido a las similitudes entre las comunidades de freza y forrajeo de bacalao capturados en el mar Celta, de Irlanda y Norte. En general, RF proporcionó una predicción muy acertada para los peces del mar Celta mientras las predicciones para los mares del Norte y de Irlanda fueron menos acertadas. La baja discriminación entre los stocks del mar Celta y de Irlanda podría estar relacionada con la proximidad geográfica y migración entre stocks de bacalao de ambos mares, mientras que las mayores tasas de clasificación errónea del mar del Norte podrían deberse a la heterogeneidad del diseño de muestreo, especialmente por la baja representación en las bases de datos de la agrupación regional "Dogger Bank" del stock de bacalao del mar del Norte.

18. Aunque los análisis indicaron notables variaciones anuales/estacionales en las comunidades parásitas del bacalao, se encontró un claro patrón de repetibilidad cuando las 2 muestras del año 2002 se usaron para predecir la procedencia de peces recogidos en la primavera siguiente. Este hecho, unido a los resultados del experimento de validación realizados con muestras "ciegas", confirmó las expectativa de partida de que los modelos de RF generalizan mejor con grupos de entrenamiento amplios y diversos y con un amplio número de variables.

19. Los datos sobre comunidades de parásitos pueden ser utilizados de forma óptima para discriminar poblaciones de origen o stocks de bacalao del Atlántico noriental utilizando RF. Los buenos resultados de discriminación obtenidos, incluso para peces migratorios con comunidades parásitas que se solapan ampliamente, reflejan el elevado potencial de RF para desarrollar modelos predictivos usando datos que son complejos y "ruidosos" e indica que se trata de una herramienta prometedora para otros estudios de biomarcadores.

12. References

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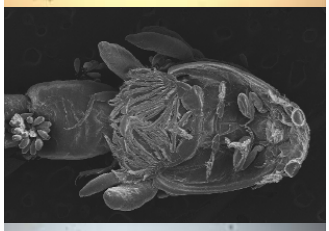

Establishing traceability for cod (Gadus morhua) in European waters: determining location of spawning and harvest