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Myxosporean gall bladder parasites of gadid fishes in the North Atlantic: Their geographical distributions and an assessment of their economic importance in fisheries and mariculture

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Abstract

Between 1992 and 2003, samples of four species of gadid fish from the northern North Sea, the Faroe Islands and northern Norway were examined for myxosporean gall bladder parasites. Total numbers of each host species examined were: 665 cod *Gadus morhua* L., 621 haddock *Melanogrammus aeglefinus* (L.), 389 saithe *Pollachius virens* (L.) and 445 whiting *Merlangius merlangus* (L.). Nine species of myxosporeans were found: *Ceratomyxa arcuata* Thélohan, 1892, *Leptotheca informis* Auerbach, 1910, *Leptotheca longipes* Auerbach, 1910, *Myxidium bergense* Auerbach, 1909, *Myxidium gadi* Georgévitch, 1916, *Myxidium oviforme* Parisi, 1912, *Myxidium sphaericum* Thélohan, 1895, *Sphaeromyxa hellandi* Auerbach, 1909, and a hitherto undescribed species of *Myxidium*. The taxonomy and likely geographical distributions of these and other gall bladder myxosporeans of gadid fish reported from both sides of the North Atlantic are discussed. These myxosporeans fulfil most criteria for use as biological tags in host population studies and some have been used successfully already. They also have potential use as indicators of environmental change and marine pollution. Some species are likely to become serious pathogens in mariculture, particularly of cod and haddock. It is clear from our assessment that a great deal has still to be learned about their taxonomy, host specificities, life cycles and general ecology. For their more efficient use as tags and indicators, and for successful control of infections and the application of preventative measures in mariculture, more information on the their biology and ecology is essential.

Keywords: Myxosporean parasites; Gadid fish; North Atlantic; Economic importance

1. Introduction

A variety of myxosporean species have been reported from the gall bladders of gadid fishes in the North Atlantic (Kabata, 1967; Khan et al., 1986;

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MacKenzie and Kalavati, 1995; Kalavati and MacKenzie, 1999). This paper brings together the results of several surveys of these myxosporeans carried out by us in the northeast Atlantic and those of earlier studies throughout the North Atlantic. We describe the likely geographical distributions, host ranges and patterns of infection with host length/age of these parasites and attempt to assess their potential value as biological tags in population studies of gadid fishes throughout the North Atlantic and their importance as pathogens, particularly in the developing field of gadid mariculture.

Some gall bladder myxosporeans infecting gadid fishes have previously been shown to be of value as biological tags in population studies of their hosts. Species in the genera *Ceratomyxa*, *Leptotheca*, *Myxidium* and *Sphaeromyxa* were all used by Kabata (1963, 1967) as biological tags for stock identification of whiting, *Merlangius merlangus* (L.), and haddock, *Melanogrammus aeglefini* (L.), in British and Faroese waters, while *Myxidium gadi* and *M. oviforme* were used to help identify stocks of cod, *Gadus morhua* L., off Newfoundland and northern Norway by Khan and Tuck (1995) and Larsen et al. (1997), respectively. Kabata (1967) commented on the pathology associated with gall bladder myxosporeans in general, but with particular reference to those infecting gadids. He described hypertrophy and increased thickness of the gall bladder wall and loss of contractility of the bladder, with the likely final outcome of a heavy infection being complete functional elimination of the bladder. The pathology of myxosporean parasites in mariculture was reviewed by Alvarez-Pelliterro and Sitjà-Bobadilla (1993a), who described the pathogenic effects of several gall bladder myxosporeans.

Little use has so far been made of myxosporeans as indicators of aquatic pollution, but Bucher et al. (1992) and Marcogliese and Cone (2001) found that levels of infections with gall bladder myxozoans in freshwater fish increased at sewage-contaminated sites. The latter authors suggested that increased populations of oligochaete hosts of actinosporean stages in sewage-enriched sediments could have accounted for the increased levels of infection in the fish hosts. In

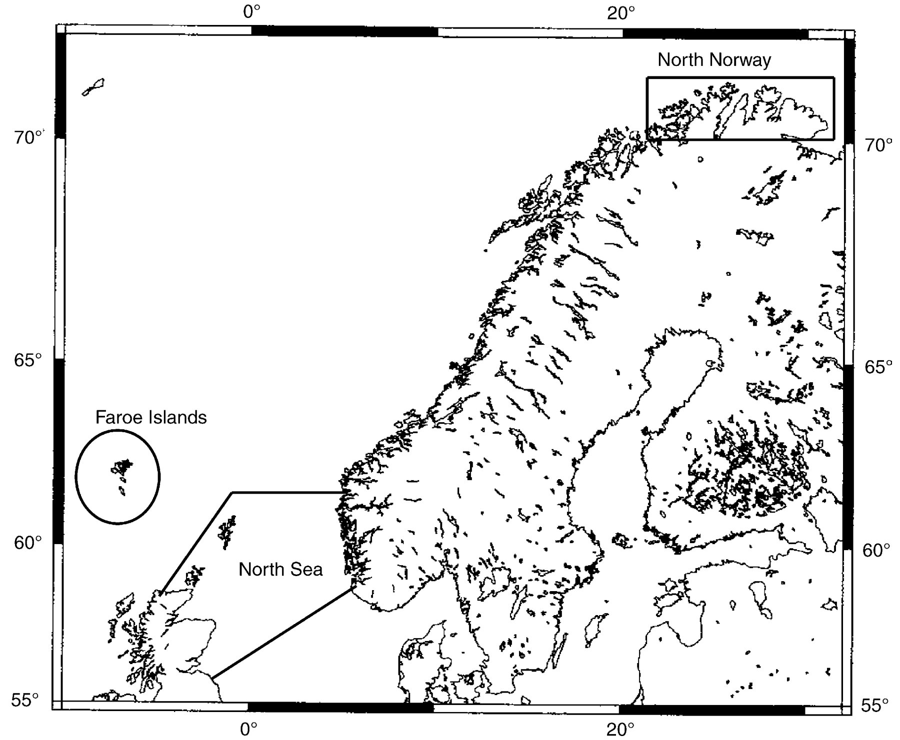

Fig. 1. Map of the northeast Atlantic showing areas from which samples of fish were taken.

contrast, Khan (1998, 1999) found that levels of infection of a gall bladder myxozoan of a marine fish were significantly lower at sites contaminated with polychlorinated biphenyls (PCBs) and polycyclic aromatic hydrocarbons (PAHs) than at cleaner reference sites. The important point about these studies is that they clearly demonstrate that myxosporeans are highly sensitive to environmental change.

2. Materials and methods

The gadid species sampled by us were cod *G. morhua*, haddock *M. aeglefinus*, saithe *Pollachius virens* (L.) and whiting *M. merlangus*. Areas in the northeast Atlantic from which our samples were taken are shown in Fig. 1. Northern North Sea samples were collected in 1992 and 1993, northern Norway samples in 1993, 1998, 2001 and 2003, and Faroese samples in 1998. Totals of 665 cod, 621 haddock, 389 saithe and 445 whiting were examined (Table 1). Some gall bladders were examined fresh, while others were removed from deep-frozen fish after defrosting, or were preserved in 10% buffered formalin at sea. Each gall bladder was examined by scanning a drop of its contents on a microscope slide at a magnification of 400×. The measure of infection level used in this paper is prevalence, as defined by Bush et al. (1997).

The statistical significance of variations in prevalence of infection with host length was tested using Fisher's exact test.

3. Results

We found nine species of myxosporeans in the gall bladders of the four host species examined. They were: *Ceratomyxa arcuata* Thélohan, 1892, *Leptotheca informis* Auerbach, 1910, *Leptotheca longipes* Auerbach, 1910, *Myxidium bergense* Auerbach, 1909, *Myxidium gadi* Georgévitch, 1916, *Myxidium oviforme* Parisi, 1912, *Myxidium sphaericum* Thélohan, 1895, *Sphaeromyxa hellandi* Auerbach, 1909, and a hitherto

Table 1
Samples of gadid fishes examined for gall bladder myxosporeans

Host species	Date	Number examined	Location
Cod	June 1992	21	Northeastern North Sea
	June 1993	150	Northern North Sea
	August 1993	71	Northern North Sea
	October 1993	101	Balsfjord, North Norway
	October 1998	36	Off Bergen, western Norway
	Summer 1998	256	Faeroe Islands
	October 2003	30	Finnmark, North Norway
Haddock	June 1992	50	Northeastern North Sea
	June 1993	151	Northern North Sea
	August 1993	157	Northern North Sea
	October 1993	134	Northeastern North Sea
	October 1998	100	Finnmark, North Norway
	October 2003	29	Finnmark, North Norway
Whiting	June 1992	50	Northeastern North Sea
	August 1993	166	Northern North Sea
	October 1993	152	Northern North Sea
	October 2001	33	Finnmark, North Norway
	October 2003	44	Finnmark, North Norway
Saithe	June 1992	12	Northeastern North Sea
	June 1993	101	Northern North Sea
	August 1993	51	Northern North Sea
	October 1993	40	Northeastern North Sea
	November 1993	56	Off Bergen, western Norway
	October 2003	129	Finnmark, North Norway

Table 2
Prevalence of *Ceratomyxa arcuata* in different length classes of whiting from the northern North Sea (1992–1993)

Length class (cm)	No. of whiting examined	No. of whiting infected	Prevalence (%)
10–13	38	1	3
14–21	43	20	47
22–25	80	34	43
26–29	118	63	53
30–33	58	38	66
34+	31	21	68
Total	368	177	48.1

undescribed species of *Myxidium.* Infection details for each species are described below.

3.1. *Ceratomyxa arcuata* (Table 2)

Found in 48.1% of whiting in samples from the northern North Sea, but not in whiting from northern Norway. The smallest infected whiting was 13 cm long and prevalence of infection in North Sea whiting increased significantly ($P < 0.0001$) with length.

3.2. *Leptotheca informis* (Table 3)

Found in 6.3% of whiting in samples from the northern North Sea, but not found in the southernmost sample taken south of 57°N or in northern Norway. The smallest infected whiting was 17 cm long and prevalence in North Sea samples peaked at between 14 and 21 cm. Variations in prevalence with host length were not statistically significant at the 5% level ($P = 0.06$).

Table 3
Prevalence of *Leptotheca informis* in different length classes of whiting from the northern North Sea (1992–1993)

Length class (cm)	No. of whiting examined	No. of whiting infected	Prevalence (%)
10–13	38	0	0
14–21	43	6	14
22–25	80	8	10
26–29	118	4	3
30–33	58	3	5
34+	31	2	6
Total	368	23	6.3

Table 4
Prevalence of *Leptotheca longipes* in different length classes of haddock from the northern North Sea (1992–1993)

Length class (cm)	No. of haddock examined	No. of haddock infected	Prevalence (%)
12–16	56	1	2
17–21	21	2	10
22–26	92	13	14
27–31	187	13	7
32–36	112	7	6
37+	24	1	4
Total	492	37	7.5

3.3. *Leptotheca longipes* (Table 4)

Found in 7.5% of haddock from the northern North Sea. All infected samples were taken between 57 and 60°N. No infected haddock were found in one sample taken south of 57°N or in two taken north of 60°N, and none was found in samples from northern Norway. The smallest infected haddock was 15 cm long and prevalence in North Sea samples peaked at between 22 and 26 cm. Variations in prevalence with host length were not statistically significant ($P = 0.07$).

3.4. *Myxidium bergense*

Found in 59 and 79% of haddock from two samples taken in northern Norway, but in only 1.6% of haddock from the northern North Sea, in two of seven samples taken between 56 and 61°N, with the greatest prevalence in the furthest north of these samples. Most haddock in the North Sea samples were <30 cm long, but all eight infected fish were amongst the largest examined (32 cm and over). Haddock from northern Norway were larger, ranging in length from 37 to 68 cm, and showed no variation in prevalence with length. We also found *M. bergense* in 5% of cod from a sample taken in Balsfjord, northern Norway in 1993.

3.5. *Myxidium gadi* (Table 5)

Found in 54.2% of saithe from the northern North Sea, in 50% caught off Bergen in western Norway, and in 29.5% from northern Norway. In the North Sea saithe as small as 10 cm were infected and prevalence decreased significantly with length ($P < 0.0001$), whereas in northern Norway prevalence was lowest in

Table 5

Prevalence of *Myxidium gadi* in different length classes of saithe from two areas

Area	Length class (cm)	No. of saithe examined	No. of saithe infected	Prevalence (%)
Northern North Sea (1992–1993)	10–19	22	22	100
	20–29	24	17	71
	30–39	32	15	47
	40–49	24	12	50
	50–59	25	12	48
	60+	26	5	19
	Total	153	83	54.2
Northern Norway (2003)	20–29	21	4	19
	30–39	24	10	42
	40–49	33	12	36
	50–59	18	8	44
	60+	33	4	12
	Total	129	38	29

the smallest (20–29 cm) and largest (60+ cm) length classes sampled but was similar to those from the North Sea in the intermediate length range, the variation being statistically significant ($P = 0.04$). Lengths were not recorded in the sample from western Norway. Found in cod from the Faroe Plateau only, at two out of seven stations and at an overall prevalence of 3.5%.

3.6. *Myxidium oviforme* (Table 6)

Found in 7.0% of cod from the northern North Sea, in 19.0% from the Faroe Plateau, and in 17.0 and 20.8% (mean 19.8%) in two samples from northern Norway. In the North Sea prevalence of infection was lowest in both the smallest and the largest cod and peaked at between 44 and 63 cm. The smaller length classes examined in the North Sea were absent from the samples taken in northern Norway, where the greatest prevalence was in the highest length class. Variations in prevalence with length were not statistically significant in either area ($P = 0.14$ and $P = 0.24$, respectively).

3.7. *Myxidium sphaericum*

Found in only four whiting in two samples taken south of 58°N (3.0% prevalence), but not found in North Sea samples of whiting taken north of 58°N or in northern Norway.

3.8. *Sphaeromyxa hellandi* (Table 7)

Found in 10.7% of haddock from the northern North Sea, but not from northern Norway. The smallest length classes of haddock (12–21 cm) were not infected, the

Table 6

Prevalence of *Myxidium oviforme* in different length classes of cod from two areas

Area	Length class (cm)	No. of cod examined	No. of cod infected	Prevalence (%)
Northern North Sea (1992–1993)	24–33	44	1	2
	34–43	89	6	7
	44–53	63	8	13
	54–63	20	2	10
	64+	26	0	0
	Total	242	17	7.0
Northern Norway (1993)	40–45	24	3	12
	46–50	46	11	24
	51–55	20	2	10
	56+	11	5	45
	Total	101	21	20.8

Table 7
Prevalence of *Sphaeromyxa hellandi* in different length classes of haddock from the northern North Sea (1992–1993)

Length class (cm)	No. of haddock examined	No. of haddock infected	Prevalence (%)
12–16	56	0	0
17–21	21	0	0
22–26	92	12	13
27–31	187	24	13
32–36	112	13	12
37+	24	4	17
Total	492	53	10.7

smallest infected individual being 22 cm, after which there was no increase or decrease in prevalence with length. The variations in prevalence with length were statistically significant ($P = 0.02$).

3.9. *Myxidium sp.*

This apparently undescribed species, resembling *M. sphaericum*, was found only in whiting from a small sample of 33 fish taken in northern Norway, at a prevalence of 67%.

4. Discussion

The zoogeography, host specificity and possible pathogenicity of each myxosporean species reported from gadid fishes of the North Atlantic are discussed below in order to assess their value as biological tags and their potential impact on the health of wild and cultivated gadid hosts. A major impediment to such assessment is the fact that we do not know if all marine myxosporeans have obligate alternative invertebrate hosts or if direct transmission from fish to fish is possible for some species, as suggested by Diamant (1997) and Yasuda et al. (2002). Køie et al. (2004) described the first life cycle of a marine myxozoan involving an actinosporean stage in polychaetes, while Hallett et al. (1999) described actinosporean stages from marine oligochaetes.

4.1. *Ceratomyxa arcuata*

All reports of this species have been from the northeast Atlantic, Mediterranean Sea and Black Sea, with the exception of that of Meglitsch (1960) from New Zealand. Differences between the description of Meglitsch and both the original description of *C. arcuata* and the redescription of Kalavati and MacKenzie (1999) suggest that Meglitsch was mistaken in his identification. From the remaining records it appears that *C. arcuata* is restricted to temperate waters of the northeast Atlantic. The fact that we found whiting to be infected in the northern North Sea but not in northern Norway suggests that *C. arcuata* could be a useful tag for following migrations and discriminating between stocks of whiting along the west coast of Norway. Within the northeast Atlantic *C. arcuata* has been reported from 15 fish species, all demersal, representing nine different families. Gadid hosts are the shore rockling *Gaidropsarus mediterraneus* (L.), whiting and cod, with the last-named considered by Kalavati and MacKenzie (1999) to be an ‘accidental’ host. Nevertheless, the fact that *C. arcuata* was found in two specimens of cod suggests that this host could be susceptible to infection under conditions of intensive cultivation. Other species of gall bladder parasitic *Ceratomyxa* have been reported as pathogens of wild and cultured marine fish. Two species of the genus *Ceratomyxa* infecting sea bass *Dicentrarchus labrax* (L.) caused severe damage to not only the gall bladder, but also to neighbouring tissues such as the pancreas and intestine (Sitjà-Bobadilla and Alvarez-Pelliterro, 1993; Alvarez-Pelliterro and Sitjà-Bobadilla, 1993b). The same two species were later described by Rigos et al. (1997) as causing severe damage and mortalities in cultured dentex *Dentex dentex* L. Another species, *C. sparusaurati*, was considered a potential threat to cultured stocks of gilthead sea bream *Sparus aurata* in the Mediterranean because of damage caused to infected gall bladders (Palenzuela et al., 1997).

4.2. *Leptotheca informis*

Reports of this species are from two main areas: the northeast Atlantic and the eastern Pacific. Differences between descriptions of the parasite from different host species led Kalavati and MacKenzie (1999) to suggest that the species in the Pacific may be different from *L. informis* as originally described from ling *Molva molva* (L.) off western Norway by Auerbach (1910). If we exclude the Pacific records, we are left with a distribution of *L. informis* restricted to temperate waters of the northeast Atlantic, including one report from the Black Sea (Pogoreltseva, 1952) and with a host range of two gadid species, ling and whiting. This species, like *C. arcuata*, was not found in whiting from northern Norway and so could be a useful biological tag for population studies of whiting along the west coast of Norway.

4.3. *Leptotheca longipes*

This species has also been reported from the northeast Atlantic and the eastern Pacific, but again Kalavati and MacKenzie (1999) suggested that the Pacific reports may have been of a different species. It has been reported from only two host species in the northeast Atlantic—tusk *Brosme brosme* (Ascanius) and haddock. Its absence from haddock in northern Norway suggests a distribution restricted to temperate waters of the northeast Atlantic, but in contradiction to this we have found tusk infected in northern Norway (unpublished data). Further surveys are therefore required to determine the geographical distribution of *L. longipes* in both hosts.

4.4. *Myxidium bergense*

This species was originally described by Auerbach (1910) from saithe caught off Bergen in western Norway, but we did not find it in saithe from the North Sea, including a sample taken from the type locality, or from northern Norway. Instead these saithe were infected with *M. gadi* only. This suggests that Auerbach's (1910) report may have been based on a wrong host identification and that saithe was not the host species from which his material originated. Seven of the eight haddock infected with *M. bergense* in the North Sea samples were found in the northernmost samples north of 60°N, but prevalence was highest in samples from northern Norway. All other reports of *M. bergense* in the northeast Atlantic are from north of 58°N, with the exception of that of Gaevskaya and Kovaleva (1984), who reported it from whiting to the southwest of the British Isles. However, significant differences between the description of Gaevskaya and Kovaleva and both the original description of Auerbach (1910) and the redescription by MacKenzie and Kalavati (1995) suggest a different species of *Myxidium*. Reports of *M. bergense* from the Canadian Atlantic and the Barents and White Seas indicate a coldwater species with a northern distribution on both sides of the North Atlantic. Eleven fish species have been reported as hosts, including six gadids. We found prevalence and intensity of infection to be greater in haddock than in cod. *Myxidium bergense* therefore appears to have considerable potential as a biological tag in population studies of haddock in particular, and possibly cod, in these northern waters.

4.5. *Myxidium gadi*

This species has been reported from the northeast Atlantic, from the coast of France to the Barents and White Seas, and from the northwest Atlantic. Six host species have been reported, comprising four gadids and two flatfish. In the northwest Atlantic it occurs commonly in cod and haddock (Khan et al., 1986), but in the northeast Atlantic we found it mainly in saithe, not at all in haddock, and the only cod we found infected were from the Faroe Plateau. Assuming that all previous reports of *M. gadi* are valid, this species has a much wider distribution than other species of *Myxidium* found in gadid fish, including in its range both temperate and colder waters over the entire North Atlantic. The important question, however, is why the same parasite species should infect different hosts in different parts of its distribution. Either distinct populations or stocks of cod and haddock vary markedly in their susceptibility to infection, or the name *M. gadi* actually includes two or more species that are virtually indistinguishable morphologically. This problem urgently requires further investigation, particularly as *M. gadi* has the potential to be a serious pathogen of cultivated gadids. Feist and Bucke (1992) described necrosis of the gall bladder epithelium and an inflammatory response in sub-epithelial connective tissue resulting from heavy infections of *M. gadi* in saithe. They considered that host digestion must be affected in heavy infections, which may in turn affect condition host factor and growth rate.

Myxidium gadi infects saithe very early in life and was the only species studied by us to show a significant decrease in prevalence of infection with host length. Possible explanations for this pattern of infection are: (1) heavily infected saithe are selectively predated upon; (2) infections occur only in inshore nursery areas and have a limited life span, so adult saithe in offshore waters gradually lose their infections; (3) older saithe develop an immunity to the infection; or (4) the resident heavily infected populations we sampled are progressively diluted by immigration of uninfected adult saithe from other areas. We have no comparable length/prevalence data for infections of *M. gadi* in cod and haddock.

4.6. *Myxidium oviforme*

The taxonomic history and reported host range of this species are very complex. Firstly, the name *M. oviforme* has been given to two different forms, one infecting marine fish and the other infecting anadromous and freshwater salmonids. Shulman (1990) and Lom and Dykova (1992) considered that the species infecting salmonids is in fact the very similar *Myxidium truttae*, which had been misidentified previously. If we therefore exclude salmonids from the list of hosts reported for *M. oviforme*, this still leaves 12 species representing seven families of marine fish and a geographical range covering the northeast Atlantic, including the Mediterranean, the northwest Atlantic and the eastern Pacific. Secondly, marked differences between the description of the parasite from fishes in the eastern Pacific by Jameson (1929) and the descriptions of *M. oviforme* by Shulman (1990) and MacKenzie and Kalavati (1995) cast serious doubts on the validity of the reports from the eastern Pacific. Assuming that these reports represent a different species of *Myxidium*, this then leaves eight species of fish as hosts for *M. oviforme*, representing six families, with cod the only gadid host.

All of the infected cod we found in the North Sea came from samples taken south of 59°30′N, and cod from northern Norway and the Faroe Plateau show similarly discontinuous and localised infections (Larsen et al., 1997; Gaard, 2002), which make *M. oviforme* an excellent biological tag for population studies of cod. In the northwest Atlantic, however, Khan et al. (1986) found no cod infected with *M. oviforme*, but reported it from three species of cottid fish. This raises the same question as posed above with *M. gadi*—is it really the same parasite species infecting different hosts in different parts of its distribution? The type hosts of *M. oviforme* are apogonid and labrid species and the type locality is in the Mediterranean Sea, which further fuels suspicion that the name *M. oviforme* may include more than one species. As Shulman (1990) commented: “. . . a detailed study of this species is mandatory in the near future.”

4.7. *Myxidium sphaericum*

As with *M. oviforme*, the taxonomic history and reported host range of this species are very complex. It has been reported from 18 fish species, representing eight families, from locations as widely separated as the northeast and northwest Atlantic, Florida and the Great Barrier Reef. *Myxidium sphaericum* and *M. bergense* were considered to be conspecific by Noble (1957), Kabata (1967), Shotter (1970) and Moser et al., (1989), but MacKenzie and Kalavati (1995) tested this hypothesis and found both species, as found in gadid hosts, to be valid. They also pointed out differences between their description of *M. sphaericum* from whiting and both the original description by Thélohan (1895) and that of Lubat et al. (1989), both from the pelagic fish *Belone belone* (L.). This suggests that the species originally described as *M. sphaericum* may be a parasite of pelagic fish, while the species occurring in whiting, and possibly other demersal fish, is a different species. MacKenzie and Kalavati (1995) also noted differences between their description of the species from whiting and that described by Moser et al. (1989) from three species of Blenniidae on the Great Barrier Reef, which suggested that Moser et al. were dealing with another species different again from *M. sphaericum*. If we exclude the report of Moser et al., the remaining reports show a distribution of *M. sphaericum* in the northwest Atlantic extending from the Arctic waters of Baffin Island to Florida, and in the northeast Atlantic extending from the Mediterranean to the North Sea. In Canadian Atlantic waters eleven species of demersal fish have been reported as hosts, whereas the report from Florida is from a pelagic fish of the same family (Belonidae) as the type host. These reports support the hypothesis that the original *M. sphaericum* is a parasite of pelagic fish, perhaps specific to the family Belonidae, while the forms reported as *M. sphaericum* from demersal fish belong to at least one other species. Despite this confusion and uncertainty, the species currently identified as *M. sphaericum* from whiting was used successfully by Kabata (1967) as a biological tag. Shotter (1970) described hypertrophy of the wall of the gall bladder and occlusion and destruction of the bile duct in whiting caused by *M. sphaericum*, and he speculated that such an infection may been the cause of death of a whiting maintained in captivity.

4.8. *Myxidium virense Gaevskaya and Kovaleva, 1984*

We did not find this species in our study. It was described from saithe in the North Sea and there have been no subsequent reports of its occurrence.

4.9. *Myxidium sp.*

This appears to be a hitherto undescribed species resembling *M. sphaericum* found by us in a sample of whiting taken in northern Norway at the extreme northern part of the distribution of this host at a latitude of about 71°N. It may represent a species that has evolved in a separate geographically isolated host population and could prove to be a useful biological tag for whiting populations in western and northern Norway. This species will be described in a separate publication.

4.10. *Sphaeromyxa hellandi*

In contrast to the *Myxidium* spp. discussed above, this species has a relatively simple taxonomic history and limited host range. Its distribution appears to be confined to the northeast Atlantic from the Celtic Sea to the Barents Sea, and it has been reported from only six host species, including four gadids. One of these hosts is the whiting, but Kalavati and MacKenzie (1999) considered their finding from a single whiting to be an “accidental” infection, so whiting should not be considered to be within the normal host range. We found *S. hellandi* infecting haddock in the North Sea, but not in northern Norway, although it was reported by Polyansky (1955) from other hosts in the Barents Sea.

4.11. *Sphaeromyxa balbianii Thélohan, 1892*

We did not find this species in our study, but it has been reported from two gadid hosts, the three-bearded rockling *Gaidropsarus vulgaris* (Cloquet) and the shore rockling *G. mediterraneus* in European waters (Thélohan, 1892; Tripathi, 1948). It has also been reported from fish of four other families in both the Atlantic and Pacific Oceans. Tse et al. (1999) tentatively identified *S. balbianii* from the cottid species *Taurulus bubalis* from the North Sea and English Channel, but did not positively establish the identity of the *Sphaeromyxa* sp. they found in three-bearded rockling.

4.12. *Myxobolus sp.*

A single spore of a *Myxobolus* sp. was reported from the gall bladder of a whiting from Morecambe Bay in the Irish Sea by Feist and Ronga (1996). We found no *Myxobolus* infections in any of the fish we examined.

4.13. *Zschokkella russelli Tripathi, 1948*

We did not find this species in our study, but it was reported by Khan et al. (1986) from the gall bladders of 6 of 925 cod caught off Newfoundland and Labrador. It was originally described from the gall bladders of the three-bearded rockling and the five-bearded rockling *Ciliata mustela* from the English Channel by Tripathi (1948), and again from the latter host caught off the coast of Wales by Davies (1985). It was also reported from the urinary bladders of two macrourid fishes of the genus *Coryphaenoides* caught off the coast of Oregon (Northeast Pacific) by Yoshino and Moser (1974). Tripathi (1948) commented that changes observed in the colour and viscosity of the bile in double infections of *Z. russelli* and *Sphaeromyxa balbianii* must affect the digestion of the infected fish and ultimately its health. Alvarez-Pelliterro and Sitjà-Bobadilla (1993a) described severe pathology of the gall bladder in mugilid fishes by a species of *Zschokkella*, which they considered probably contributed to mortalities of fish held in a semi-intensive open system. The occurrence of *Z. russelli* in three species of gadid fish suggests that it should be noted as a possible pathogen in gadid mariculture.

4.14. *General comments*

Our conclusions with regard to the probable host and geographical ranges of the myxosporean species discussed above are summarised in Table 8.

Disease control is likely to be a major problem in the developing field of coldwater mariculture in the North Atlantic. Myxosporeans were one of the taxonomic groups highlighted by MacKenzie and Hemmingsen (2002) in their review of parasites likely to cause problems in species new to mariculture. Cod and haddock

Table 8
Host ranges and probable geographical distributions of gall bladder myxosporeans infecting gadid fish in the North Atlantic

Myxosporean species	Host range	Probable geographical distribution
Ceratomyxa arcuata	Fifteen species from nine families. Gadid hosts: whiting, cod and shore rockling *Gaidropsarus mediterraneus*	Temperate waters of northeast Atlantic, including Mediterranean and Black Seas
Leptotheca informis	Ling *Molva molva* and whiting	Temperate waters of northeast Atlantic, including Mediterranean and Black Seas
Leptotheca longipes	Haddock and tusk *Brosme brosme*	Northeast Atlantic
Myxidium bergense	Eleven species from four families. Gadid hosts: cod, haddock, whiting, saithe, polar cod *Boreogadus saida*, and white hake *Urophycis musicki*	Northern distribution on both sides of North Atlantic (a coldwater species)
Myxidium gadi	Six species from three families. Gadid hosts: cod, haddock, saithe and pollack *Pollachius pollachius*	Temperate and colder waters over the entire North Atlantic
Myxidium oviforme	Eight species from six families. Gadid host: cod	Temperate and colder waters over the entire North Atlantic, including the Mediterranean
Myxidium sphaericum	Fifteen species from seven families. Gadid hosts: whiting and poor cod *Trisopterus luscus*	Northwest Atlantic from Florida to Baffin Island; northeast Atlantic from the Mediterranean to the North Sea
Myxidium virense	Saithe	Single record from the North Sea
Myxidium sp.	Whiting	Northern Norway
Sphaeromyxa hellandi	Six species from three families. Gadid hosts: haddock, whiting, ling and tusk	Northeast Atlantic from the Celtic Sea to the Barents Sea
Sphaeromyxa balbianii	Seven species from four families. Gadid hosts: shore rockling and three-bearded rockling *Gaidropsarus vulgaris*	North Atlantic and North Pacific
Myxobolus sp.	Whiting	Single record from the Irish Sea
Zschokkella russelli	Cod, three-bearded rockling and five-bearded rockling *Ciliata mustela*. Also *Coryphaenoides abyssorum* and *C. filifer* (Macrouridae)	North Atlantic and North Pacific

are favoured species for cultivation and some of the myxosporeans discussed in this paper, particularly the *Myxidium* species, could well feature prominently as serious hazards in their cultivation. There is no known treatment for these parasites once they have become established in a fish farm, so the strategy must be to prevent them gaining access in the first place. To put preventative measures into effect it is necessary to have good information on the parasites' life cycles and the optimum environmental conditions for their successful transmission, but it is clear from the foregoing assessment that at present we are far from achieving that aim. Indeed, we cannot even be sure of the true identities and host specificities of some of the species.

The efficient management of wild fish populations depends on a thorough knowledge of stock structure. These gall bladder myxosporeans fulfil most of the criteria for use as biological tags for this purpose (MacKenzie and Abaunza, 2005) and several have already been used successfully in this way. They also have the potential for use as indicators of environmental change and marine pollution. More information on the specific identities, life cycles, and general ecology of these parasites will lead to greater efficiency in their use as tags and indicators.

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