ICES Journal of Marine Science, 60: 77–84. 2003
doi:10.1006/jmsc.2002.1307

The parasite fauna of the Norwegian spring spawning herring (*Clupea harengus* L.)

A. Tolonen and E. Karlsbakk

Tolonen, A., and Karlsbakk, E. 2002. The parasite fauna of the Norwegian spring spawning herring (*Clupea harengus* L.). ICES Journal of Marine Science, 60: 77–84.

We examined 220 Norwegian spring spawning (NSS) herring for parasites. The samples included juvenile herring from coastal nursery areas and young or mature herring from feeding areas in the Norwegian Sea and from the wintering areas in fjords in Northern Norway. We detected 11 parasite species. The coccidian *Goussia clupearum* infects both young and adult fish, with increasing prevalence with age. *Eimeria sardinae*, a coccidian infecting the testes of males, is mostly restricted to mature fish. Spores of a myxozoan parasite, *Ceratomyxa auerbachi*, were only detected in fish from the wintering areas. Adult trematodes, *Hemiurus* spp., occurred only in young herring from a coastal sample. Adult and larval *Hysterothylacium aduncum* (Nematoda) infections occur predominantly in immature fish. That *H. aduncum* is rare in mature fish suggests that infections acquired as young are lost, and that there is virtually no transmission of the parasite in the feeding areas (continental shelf areas post-spawning and the Norwegian Sea). *Cryptocotyle lingua* metacercarial infections are acquired only by young herring in coastal nursery areas. The only macroparasite increasing in abundance in mature NSS herring is larvae of the nematode *Anisakis simplex*, this species infecting the fish also in the feeding areas. The parasite fauna of NSS herring is species poor, adult helminths occurring only in juveniles, while adult fish are host only to larvae, chiefly *A. simplex*.

Keywords: *Anisakis*, *Ceratomyxa*, *Clupea harengus*, *Cryptocotyle*, *Eimeria*, *Goussia*, *Hemiurus*, *Hysterothylacium*, Norwegian Sea, parasites

Received 18 February 2002; accepted 23 July 2002

A. Tolonen: Department of Limnology and Environmental Protection, PO Box 65, FIN-00014, University of Helsinki, Finland. E. Karlsbakk: University of Bergen, Department of Fisheries and Marine Biology, Bergen High Technology Centre, Postboks 7800, N-5020 Bergen, Norway. Correspondence to E. Karlsbakk: e-mail: egil.karlsbakk@ifm.uib.no

Introduction

The Norwegian spring spawning herring (NSS herring) is one of the largest and most important single fish stock units in the North Atlantic (Dragesund *et al.*, 1997). Overfishing brought the stock to a collapse in the late 1960s and the adult stock was fished out completely in 1970 (Hamre, 1990). The distribution and migration pattern of the NSS herring changed when the stock size declined. The traditional feeding and wintering areas in the Norwegian Sea were abandoned and the stock remained in coastal waters in northern Norway throughout the year early in the recovery period (Dragesund *et al.*, 1997).

In the present paper we deal with herring collected in 1993–95. In that period, the adult stock was feeding on zooplankton in the Norwegian Sea (April–August), particularly along the polar front. In late July and August an eastward movement commenced and in September the herring entered the wintering areas (Dalpadado *et al.*, 2000). In recent years (1988–), the whole spawning component and part of the juvenile stock have been wintering in a fjord system (Vestfjord-Ofotfjord-Tysfjord) in northern Norway (Dragesund *et al.*, 1997; Slotte, 1999). The herring leave the wintering area by mid-January at onset of the southbound spawning migration. Spawning occurs along the Norwegian west coast, particularly off Møre in early spring (February–March) (Dragesund *et al.*, 1997; Slotte, 1999). During wintering, migrating to spawning areas and when spawning the herring do not feed (Slotte, 1999). The larvae drift northwards with the coastal current, and the main nursery areas are the Barents Sea and the Norwegian fjords (coastal component). The juvenile period in the Barents Sea lasts 3–5 years, while fish from the coastal areas (fjords) leave at an age of 1–2 years (de Barros and Holst, 1995).

According to Arthur and Arai (1980) there are records of more than 75 parasite species, mostly from Atlantic herring. Arthur and Arai (1984), with additions by MacKenzie (1987), listed at least 41 marine parasite species from Atlantic herring (*Clupea harengus*). Though studies on Atlantic herring are numerous, there appear to be no clear records on parasites from Norwegian spring spawning (NSS) herring, the largest stock. Most NE Atlantic studies deal with Baltic herring or North Sea stocks. Murav'ev (1970) recorded larval nematodes from the areas around Iceland and Jan Mayen Island, and may have dealt with NSS herring in addition to Icelandic stocks. Polyanskii (1955) studied juvenile herring from the Murman coast, probably NSS herring, and recorded nine parasite species. Several studies on infections by the fungus-like protist *Ichthyophonus hoferi* (Plehn et Mulsow, 1911) have dealt with NSS herring (Karaseva *et al.*, 1993a,b, 1995; Hodneland *et al.*, 1997; Holst *et al.*, 1997). We set out to characterize the parasite fauna of the NSS stock, with emphasis on age related changes.

Materials and methods

Herring were collected during a cruise with R/V "G. O. Sars" 24 July–16 August 1993 from the Norwegian Sea and shelf and coastal areas (Stns 389–446), with R/V "Johan Hjort" in 2–10 December 1994 from wintering areas of Ofotfjord–Tysfjord (Stns 697, 705) and with R/V "G. O. Sars" from the feeding areas in the Norwegian Sea 22–25 April 1995 (Stns 254, 258–261) (Figure 1). All samples were taken with pelagic trawl. Samples of large herring were deep frozen in individual plastic bags on board, and later thawed and dissected in the laboratory. The 0-group herring were fixed individually in jars with 4% formaldehyde solution. Total length (mm), weight (g), sex, gonad status and age (scales and otoliths) of each fish were recorded. The samples taken are listed in Table 1.

Dissections were performed with the aid of a dissecting microscope at magnification up to 40 × using standard parasitological techniques. The following tissues and organs were examined: skin, fins, gills, mouth, liver, gallbladder, swimbladder, gonad, kidney, heart, lateral musculature, mesenteries, oesophagus, stomach, pyloric caeca, and intestine. Metazoan parasites were picked, counted and treated separately from the lumen and from the surface of the digestive tract.

Thin squash preparations were prepared from heart, liver, kidney, gonadal tissue and bile and examined using a light microscope at 100–1000 × .

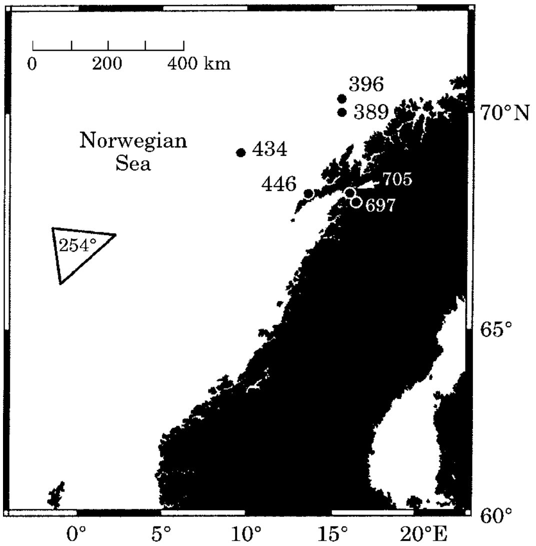

Figure 1. Locations of pelagic trawl stations where samples were taken. Triangle (254*) represents the area of Stns 254, 258–261. Stns 389 and 446 comprise juvenile fish (nursery area), Stns 254*, 396 and 434 are in the feeding area and Stns 697 and 705 are from the wintering area.

In order to reveal *Ichthyophonus* infection the skin was removed from the postero-lateral part of the fish and the red somatic muscles were examined for granulomas (Hodneland *et al.*, 1997). Macroscopic and microscopic examination of the heart for granulomas was also performed.

Prevalence is the proportion of hosts (%) infected with a particular parasite species, abundance is the number of a particular parasite species per host individual (infected or uninfected) and intensity is the number of a particular parasite species in an individual infected host.

The G-test for heterogeneity was used to analyse binomial (prevalence) data. Specific effects were revealed by the chi-square test. When expected values <5 occurred, groups were pooled to fulfil the requirements of the test (Sokal and Rohlf, 1995), or the Fisher exact test was applied. Correlations were examined with Spearman's rank correlation tests.

Results

We detected 10 parasite species in the herring samples (Table 1). The three protistans comprised two coccidians and the fungus-like *Ichthyophonus* (Ichthyosporea). Metazoans were represented by one myxozoan, four trematodes, two nematodes and one copepod. In addition, gill "cysts of unknown etiology" was found (MacKenzie, 1979).

Systemic infections with *Ichthyophonus hoferi* were found with prevalence's between 0 and 13% in the different samples. Infected fish were 4–11 years old.

Table 1. Sample prevalences and intensities (mean, standard deviation s.d., max) of parasites and gill cysts in Norwegian Spring Spawning herring from several residence areas and life cycle phases. P=prevalence (%), M=metacercariae, G=gastrointestinal , L=encapsulated larvae.

Sample no	389				446				396				434				697				705				254*			
Sample size (N)	15				46				30				31				34				34				30			
Date	Jul. 1993				Aug. 1993				Jul. 1993				Aug. 1993				Dec. 1994				Dec. 1994				Apr. 1995			
Herring length: range	50–69				155–221				210–340				245–360				213–287				243–376				250–368			
(mean ± s.d.)	(58 ± 5)				(188 ± 14)				(258 ± 28)				(292 ± 23)				(247 ± 16)				(334 ± 37)				(293 ± 30)			
Age structure: range (mode)	0 (0)				1–2 (1)				2–4 (3)				3–8 (4)				2–4 (3)				3–11 (11)				4–12 (4)			
Area	Nursery area				Nursery area				Feeding area				Feeding area				Wintering (upper)				Wintering (deep)				Feeding area**			
		Intensity				Intensity				Intensity				Intensity				Intensity				Intensity				Intensity		
	P.	Mean	s.d.	Max	P.	Mean	s.d.	Max	P.	Mean	s.d.	Max	P.	Mean	s.d.	Max	P.	Mean	s.d.	Max	P.	Mean	s.d.	Max	P.	Mean	s.d.	Max
Unknown etiology																												
Gill cysts ("CUEs")	0				0				0				3	—			0				9	—			0			
Ichthyosporea																												
Ichthyophonus hoferi	0				0				13	—			3	—			0				12	—			3	—		
Apicomplexa																												
Eimeria sardinae	0				0				0				6	—			3	—			9	—			0			
Goussia clupearum	0				7	—			0				6	—			12	—			21	—			0			
Myxozoa																												
Ceratomyxa auerbachi	0				0				0				0				12	—			0				0			
Trematoda																												
Cryptocotyle lingua M	0				57	—			0				0				0				0				0			
Hemiurus luehei	0				54	15.3	24.1	82	0				0				0				0				0			
Hemiurus communis	0				2	1	—	1	0				0				0				0				0			
Hemiurus levinseni	0				7	1	0	1	0				0				0				0				0			
Nematoda																												
Hysterothylacium aduncum G	0				50	2.1	1.4	7	30	2.4	2.2	8	39	1.3	0	2	0				0				0			
Hysterothylacium aduncum L	13	2.0	1.4	3	22	1.7	1.1	4	30	2.0	0.9	3	3	1.0	—	1	9	1.0	0.0	1	3	1.0	—	1	0			
Anisakis simplex L	7	1	—	1	54	3.7	2.9	9	83	6.0	4.7	24	100	9.6	8	33	68	3.1	2.0	7	97	17.8	13	62	90	9.9	15	62
Copepoda																												
Lernaeocera sp.	0				0				3	1	—	1	0				0				0				0			

*Stns 254,258–261, **including spent fish.

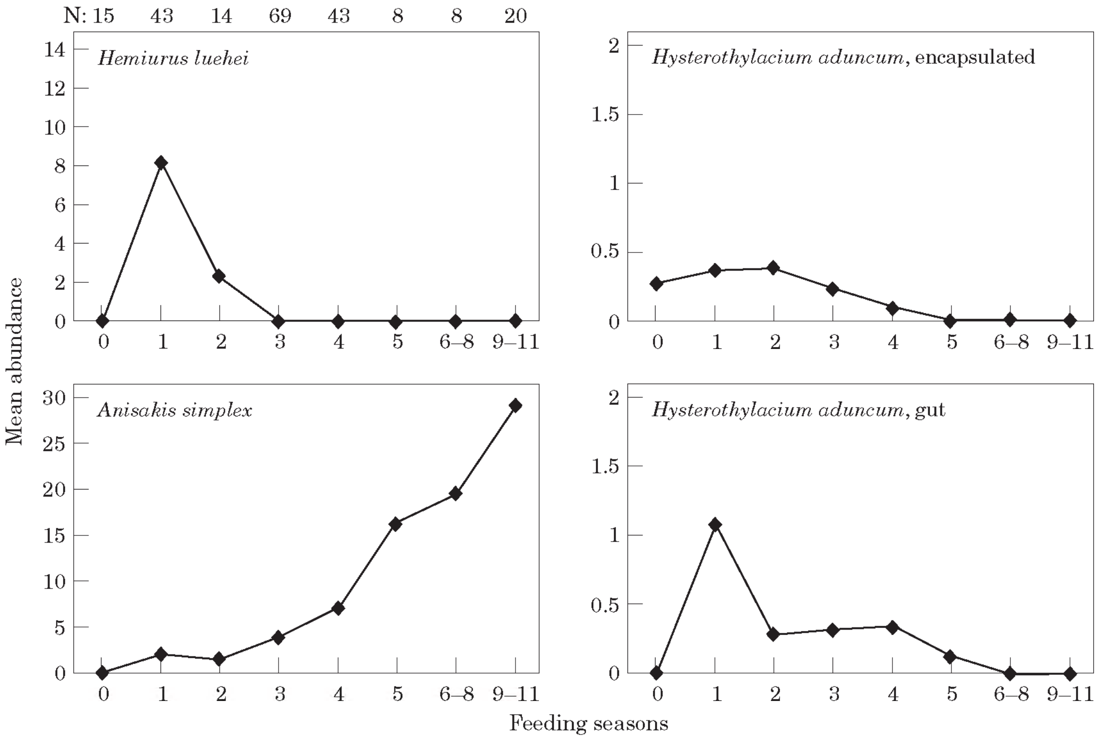

Figure 2. Patterns in infection of NSS herring with age, by some parasites that are acquired through food. Curves show sample mean abundance of parasites against number of complete feeding seasons.

Macroscopical signs of infection were most prominent in the heart and in the red body musculature.

The coccidian *Eimeria sardinae* (Thélohan, 1890) infected the testes of male herring, aged 4 years or more. Careful examinations of female gonads were all negative. The infection was significantly associated with herring belonging to the spawning stock (Fisher exact test, $p<0.01$), with a prevalence of 15% in 4+ males.

The other coccidian recovered was *Goussia clupearum* (Thélohan, 1894), which infected the liver tissue. It occurred in herring aged 1 year and more, and prevalence increased significantly with age ($G_3=18.5$, $p<0.001$), reaching 29% in 5+ fish.

The myxosporidian *Ceratomyxa auerbachi* Kabata, 1962 infects the gall bladder. It was found only in the wintering area, in immature 3–4-year-old fish (Stn 697), with a prevalence of 10% (spores). This subset of wintering herring deviated significantly with respect to *Ceratomyxa* prevalence from other life cycle phases (early/late feeding area) (Fisher exact tests, $p<0.05$).

Metacercariae of the digenean *Cryptocotyle lingua* (Creplin, 1825) were detected in the skin of 57% of the juvenile herring (1–2-year-old, Stn 446) in the frozen samples, and were not detected in the other samples. However, for this parasite additional and more comprehensive data were obtained from the examination of freshly caught NSS herring from the wintering areas in 1994, 1995, in the spawning area at Møre 1995 and the Norwegian Sea in 1995, totalling 2937 fish. Prevalences were relatively high in the 1983 and 1988 year classes, 21% (n=373) and 22% (n=73) respectively. It declined to 10% in the 1989-year class (n=307) and further to a mean of 4.6% in the 1990–92 year classes (n=2044). Within year-classes there were no prevalence differences between years or samples.

Gastrointestinal trematodes occurred only in the coastal sample from the nursery area (Stn 446), in herring aged 1–2 years (Figure 2). All three species found occurred in the stomach. *Hemiurus luehei* Odhner, 1905 was the dominant species representing 99% of the stomach trematode individuals and with a sample prevalence of 61%. Nearly all *H. luehei* were large and oviferous. *Hemiurus communis* Odhner, 1905 (n=3) and *Hemiurus levinseni* Odhner, 1905 (n=1) were oviferous but with few eggs.

Hysterothylacium aduncum (Rudolphi, 1802) occurred both as encapsulated III stage larvae in the viscera and as freely moving larvae, preadults (stage IV) and adults in the gut. In the 1993 samples, encapsulated larvae occurred in immature herring (age 0–4), with low mean abundances (<0.5). *H. aduncum* larvae did not occur in sexually mature herring in any of the samples (Figure 2), but a larva was observed in a 10 year-old fish. Most *H. aduncum* larvae were encapsulated on or between the caeca (84%), while the rest occurred elsewhere on the gut. Lumenal *H. aduncum* were almost exclusively preadult and adult worms. These occurred in the caeca (78%), the intestine (19%) and the stomach (2%). In 1993, lumenal *H. aduncum* infections were not found in 0-group, were most common in 1–2-year-old herring and had decreasing abundances in fish 3–5 years old. In addition, we observed an 8-year-old fish infected with a single *H. aduncum*. Lumenal infections did not occur in wintering fish (1994) or in the 1995 samples from the Norwegian Sea (Figure 2).

Larvae of the nematode *Anisakis simplex* (Rudolphi, 1809) were recovered from all samples, including from a 59 mm long 0-group fish. Abundance of *Anisakis* increased with host age and length in most samples, the exception being samples of relatively uniform age (e.g. Stn 446) where abundance correlated with length. The main sites for *Anisakis* larvae were the serosal coverings of the stomach including its extension towards the pneumatic duct (60%), the pyloric caeca (23%) the intestine (13%) and the liver (2%). This pattern was not significantly affected by herring age. Intramuscular *Anisakis* (belly flaps) were rare.

A single pre-metamorphosis stage *Lernaeocera* was found on a gill of a 2-year-old herring (Stn 396). In addition, when examining freshly caught herring (>3000) in the Norwegian Sea, wintering area and spawning area, adult *Caligus elongatus* Nordmann, 1832 were occasionally found on the skin, despite significant scale loss.

Parasite community

The average number of endoparasite species was highest in the 1–2-year-old fish, with 2.2–2.8 species. In the 0-group *H. aduncum* larvae were most common, representing 0.2 species per individual. In 3-year-old fish there were 1.4 species, while in older fish (4–12 years) the average number was close to 1 (0.9–1.1). The same pattern is valid for the number of metazoan macroendoparasite species, demonstrating the rarity of infections with coccidians and the myxozoan *C. auerbachi*. The average number of metazoan parasite individuals increased from 0.3 in the 0-group to a temporary maximum of ca. 18 in the 1–2-year-olds, followed by a decline to 6.4 in 3-year-olds and 4.7 in 4-year-old herring. Thereafter, the average number of parasite individuals gradually increased reaching 24.5 in the 11-year-old herring. The dominant species were *H. aduncum* in the 0-group, *C. lingua* in 1–2-year-old herring (closely followed by *H. luehei*), and *A. simplex* in fish 3 years or older. Larval helminths constituted 100% of the individuals in 0-group, about 50% in the 1–2-year-old herring and 90–95% in those 3–4 years old. In older herring (5–12 years), larvae represented >99% of all metazoan endoparasite individuals, *A. simplex* representing 99.9% of these. Gastrointestinal helminths were represented by a total of four species. Gut parasites were not found in the 0-group fish examined, but were common in 1–2-year-old herring with an average of 1.0–1.1 species. In 3-year-old fish there were 0.3 gastrointestinal parasite species per individual, and this declined further to close to 0 in 5–12-year-old herring.

Discussion

Ichthyophonus hoferi, a fungus-like ichthyosporean parasite that produces systemic infections, has previously been reported from the NSS herring (Hjeltnes and Skagen, 1992; Karaseva *et al.*, 1993a,b, 1995; Hodneland *et al.*, 1997; Holst *et al.*, 1997). The coccidian *Eimeria sardinae* occurs in testes of Barents Sea and White Sea herrings (Shulman and Shulman-Albova, 1953; Polyanskii, 1955; Polyanskii and Shulman, 1956; Shulman, 1956), but is more prevalent in North Sea and Baltic stocks (Kabata, 1963; Gaevskaya, 1977; Turovsky *et al.*, 1993). Prevalences in the NSS herring are intermediate between these two main areas. In North Sea and NW Atlantic herring, *E. sardinae* infections are particularly associated with sexual maturity in males, infections in immature (1–2-year-old) herring being rare (Kabata, 1963; McGladdery and Burt, 1985). Our findings corroborate such a pattern of infection, but the prevalence in NSS herring (at age) is lower. *Goussia clupearum* infects the liver tissue of 16 unrelated fish species (cf. Daoudi *et al.*, 1989; Diouf and Toguebaye, 1993; Karlsbakk *et al.*, 2000; Azevedo, 2001), with certain pelagic clupeid, scombrid and gadid fishes being common hosts in NE Atlantic waters including Norway. This parasite has not been recorded from Barents Sea and White Sea herring, but was found by Karasev (1990) in Barents Sea and Norwegian Sea blue whiting [*Micromesistius poutassou* (Risso, 1826)]. The present records are the northernmost known from herring. In herring, *G. clupearum* prevalence typically increases with host age (Kabata, 1963), but there may be a decrease in prevalence in older fish. *Ceratomyxa* infections occur in White Sea herring, *Clupea pallasii marisalbi* Berg, 1923, but have been identified as *C. orientalis* (Dogel', 1948) (Shulman, 1953; Shulman and Shulman-Albova, 1953). *Ceratomyxa orientalis* from herrings (*Clupea* spp.) in the Atlantic and Pacific is morphologically distinct from *C. orientalis* sensu Dogel' (1948) (cf. Arthur and Arai, 1984) so it is likely that *Clupea* spp. in these areas are infected with a single species, *C. auerbachi* Kabata, 1962. *Ceratomyxa auerbachi* was reported from coastal herring caught near Bergen, W Norway, by Auerbach (1909) [as *C. sphaerulosa* Thélohan, 1895 see Kabata (1962)]. Therefore, *C. auerbachi* infections in coastal NSS herring from northern Norway were to be expected. Myxozoan life cycles involve benthic invertebrates as intermediate hosts, so transmission in oceanic waters over great depths seems unlikely. The absence of *Ceratomyxa* spores in NSS herring in its oceanic phase (feeding areas) may reflect parasite adaptation to transmission when close to the substrate. The crowded conditions in the wintering areas, where we found herring with *C. auerbachi* spores in their bile, could provide good opportunities for transmission.

Prevalence of *Cryptocotyle lingua* metacercariae ("black spot disease") was highest in the 1983 and 1988 year classes (>20%), ca. 10% in the 1989 year class and <5% in 1990–92 year class herring. Since *C. lingua* cercariae are dispersed from intertidal snails (*Littorina* spp.), infected herring must have visited shallow waters in the warmer part of the year (i.e. summer and early autumn). Our sample 446 represent such fish, with a *C. lingua* prevalence of 57% in herring of the 1991–92 year classes. The spawning stock is not exposed to this parasite, since it only resides in nearshore waters when wintering and spawning. The nursery area of NSS herring extends from about 60°N on the west coast of Norway to ca. 80°N in the Barents Sea. Barents sea juveniles have slower growth and spend 3–5 years in the nursery areas, while fish from the Norwegian west coast leave at an age of 1–2 years (de Barros and Holst, 1995). Since NSS herring cannot become infected with the parasite offshore in the Barents Sea, *C. lingua* prevalence in 3+ fish should reflect the proportion spending their juvenile period in coastal waters (coastal component). Therefore, the level of *C. lingua* infection suggests a decreasing coastal component from the 1983 and 1988 year classes compared to the 1990–92 spawned fish. Following the arguments above, findings of live *C. lingua* metacercariae in the skin of 1983 year-class herring in summer 1995 (unpubl.), suggests that the longevity of these metacercariae in NSS herring may be 8 years or more. Gastrointestinal trematodes, chiefly the clupeid specialist *H. luehei*, occurred only in a coastal sample of 1–2-year-old herring. The life cycles of *Hemiurus* spp. involve a benthic opisthobranch as first intermediate host, which release cystophorous cercariae that infect planktonic copepods (Køie, 1990, 1995). Therefore, NSS herring should only become infected in coastal waters. Since mature herring generally do not feed when wintering, migrating to spawning areas and when spawning (Slotte, 1999), infections with these trematodes seem to be restricted to juvenile herring in coastal nursery areas. The lack of *H. luehei* in 3+ fish also indicates that the life span of the parasite is short.

Hysterothylacium aduncum is a common parasite of NE Atlantic marine fishes (Punt, 1941; Polyanskii, 1955; Berland, 1961), and occurs in herring throughout its range (Arthur and Arai, 1984; MacKenzie, 1987). In herring, it may occur both as encapsulated III-stage larvae on the viscera, and as maturing and mature nematodes in the gut (Punt, 1941; Hartwich, 1975). In most fish species studied, larvae tend to accumulate with host size/age. In the NSS herring (this study), there was an initial accumulation in immature herring (0–4 years old), while the parasite was virtually absent in mature fish. Roskam (1967) found the same pattern in North Sea herring, and he interpreted the disappearance of *H. aduncum* III larvae in older herring as possible evidence for 70–95% parasite-induced mortality. However, such an interpretation assumes a long life span of the *H. aduncum* larvae. Khalil (1969) demonstrated that encapsulated *H. aduncum* larvae are eventually killed and degraded in herring, and that such parasite mortality probably accounts for the disappearance of the larval nematode in older herring. Lumenal infections with *H. aduncum* in our material showed similar age-dynamics to the larvae (Figure 2). Our results suggest that in the feeding areas in the Norwegian Sea, there is virtually no transmission of this nematode to herring. Acquisition appears to be largely restricted to coastal waters, where the mature part of the stock is wintering, migrating or spawning and do not feed. The opportunity for these to acquire the infection is therefore slight, and nematodes acquired as juveniles are largely lost before the fish becomes sexually mature.

Anisakis simplex larvae in NE Atlantic fish may belong to two sibling species, which cannot be separated by morphology. According to Mattiucci *et al.* (1997) larvae in fish from the Baltic-, North- and Norwegian Seas belong to *Anisakis simplex* sensu stricto. *Anisakis simplex* larvae are acquired through feeding on euphausiacean intermediate hosts (Smith, 1983). We found a larva in a 59 mm long 0-group fish, which probably is too small to be able to devour even small *Thysanoessa*. Free *A. simplex* larvae have occasionally been detected in zooplankton samples (Karasev, 1993; Køie, 2001), and represent a way that such small fish may become infected (see also Køie, 2001). Abundance of *Anisakis* increases with host age and length, reflecting accumulation of a long-lived parasite with age. Unlike the other helminths, *Anisakis* abundance increases also in mature herring (Figure 2). This reflects the presence and transmission of this parasite also in the feeding areas.

When considering abundance, the parasite assemblage of the NSS herring is similar to that of other N Atlantic marine stocks (Polyanskii, 1955; Reimer and Jessen, 1972; McGladdery and Burt, 1985). Notable is the apparent absence of *Renicola* metacercariae and *Lacistorhynchus* metacestodes, used as biological tags for several North Sea and British stocks (MacKenzie, 1985). Also, *H. luehei* is absent in the NW Atlantic.

In Baltic herring 31 parasite species have been recorded, in the Barents and White Seas 33 and in the North Sea 23 (MacKenzie, 1987). The NSS herring is known to be infected by 16 species; in addition to the 11 reported in this study, Karlsbakk & Nilsen (1993) and Karlsbakk *et al.* (2000) recorded *Trichodina* sp.

Gyrodactylus harengi Malmberg, 1957, *Gyrodactyloides baueri* Kulachkova, 1970 and *Contracaecum* sp. larvae from NSS herring, and small (40–100 μm) unilocular metacestodes may occur in the caeca of 0-group NSS herring (Karlsbakk, unpublished). In addition come *Ichthyophonus* infections, not considered by MacKenzie (1987). Some common herring parasites, *Derogenes varicus* (Müller, 1784), *Brachyphallus crenatus* (Rudolphi, 1802) and *Lecithaster* spp. (Arthur and Arai, 1984; MacKenzie, 1988), occur along the Norwegian coast in other fish species. The absence of these in our samples probably reflects the limited number of young NSS herring examined from coastal waters.

The common endoparasites in juvenile NSS herring are *Hemiurus luehei*, *Cryptocotyle lingua* metacercariae and *Hysterothylacium aduncum*. *Hemiurus* and *Hysterothylacium* disappear with age, while prevalence of the coccidians and the intensity of *Anisakis* increase. Thus NSS herring act as a final host to endohelminths only when young. Endohelminths in mature NSS herring are virtually exclusively larval stages of generalists. It may transmit *C. lingua* to piscivorous birds throughout life, but probably predominantly when young (and small). In the feeding areas, it acts as a paratenic host for *Anisakis simplex*, probably being a major source of *Anisakis* infection in toothed whales such as killer whales (*Orcinus orca*).

With the possible exception of the coccidians and *Ceratomyxa auerbachi*, which have unknown life cycles, and *C. lingua* whose cercariae directly penetrate the fish in shallow waters, all NSS herring parasites detected are acquired through feeding on zooplankton. Polyanskii (1955, 1958) stated that helminth faunas of pelagic planktivorous fishes tend to be species poor and with low intensities. This is particularly evident for mature NSS herring, which however can have high *Anisakis* intensities (Polyanskii, 1955). Juveniles of the coastal component are exposed to additional helminths whose life cycles involve benthic hosts. Following this, it is to be expected that local fjord stocks have richer parasite communities than NSS herring.

Acknowledgements

This study was supported by grants from The Nordic Academy for Advanced Study (NorFa) (A.T.) and by the Norwegian Research Council project No. 121117/120 (E.K.).

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