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FEATURE ARTICLE

Parasite faunas of farmed cod and adjacent wild cod populations in Norway: a comparison

Peter A. Heuch[1,*], Peder A. Jansen[1], Haakon Hansen[1], Erik Sterud[1,4], Ken MacKenzie[2], Paal Haugen[3], Willy Hemmingsen[3]

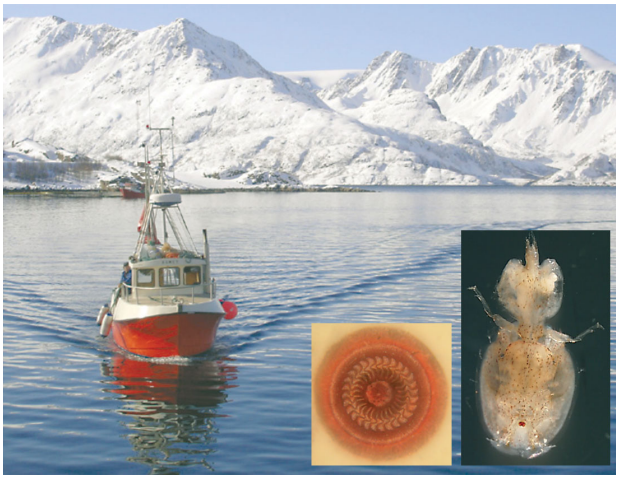
[1]National Veterinary Institute, PO Box 750 sentrum, 0106 Oslo, Norway

[2]University of Aberdeen, Aberdeen, Scotland, UK

[3]Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, University of Tromsø, 9037 Tromsø, Norway

[4]*Present address:* Norske Lakseelver, PO Box 9354 Grønland, 0135 Oslo, Norway

ABSTRACT: Atlantic cod *Gadus morhua* L. is host to more than 120 parasite species. Background abundance of these parasite species on adjacent wild hosts determines the infection pressure on cod farmed in open pens. In 2006, 2007 and 2008, 343 cod were collected from 4 locations along the coast of Norway: Øksfjord, Kvarøy, Brønnøysund and Ålesund. Freshly killed wild local cod, wild migratory cod, hatchery-reared farmed cod and wild-caught farmed cod were given a complete autopsy according to a standardized protocol. A total of 343 cod were examined, from which 48 parasite taxa, including 37 named species, were recorded. Wild local cod had the most diverse parasite fauna. Wild-caught farmed cod had a more diverse parasite fauna than the wild migratory cod, and the latter had 2 more parasite taxa than the hatchery-reared cod. The most common parasites in hatchery-reared cod were the digenean *Cryptocotyle lingua*, the monogenean *Gyrodactylus marinus* and the protozoans *Spironucleus torosa* and *Trichodina* spp. Other parasites occurring frequently in hatchery-reared cod were the parasitic copepod *Cresseyus confusus*, the myxosporean *Zschokkella hildae* and the nematode *Hysterothylacium aduncum.* The nematode and digenean fauna of the hatchery-reared fish was sparse compared to wild cod and the wild-caught farmed cod. Caligid copepods were very rare on the hatchery-reared cod. These results support the hypothesis that food-borne parasites, such as nematodes and mature stages of digeneans, are most unlikely to become a health problem for farmed cod, and that parasites with simple life cycles and pelagic transmission stages, such as monogeneans and trichodinids, may dominate the parasite fauna of farmed cod in the future



Wild and farmed cod *Gadus morhua* were sampled at Øksfjord, Norway. Insets: ectoparasites *Trichodina* sp. (left) and *Caligus* sp. (right). *Photos:* Erik Sterud, Ken MacKenzie

KEY WORDS: *Gadus morhua* · Cod farm · Parasites · Transmission · Wild cod

INTRODUCTION

Parasites may move freely between farmed fish kept in net pens and adjacent wild fish populations. The background prevalence and intensity of the different parasite species determines the infection pressure on net-penned populations, especially of naïve juvenile

*Email: peter-andreas.heuch@vetinst.no

fish. Knowledge of the natural infection levels is essential for parasite control as well as for assessment of parasite transfer rates from farms into the environment and for public management of marine farming activity.

Atlantic cod *Gadus morhua* L. is host to more than 120 parasite species (Hemmingsen & MacKenzie 2001, MacKenzie & Hemmingsen 2003). Some of these will infect the cod in the farm, and eventually, depending on the life cycle of the parasite, may represent a source of infection for wild cod. It is not yet known, however, which parasites will create problems and which will be present but will remain harmless. Along the Norwegian coastline there are many wild local cod populations, and migratory cod feeding on offshore banks enter the fjords to spawn (Larsen et al. 1997, Robichaud & Rose 2004, Sarvas & Fevolden 2005). These populations are natural reservoirs for parasites which may infect farmed cod. Research on assemblages of wild fish around Norwegian salmon farms shows that these are dominated by gadids. Atlantic cod and saithe *Pollachius virens* in particular are likely to act as reservoirs for parasites because they occur in high numbers in the close vicinity of farms (Dempster et al. 2009).

Commercial cod farming has 4 main phases (Moksness et al. 2004). (1) Eggs are produced and fertilized by brood fish. (2) Hatcheries produce larvae, which are weaned from cultured rotifers and *Artemia* to particulate commercial diets in ca. 4 mo. The larvae are then 5 to 10 g wet weight. (3) The larvae are on-grown to juveniles. These first phases are carried out in tanks supplied with filtered seawater. (4) Juveniles are on-grown in sea cages. The standing stock of Atlantic cod farmed from hatched juveniles in Norway on 31 December 2009 was ca. 18.1 million fish. A varying number of wild-caught cod (length >40 cm) are also on-grown in farms (DFN 2010). The growth and sustainability of the cod farming industry is critically dependent on control of parasites. Norwegian authorities have stated that experience from salmon farming shows that the greatest environmental problems following the domestication of a new aquaculture species are related to transfer of parasites and disease between wild and farmed fish (Anonymous 2003). The transfer of infections between farmed species is also identified as an important area of research, and the importance of establishing basic knowledge on the parasite infection status of wild cod before cod farming grows to a large industry is emphasized. Such information was scarce for Atlantic salmon *Salmo salar* L. before salmon farming grew to become a major industry in Norway, Scotland, Ireland and Canada. This resulted in conflicts between salmon farmers, environmentalists and anglers with respect to the natural levels of the parasitic copepod *Lepeophtheirus salmonis* (Krøyer, 1837) (Pike & Wadsworth 1999, Heuch et al. 2005).

A number of authors have tried to predict which parasites will become important pests in cod farms based on characteristics of the life cycles of different species and on their occurrence in wild cod (Burt & MacKinnon 1997, Hemmingsen & MacKenzie 2001, MacKenzie & Hemmingsen 2003, Bricknell et al. 2006). A feature common to these publications is the prediction that parasites with one-host life cycles will pose the greatest threat to mariculture, as transmission of these will be favoured by the high density of potential hosts within the farm. For cod culture specifically, these include the copepods *Caligus elongatus* and *C. curtus*, species of the monogenean genus *Gyrodactylus*, the protozoans *Cryptobia* sp., *Cryptocaryon irritans*, *Goussia gadi*, *Loma branchialis*, *Pleistophora* sp., *Spironucleus torosa, Trichodina* spp. and species of the genera *Paramoeba* and *Neoparamoeba* (see Burt & MacKinnon 1997, MacKenzie & Hemmingsen 2003, Bricknell et al. 2006). Some parasites with 2 or more hosts in their life cycles have been identified as pests in the culture of other fish, and species related to these have on this basis also been put forward as possible cod disease agents. These include mostly myxosporeans, which have oligochaetes and polychaetes as alternate hosts, and the well-known parasitic copepod *Lernaeocera branchialis*. Finally, it has been hypothesised that ascaridoid nematodes will not be found in farmed cod, as these parasites are absent from the dry pelleted feed used in farms (Hemmingsen et al. 1993). In a recent survey of North East Atlantic cod parasites, 58% of the macroparasite individuals discovered were larval anisakids (Perdiguero-Alonso et al. 2008); thus, a large difference between the parasite faunas of wild and farmed cod may be expected.

This communication presents the results of a parasite screening programme (CODPAR) of wild and farmed cod from the 3 Norwegian counties Finnmark, Nordland and Møre og Romsdal. The aim of CODPAR was to assemble a database of the protozoan and metazoan parasites infecting wild and farmed cod in different parts of the Norwegian coast, to compare the parasite faunas of wild and farmed cod from the same location, to assess the likelihood of parasite transfer between the 2 populations, and to identify those parasites most likely to cause problems in cod culture.

MATERIALS AND METHODS

Collection of cod. During 2006, 2007 and 2008, cod were collected from 4 locations along the coast of Norway: Øksfjord (Finnmark), Kvarøy (Nordland), Brønnøysund (Nordland) and Ålesund (Møre og Romsdal) (Fig. 1). Four different groups of cod were sampled: wild local cod, wild migratory cod (Øksfjord

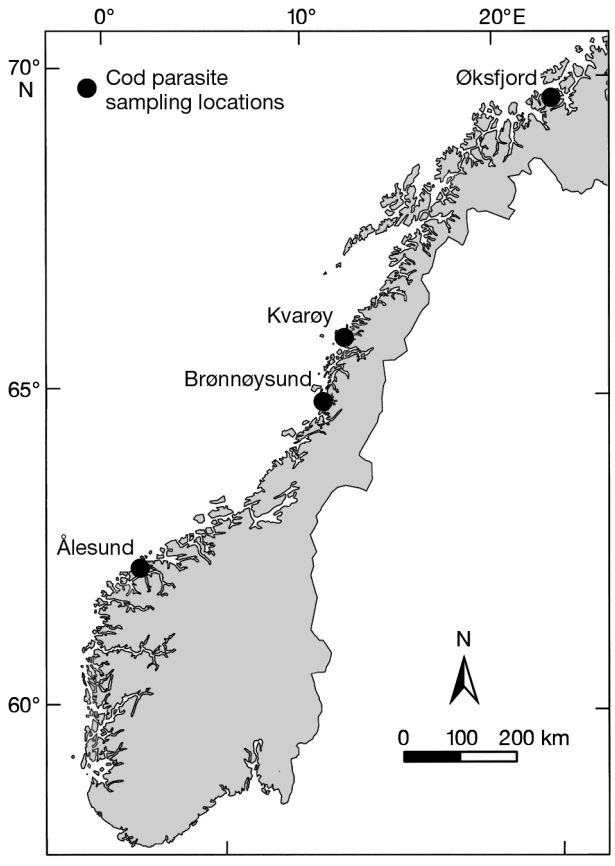


Fig. 1. Cod sampling areas in Norway

only), hatchery-reared farmed cod and wild-caught farmed cod (Øksfjord only). The last category were cod that had been captured in the wild in northeast Finnmark about 1 yr before sampling, held in cages and fed commercial pelleted fish food. The farmed cod were provided by farm staff; wild cod were either caught in traps by local commercial fishermen or by CODPAR partners using hook and line. Wild local cod were not caught in the immediate vicinity of fish farms but in the same area as the investigated cod farms. These fish correspond to 'farm unassociated' fish of Dempster et al. (2011). Øksfjord was sampled in April and October 2006, Kvarøy in June and September 2007, Brønnøysund in August 2006, April 2007 and June 2008, and Ålesund in October 2007 and April 2008.

Examination for parasites. The cod were held alive in tanks of aerated seawater until complete autopsies were carried out according to the following protocol.

(1) Each fish was killed with a sharp blow to the head.

(2) A blood smear taken from the caudal vein was air-dried, fixed in methanol, labelled and stored. For later microscopic examination, the slide was stained with Giemsa, a drop of DePeX mountant was placed on the smear, a 20 × 50 mm coverslip placed over it, and the entire surface was scanned at a magnification of 125×.

(3) A skin smear was taken by scraping a microscope slide along the flank of the cod, which was then scanned under a compound microscope at 100 to 200× magnification.

(4) The following organs were removed, placed in petri dishes under seawater, and scanned under a dissecting microscope at 20 to 40× magnification: the dorsal, ventral and tail fins, plus pectoral and pelvic fins from the left side only; the operculum and jaw from the left side; the nostril from the left side, complete with the olfactory rosette; the eye from the left side; the gill arches from the left side; and the pharynx. Any parasites found were removed and examined under higher magnifications where necessary.

(5) A smear was taken from the gill filaments and scanned under a compound microscope at 200 to 400× magnification.

(6) The abdominal and pericardial cavities were opened and all internal organs, including the swim bladder, removed and isolated. Each organ was scanned under a dissecting microscope at 20 to 40×. Smears were taken from the liver, spleen, gonads, gall bladder, urinary ducts, and from any lesions observed, and examined at 200 to 400×. Samples of gall and urine were extracted with a syringe and scanned under a compound microscope at 200 to 400×. In addition, squash preparations were made from any abnormal tissue from the liver, spleen and gonads and examined at 200 to 400×.

(7) The alimentary tract was divided into stomach, pyloric caeca, fore-, mid- and hind-intestine. Apart from the pyloric caeca, each section was opened longitudinally and examined under a dissecting microscope at 20 to 40×. Some of the contents of the pyloric caeca were squeezed onto a slide and examined at 20 and 200×. Smears from the stomach and intestinal mucosa were examined at 200 to 400×. All metazoan parasites found were removed and placed in watch glasses of seawater. Any unidentified specimens were fixed in 10% formalin for later examination.

(8) Samples of head and rear kidney were squashed on a slide and examined at 200 to 400×.

(9) A scraping from the swimbladder was examined at 200 to 400×.

(10) The head was split longitudinally and the cranial cavity examined under a dissecting microscope at 20 to 40×. A smear was taken from the brain and surrounding fluid and examined at 200 to 400×.

(11) The carcass was filleted and the left side fillets examined by eye over a light box for metazoan parasites or lesions.

(12) The skin from the left side of the fish behind the head was examined for *Cryptocotyle lingua* metacercaria on a light box. The number of metacercaria within a standardised area was counted. If the skin was

more than 9 cm wide, a circular area with this diameter was examined. In smaller fish 25% of this area was examined and the count multiplied by 4. The counts were binned into 4 categories: 1 = 0; 2 = 1 – 10; 3 = 11 – 100; 4 = >100 *C. lingua* metacercaria within the circle.

(13) Representative specimens of each helminth species found were washed in seawater then fixed and preserved in either 10% formalin (for morphological identification) or ethanol (for molecular study). Adult caligid copepods were identified to species in the field laboratory, whereas larvae of this family and all isopods were stored in ethanol for later examination. Only adult female *Clavella adunca* were counted.

(14) The number of *Anisakis simplex* from the surface of the liver was noted.

All compound microscope examinations were carried out using phase contrast.

Parasite identification. As far as possible the parasites were identified to species in the field laboratory using relevant literature. *Caligus* and isopod larvae (Crustacea) and specimens of *Gyrodactylus* (Monogenea) could not be identified to species in the field laboratory. Representative specimens of *Gyrodactylus* and larval *Caligus* and isopods in 96% ethanol were brought back to the laboratory of the National Veterinary Institute for further characterisation.

Larval Caligus and isopods: Larval caligids were identified by DNA sequencing of a fragment of the mitochondrial cytochrome oxidase 1 (CO1) gene and then comparing the obtained sequences to sequences in GenBank. DNA was extracted from 98 specimens using the GeneMole DNA Tissue Kit on a Genemole extraction machine (Molegenetics) and the CO1 sequences were obtained following the protocols outlined by Øines & Heuch (2005). In instances where no sequences were obtained, the parasite was noted as *Caligus* sp. Attempts were made to identify the larval isopods morphologically.

Gyrodactylus: Ethanol preserved gills, fins and pharynx infected with *Gyrodactylus* specimens or individual specimens of *Gyrodactylus* preserved in ethanol were brought back to the laboratory for identification. A sub-sample of individual parasites from the different sites and organs were identified to species level using morphological criteria. The soft tissue of the haptor was digested following the protocol of Harris et al. (1999), and following digestion, the parasites were identified morphologically following Malmberg (1970).

Table 1. *Gadus morhua*. Numbers and types of cod sampled in different areas and mean (±SD) wet weight. WC: wild cod

Sample no.	Area	Date	Category	n	Wet weight (kg)
1	Øksfjord	Apr 2006	Farmed WC	18	2.12 ± 0.66
2			Local WC	19	2.24 ± 0.91
3			Wild migratory	17	3.26 ± 0.53
4		Oct 2006	Farmed WC	17	3.02 ± 0.71
5			Local WC	17	2.09 ± 0.77
6	Brønnøysund	Aug 2006	Hatchery-reared	20	0.38 ± 0.21
7			Local WC	14	1.20 ± 1.32
8		Apr 2007	Hatchery-reared	20	1.12 ± 0.35
9			Local WC	15	1.20 ± 0.48
10	Kvarøy	Jun 2007	Hatchery-reared	20	0.24 ± 0.10
11			Local WC	20	0.50 ± 0.23
12		Sep 2007	Hatchery-reared	20	0.32 ± 0.06
13			Local WC	12	1.06 ± 0.32
14	Ålesund	Oct 2007	Hatchery-reared	16	1.20 ± 0.25
15			Local WC	18	1.22 ± 1.02
16		Apr 2008	Hatchery-reared	20	2.24 ± 0.57
17			Local WC	20	1.92 ± 1.86
18	Brønnøysund	Jun 2008	Hatchery-reared	20	3.16 ± 0.75
19			Local WC	20	1.20 ± 0.72

Table 2. Mean abundance (±SD) of the parasites entered in the multi-dimensional scaling analysis. Data were pooled for season and for samples comprising wild (including local and migratory cod), wild-caught farmed and hatchery-reared cod

Parasite	Wild	Wild-caught farmed	Hatchery-reared farmed
Gyrodactylus callariatis	5.2 ± 11.4	0.3 ± 0.7	1.2 ± 5.8
Gyrodactylus marinus	7.2 ± 41.3	42.2 ± 70.8	33.4 ± 117.4
Gyrodactylus pharyngicus	3.1 ± 14.3	0.1 ± 0.4	0.4 ± 2.1
Cryptocotyle lingua[a]	1.8 ± 1.1	1.1 ± 0.6	1.4 ±1.1
Derogenes varicus	16.8 ± 20.0	20.3 ± 27.8	0.1 ± 0.5
Hemiurus communis	44.0 ± 84.9	0.0 ± 0.0	0.0 ± 0.1
Hemiurus levinseni	1.9 ± 7.5	1.1 ± 2.2	0.0 ± 0.0
Diphyllobothrium phocarum	0.0 ± 0.3	0.1 ± 0.6	0.0 ± 0.0
Anisakis simplex	10.9 ± 26.4	20.1 ± 28.9	0.0 ± 0.3
Hysterothylacium aduncum	8.7 ± 13.3	6.3 ± 33.7	0.2 ± 0.6
Pseudoterranova decipiens	0.2 ± 1.0	0.1 ± 0.4	0.0 ±0.0
Cucullanus cirratus	2.2 ± 4.0	0.0 ± 0.2	0.0 ± 0.2
Echinorhynchus gadi	4.5 ± 10.0	0.7 ± 1.3	0.0 ± 0.3
Caligus spp.	1.2 ± 5.5	0.1 ± 0.2	0.0 ± 0.1
Caligus curtus	0.5 ± 2.0	0.0 ± 0.2	0.0 ± 0.1
Caligus elongatus	0.1 ± 0.5	0.2 ± 0.5	0.0 ± 0.0
Clavella adunca	1.7 ± 2.4	1.7 ± 3.4	0.2 ± 0.7
Cresseyus confusus	4.5 ± 5.6	0.7 ± 1.5	0.9 ±1.9
Lernaeocera branchialis	0.1 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Praniza larvae	0.0 ± 0.2	0.0 ± 0.0	0.0 ± 0.0

[a]Tabulates the mean of 4 categories (see 'Materials and methods') for *C. lingua*

Statistical analyses. Multivariate ordination techniques were used to compare similarities in parasite species composition at the level of 19 different samples of cod (Table 1). All parasite species for which a measure of infection intensity was obtained were entered in the analyses (Table 2). Prior to the analyses, the data for each parasite were reduced to sample mean abundance, with the exception of *Cryptocotyle lingua*, for which the mean of 4 abundance categories was used. Classical metric multi-dimensional scaling (MDS) for dissimilarity in parasite species composition between samples was performed in the STATA (9.2) statistical package. The square of the Minkowski distance metric (L2 squared in STATA) was used as the measure of dissimilarity between samples. Fourth root transformations of sample means were performed and the data were scaled to min. = 0 and max. = 1 prior to computation of dissimilarities. Transformation of the data decreased the stress value of the MDS representation, hence increasing the adequacy of the MDS representation (Appendix A, Primer; http://eprints.utas.edu.au/419/7/07appendix.pdf).

RESULTS

General

A total of 343 cod were examined (Table 1, Supplement www.int-res.com/articles/suppl/q002p001_supp.xls) from which 48 parasite taxa, including 37 named species, were recorded (Table 3). These included one hitherto undescribed species of the protozoan genus *Trichodina* and 2 new host records for cod—the digenean *Lampritrema mieschери* and the nematode *Hysterothylacium cornutum* (see MacKenzie et al. 2009). The subsamples of gyrodactylids were identified by morphological methods as *Gyrodactylus marinus* infecting the gills, *G. callariatis* infecting the skin and *G. pharyngicus* infecting the pharynx (Table 3). In the following, all *Gyrodactylus* from the gills are regarded as *G. marinus*, all *Gyrodactylus* from the skin and fins as *G. callariatis*, and all *Gyrodactylus* from the pharynx as *G. pharyngicus*.

Table 3. *Gadus morhua*. Parasites found and sites of infection

Parasite	Site of infection
Protozoa	
Goussia spraguei Morrison & Poynton, 1989	Kidney
Trichodina cooperi Poynton & Lom, 1989	Skin, fins, gills
Trichodina murmanica Polyansky, 1955	Skin, fins, gills
Undescribed *Trichodina* sp.	Skin
Ichthyobodo sp.	Nares
Unidentified microsporidian	Urinary bladder
Spironucleus torosa Morrison & Poynton, 1989	Rectum
Hexamita sp.	Rectum
Trypanosoma sp.	Blood
Myxosporea	
Myxidium oviforme Parisi, 1912	Gall bladder
Myxidium bergense Auerbach, 1909	Gall bladder
Gadimyxa sp.	Kidney, urinary bladder
Zschokkella hildae Auerbach, 1910	Kidney, urinary bladder
Monogenea	
Gyrodactylus callariatis Malmberg, 1957	Skin, fins
Gyrodactylus marinus Bychowsky & Polyansky, 1953	Gills
Gyrodactylus pharyngicus Malmberg, 1964	Pharynx
Digenea (metacercariae)	
Cryptocotyle lingua (Creplin, 1825)	Skin, fins, gills
Prosorhynchoides gracilescens (Rudolphi, 1819)	Cranial cavity
Otodistomum sp.	Body cavity
Digenea (adults)	
Derogenes varicus (Müller, 1784)	Oesophagus, stomach
Hemiurus communis (Odhner, 1905)	Stomach
Hemiurus levinseni (Odhner, 1905)	Stomach
Lampitrema mieschери (Zschokke, 1890)	Intestine
Lecithaster gibbosus (Rudolphi, 1802)	Intestine
Lepidapedon elongatum (Lebour, 1908)	Intestine, pyloric caeca
Lepidapedon rachion (Cobbold, 1858)	Intestine
Stephanostomum pristis (Deslongchamps, 1824)	Pyloric caeca
Eucestoda (plerocercoids)	
Diphyllobothrium phocarum (Fabricius, 1780)	Body cavity outside pyloric caeca
Grillotia erinaceus Van Beneden, 1858	Body cavity
Tetraphyllidea sp. 1	Pyloric caeca
Tetraphyllidea sp. 2	Intestine
Eucestoda (adults)	
Abothrium gadi Van Beneden, 1871	Pyloric caeca, intestine
Nematoda (larvae)	
Anisakis simplex (Rudolphi, 1809)	Body cavity, musculature, liver
Contracaecum osculatum (Rudolphi, 1802)	Liver, body cavity
Hysterothylacium aduncum (Rudolphi, 1802)	Stomach, intestine, body cavity
Hysterothylacium cornutum (Stossich, 1904)	Stomach
Pseudoterranova decipiens (Krabbe, 1878) sensu lato	Musculature
Nematoda (adults)	
Ascarophis filiformis Polyansky, 1952	Stomach
Capillaria gracilis (Bellingham, 1840)	Intestine
Cucullanus cirratus Müller, 1777	Pyloric caeca, intestine
Hysterothylacium aduncum (Rudolphi, 1802)	Stomach, intestine
Hysterothylacium cornutum (Stossich, 1904)	Stomach
Acanthocephala (juveniles)	
Corynosoma sp.	Body cavity
Acanthocephala (adults)	
Echinorhynchus gadi Zoega in Müller, 1776	Intestine
Copepoda	
Caligus curtus Müller, 1785	Skin, fins
Caligus elongatus Nordmann, 1832	Skin, fins
Clavella adunca (Strøm, 1762)	Skin, mouth, pharynx
Cresseyus confusus (Stock, 1953)	Nares
Lernaeocera branchialis (L., 1767)	Gills
Isopoda	
Praniza larvae	Fins

Altogether, 96 adult specimens of *Caligus curtus* and 25 adult *C. elongatus* were found. Sequences of the CO1 gene were obtained from 83 specimens of larval caligids and these sequences identified 77 specimens as *C. curtus*, 5 specimens as *C. elongatus* Genotype 1 and 1 specimen as *C. elongatus* Genotype 2 (Øines & Heuch 2005).

There were marked differences between the parasite faunas of the different groups of cod (Tables 4 & 5). As expected, local wild cod had the most diverse parasite fauna. Wild-caught farmed cod had a more diverse parasite fauna than the wild migratory cod, with the latter having only 2 parasite taxa more than the hatchery-reared cod (Table 5). The most common parasites in hatchery-reared cod were the metacercarial stage of the digenean *Cryptocotyle lingua* encysted in the skin, the monogenean *Gyrodactylus marinus* and the protozoans *Spironucleus torosa* and *Trichodina* spp.

However, the only parasites which were significantly more prevalent on farmed than on wild cod were *Gyrodactylus marinus* and *Trichodina* spp. The prevalences of *G. marinus* on the gills of both wild-caught farmed and hatchery-reared cod were higher than those on local wild cod, whereas the reverse was true for *G. callariatis* on the skin and fins, and *G. pharyngicus* in the pharynx (Fig. 2). However, *G. callariatis* was the only gyrodactylid found on both farmed and wild fish at all sites. *Trichodina* spp. were also clearly more prevalent on both wild-caught farmed and hatchery-reared farmed than on wild cod (Table 4). Other parasites occurring frequently in hatchery-reared cod were the parasitic copepod *Cresseyus confusus* (formerly *Holobomolochus*; see Ho & Lin 2005), the myxosporean *Zschokkella hildae* and the nematode *Hysterothylacium aduncum.* The gall bladder myxosporean *Myxidium bergense* was found at the same low level of prevalence on both wild and hatchery-reared cod (Table 4).

Parasites frequently present in wild cod and rarely in farmed cod included food-borne helminths, but also *Myxid-*

Table 4. *Gadus morhua*. Prevalences (%) of parasite taxa in 3 groups of cod in spring and autumn samples. Local (from all sampling sites) and migratory (from Øksfjord) wild cod are combined in this table. Full species names given in Table 3

Parasite	Wild		Wild-caught farmed		Hatchery-reared	
	Spring	Autumn	Spring	Autumn	Spring	Autumn
Protozoa						
G. spraguei	1	0	0	0	0	0
Trichodina spp.	25	16	56	76	35	46
Ichthyobodo sp.	4	5	0	0	14	5
Microsporidian	7	15	33	29	0	0
S. torosa	70	77	39	47	48	79
Hexamita sp.	1	0	0	0	0	0
Trypanosoma sp(p).	3	0	6	6	0	0
Myxosporea						
M. oviforme	32	34	0	0	6	2
M. bergense	9	5	0	0	9	2
Gadimyxa sp(p).	12	25	0	35	5	5
Z. hildae	27	34	44	41	35	20
Monogenea						
G. callariatis	50	46	22	24	18	29
G. marinus	43	26	100	82	55	61
G. pharyngicus	10	26	6	6	0	14
Digenea						
C. lingua	75	93	94	100	55	79
P. gracilescens	13	15	0	0	1	0
Otodistomum sp.	0	0	6	0	0	0
D. varicus	90	80	56	94	4	5
H. communis	63	57	0	0	0	2
H. levinseni	16	11	0	71	0	0
L. miescheri	1	0	0	0	0	0
L. gibbosus	0	3	0	0	0	0
L. elongatum	11	11	0	0	0	2
L. rachion	3	0	6	0	0	2
S. pristis	0	5	0	0	0	0
Eucestoda						
D. phocarum	2	0	0	12	0	0
G. erinaceus	8	11	0	0	0	0
Tetraphyllidea spp.	14	18	6	82	0	0
A. gadi	2	2	0	0	0	0
Nematoda						
A. simplex	86	87	100	100	1	0
C. osculatum	0	0	0	12	0	0
H. aduncum	63	75	17	41	13	20
H. cornutum	0	0	0	6	0	0
P. decipiens	6	11	17	0	0	0
A. filiformis	1	2	0	6	0	0
C. gracilis	5	5	0	0	0	0
C. cirratus	41	64	0	6	0	2
Acanthocephala						
Corynosoma sp.	0	0	0	12	0	0
E. gadi	54	44	11	47	3	2
Copepoda						
Caligus spp.	26	23	0	12	1	0
C. curtus	16	21	0	6	0	2
C. elongatus	3	11	0	24	0	0
C. adunca	56	49	61	47	24	0
C. confusus	65	82	22	53	36	29
L. branchialis	7	15	0	0	0	0
Isopoda						
Praniza larva	2	7	0	0	0	0

Table 5. *Gadus morhua*. Numbers of different parasite taxa recorded from the different groups of cod

	Wild		Wild-caught farmed	Hatchery-reared
	Local	Migratory		
Protozoa	9	4	6	4
Myxosporea	4	3	2	4
Monogenea	1	1	1	1
Digenea	10	3	5	4
Cestoda	5	2	2	0
Nematoda	6	4	6	2
Acanthocephala	1	1	2	1
Crustacea	6	3	4	3
Total	**42**	**21**	**28**	**19**

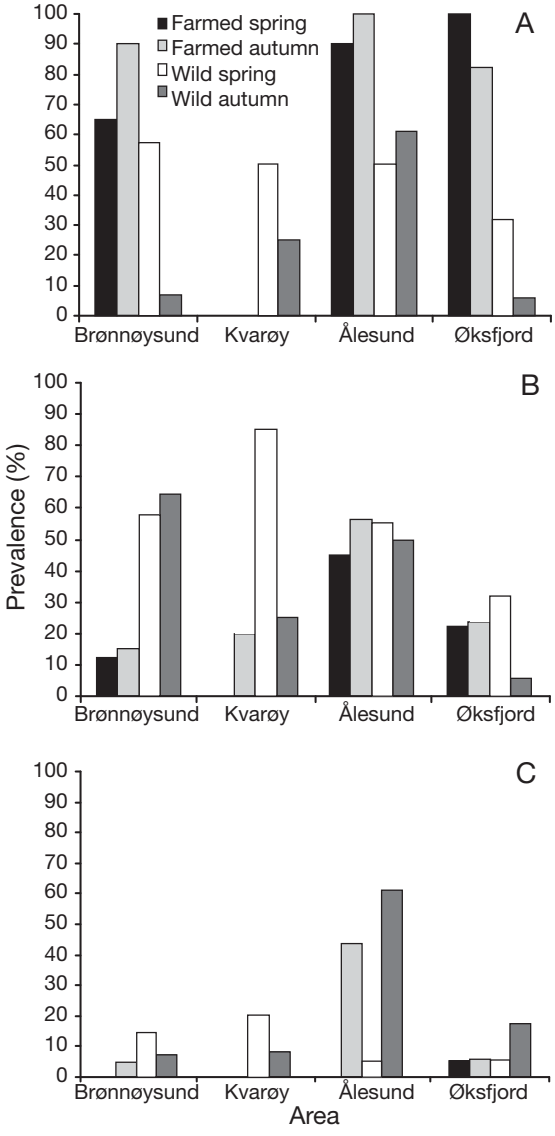


Fig. 2. *Gyrodactylus* spp. on wild and farmed *Gadus morhua*. Prevalence in spring and autumn. In Øksfjord the farmed fish were wild-caught. *Gyrodactylus* on (A) gills (*G. marinus*), (B) skin (*G. callariatis*), and (C) in pharynx (*G. pharyngicus*)

ium oviforme, *Gyrodactylus pharyngicus* and parasitic copepods of the genera *Caligus, Clavella and Cresseyus* (Table 4). Of the parasites with a zoonotic potential, the nematode *Anisakis simplex* was the most abundant at a prevalence of 87% in wild cod and 100% in wild-caught farmed cod (Table 4). Only about 1% of the hatchery-reared farmed fish harboured this worm. No hatchery-reared cod had *Pseudoterranova decipiens*, but this species was found in ca. 10% of the wild cod and 0 to 17% of the wild-caught farmed cod. Parasite prevalences were rarely different between spring and autumn samples in wild cod (Table 4).

Multi-dimensional scaling analyses

Species composition of parasites in samples of wild versus hatchery-reared cod grouped along Dimension 1 in the MDS plot (Fig. 3). Fish category was significantly associated with Dimension 1 coordinates (Spearman rank test, $p = 0.002$, $df = 3$) but not with Dimension 2 coordinates. Neither sample season nor sample location was significantly associated with Dimension 1 or 2 coordinates (Spearman rank tests). Fish weight was significantly correlated with Dimension 2 (Spearman rho = 0.49; $p = 0.03$) but not with Dimension 1. There are qualitative differences between samples sharing low (wild cod) versus high (hatchery-reared cod) Dimension 1 coordinates (Fig. 3). Food-borne infections are practically non-existent in hatchery-reared farmed cod, whereas *Gyrodactylus marinus* tended to be more abundant on farmed than on wild cod (Table 2).

DISCUSSION

General

As mentioned in the introduction, several authors have predicted that parasites with one-host life cycles would pose the greatest threat to the culture of cod and other marine fish (Burt & MacKinnon 1997, Hemmingsen & MacKenzie 2001, MacKenzie & Hemmingsen 2003, Bricknell et al. 2006). The results of our study support this prediction in that the only parasite taxa that were clearly more common on farmed hatchery-reared and wild-caught than on wild cod (both groups) have such life cycles: *Gyrodactylus marinus* on the gills and *Trichodina* spp. on the body surface. The importance of *Gyrodactylus* spp. and *Trichodina* spp. as pathogens of farmed fish is well documented (e.g. Vadstein et al. 2004, Basson & Van As 2006). Furthermore, the nematode and digenean fauna of the hatchery-reared fish was sparse compared to the wild cod and the wild-caught farmed cod (Table 4). An excep-

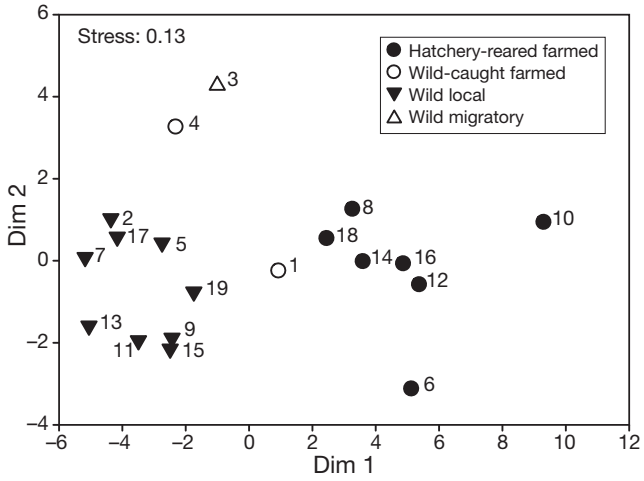


Fig. 3. Multi-dimensional scaling (MDS) plot of dissimilarities of parasite species composition in samples of cod. Different samples are shown according to the category of cod they represent (see key) and according to Dimension 1 (Dim 1) and Dimension 2 (Dim 2) of the MDS scales. Numbers to the right of each data point refer to sample no. in Table 1

tion was *Cryptocotyle lingua* metacercaria, which occurred at high prevalences in all fish groups. A surprising finding was the near absence of caligid copepods on the hatchery-reared cod. The apparent separation of hatchery-reared farmed cod from all wild cod samples along Dimension 1 in the multi-dimensional scaling analysis was due to higher abundances of all entered taxa in wild cod, except for *G.* marinus, where the opposite was true. In the following, these differences are discussed in more detail.

Parasites with direct life cycles

Protozoa

The most common protozoan parasite of both wild and farmed cod was the intestinal flagellate *Spironucleus torosa* (Table 4). Although this species has not been associated with pathological changes in its gadid hosts, another member of the same genus, *S. salmonicida,* has caused systemic disease in farmed Atlantic salmon in Norway (Sterud et al. 1998, Jørgensen & Sterud 2006). *S. torosa* must therefore be regarded as having the potential to be a pathogen of any farmed cod. About 10% of hatchery-reared cod were infected with *Ichthyobodo* sp. *Ichthyobodo* is a genus of flagellate protozoan that is well documented as a serious pathogen of farmed fish worldwide (Woo 2006). A single species, *Ichthyobodo necator,* was originally considered to be responsible for all infections, until Todal et al. (2004) showed that *I. necator* is in fact a complex of sibling species. Callahan et al. (2005) identified a complex of 9 different species with low host specificity, one of which was capable of infecting both marine and freshwater fish. A species of *Ichthyobodo* was reported from cod by Isaksen et al. (2007). Clearly *Ichthyobodo* is a potentially serious pathogen in cod mariculture.

Three species of *Trichodina* were identified from cod in the present study, by far the most common of which was *T. murmanica.* The undescribed species of *Trichodina* is highly distinctive, its most outstanding feature being a much larger number of denticles (about 40) than is usual for *Trichidina* spp. infecting fish. A species possibly identical to this was reported from cod caught off Nova Scotia, Canada, by Poynton & Lom (1989), and from saithe *Pollachius virens* caught off Bergen, Norway, by Nilsen (1993). As in the present study, these authors found too few specimens of this fragile species to allow them to prepare a full description.

Trichodinids are commensals using fish as a substrate (Basson & Van As 2006). They feed on waterborne particles, and thrive in fish farms where such are plentiful. Their movement and growth irritate the fish skin, which reacts by increased mucous production, adding food particles to the water (Basson & Van As 2006). Trichodinids disperse through the water and therefore are expected to be are more prevalent in cod farms, where the possible hosts are closer than in wild fish populations.

The process of capture at depths down to several hundred meters, subsequent transport and stocking in cages is stressful and harms the cod skin. This is a likely reason why wild-caught cod had a markedly higher prevalence of trichodinids in the present survey.

Monogenea

Six species of the genus *Gyrodactylus* have been reported from cod, some of them highly site-specific (Appleby 1994). In this survey, *G. marinus* in particular appeared to be associated with the farming situation (Fig. 2 & Table 4). It is not clear what makes this parasite thrive on the farmed fish, contrary to *G. callariatis* and *G. pharyngicus*, which were more prevalent on wild cod. On some of the sites visited in the course of the CODPAR study the fish had previously shown gill pathology associated with *Gyrodactylus* sp(p). that necessitated chemical treatment.

Parasitic Copepoda

The most common parasitic copepod on hatchery-reared cod was *Cresseyus confusus.* About one-third of the fish were infected at intensities of up to 14 copepods per cod. Karlsbakk et al. (2001) found *C. confusus*

to be the most common metazoan parasite of postlarval cultured cod that had been fed natural plankton, with almost one-third of their cod infected. On the southwest coast of Sweden, a 77% prevalence of this copepod on wild Atlantic cod was found by Linderby & Thulin (1983). Boxshall (1974) reported *C. confusus* from 9 species of marine fish in the North Sea, including some, such as Atlantic cod, saithe *Pollachius virens* and pollack *Pollachius pollachius,* that are commonly found in the vicinity of sea cages of aquaculture fish (Carss 1990, Dempster et al. 2009). It is therefore obvious that this copepod can access farmed cod very easily. Although the pathology of *C. confusus* infections has not been investigated, Kabata (1984) found infected nasal capsules of cod full of opaque, pus-like mucous. He considered that the olfactory function of an infected nose is probably adversely affected. This copepod could therefore be considered a potential health and welfare problem for farmed cod.

The only other parasitic copepod found on hatchery-reared cod at more than a few percent prevalence was *Clavella adunca.* Janusz (1980) reported confusing variations in the relationship between *C. adunca* infection and weight of wild cod, but the only evidence of pathology associated with this parasite is some erosion of the fin margins or the formation of small hyperplastic tumours around their points of attachment (Kabata 1984). Possible sources for this copepod are common coastal fish species such as wild cod, whiting, saithe and haddock (Boxshall 1974, Dempster et al. 2009).

Contrary to the predictions referred to above, hatchery-reared cod carried only 0 to 1% *Caligus* spp., and *C. curtus* was much more abundant than *C. elongatus*. It must be noted that the hand netting in farms, subsequent transport and storage in tanks before examination would most likely have dislodged some of the highly agile *C. elongatus* (Neilson et al. 1987, Øines et al. 2006). Thus, the prevalence of adult lice may have been reduced, but the sessile chalimus stages, which are anchored to the fish skin by a chitinous thread (Pike et al. 1993), would have remained. Had the *Caligus* population been large, a high number of chalimus larvae would have been found on the farmed hosts. This was, however, not the case.

Parasites with indirect life cycles

Parasites with complex indirect life cycles involving developmental stages in 2 or more different hosts are usually adapted to low host densities and can persist in a population of farmed fish only if all the other hosts necessary for the completion of their life cycles are present in the immediate vicinity of the farm site. Given this scenario, however, many such parasites can become serious threats to farmed fish.

Myxosporea

Myxosporeans are amongst the most serious pathogens of farmed fish (Alvarez-Pellitero & Sitja-Bobadilla 1993, Rigos et al. 1999). At least 4 species were found in both wild fish groups and in hatchery-reared cod in the present study (*Gadimyxa* may include 2 species, see Køie et al. 2007). The most important factor that will determine whether or not these myxosporeans will become problems in cod mariculture is the nature of their life cycles. All life cycles of myxosporeans infecting freshwater fish and those of the few marine species so far described have included an alternate invertebrate host in the form of an oligochaete or polychaete, but direct fish-to-fish transmission has also been confirmed for the pathogenic marine myxosporean *Enteromyxum leei* (see Sitjà-Bobadilla et al. 2007). *E. leei* and other species of *Enteromyxum* were originally assigned to the genus *Myxidium,* to which they are closely related. This raises the possibility that the 2 *Myxidium* species found in the gall bladders of cod in the present study may also be capable of direct fish-to-fish transmission. This possibility is of practical importance because *Myxidium,* like *Enteromyxum,* is a genus that includes species pathogenic to marine fish (Shotter 1970, Feist & Bucke 1992, Al-Jahdali & El-Said Hassanine 2010)

Zschokkella hildae was the most common myxosporean in hatchery-reared cod in the present study and was found at the same prevalence in both wild and hatchery-reared cod. Holzer et al. (2010) reported 100% prevalence of *Z. hildae* infection in 45 Atlantic cod sampled from a culture facility in Scotland. No *Zschokkella* species infecting the kidneys and urinary bladders of fish has been associated with any pathological effects, but damage to the gall bladder and hepatic ducts due to *Z. russelli* was described by Davies (1985). *Gadimyxa* infections were rare in hatchery-reared cod. While no pathogenicity has been reported associated with *Gadimyxa*, the closely related genus *Parvicapsula* includes 2 species that are serious pathogens of both wild and farmed salmonids (Sterud et al. 2003, Bradford et al. 2010).

Digenea

The only digenean to be found commonly on hatchery-reared cod was the metacercarial stage of *Cryptocotyle lingua.* Cod and many other inshore species of fish serve as second intermediate hosts for this parasite, which is the agent of the condition known as 'black-spot'. Farmed fish become infected with *Cryptocotyle lingua* when cages are sited close to rocky shores with large populations of the mollusc first intermediate host, the periwinkle *Littorina littorea,* from which large numbers of infective cercariae emerge to seek out a fish

host. The cercariae penetrate the skin of the fish and encyst in the subcutaneous tissues, while the fish reacts by depositing melanin pigment around the cysts. The usual final hosts are seagulls, which tend to be attracted to fish farm sites, so that the coexistence of large numbers of periwinkles, fish and seagulls guarantee a high rate of transmission for this parasite. The design of the fish cages can also be a factor in determining the infection pressure of *C. lingua.* Lysne et al. (1998) found that cod held in cages close to the surface became infected with significantly more cysts of *C. lingua* than those held in cages lower in the water column.

The problems caused by this parasite are not so much related to its effects on fish health, but to the spoilage effect of heavy infections, with fillets being rendered unmarketable as a result. However, pigmented cysts may develop in the cornea of the eye, which may impair sight at high intensity infections.

Cestoda

No adult cestodes were found in hatchery-reared fish, but plerocercoid larvae of *Grillotia erinaceus* and tetraphyllideans were common in wild-caught farmed and wild cod. The final host of *Diphyllobothrium phocarum* is the bearded seal *Erignathus barbatus* (see Polyansky 1955). This seal has an arctic distribution, which accounts for the occurrence of the larvae only in cod from Øksfjord. Final hosts of tetraphyllidean cestodes are elasmobranch fish; cod and other teleost fish become infected by eating infected invertebrate intermediate hosts.

Nematodes and Acanthocephala

The most common nematode found in hatchery-reared cod was *Hysterothylacium aduncum,* which occurred as 4th-stage larvae and adults in the alimentary tract at a prevalence of 15.4%. No serious pathology has been reported to be associated with infections of this nematode.

The adult acanthocephalan *Echinorhynchus gadi* is one of the most common parasites of cod and other gadid fish, but it was found in only 3 hatchery-reared cod. Again, this must be ascribed to the artificial diet of the fish. To become infected, farmed cod would have to eat the mainly benthic crustacean intermediate hosts (Marcogliese 1994), and it is apparent that most cod do not have access to such food items. The 3 infected cod in the present study may have eaten crustaceans such as amphipods off the cage net.

Helminths in cod farms

Intestinal digeneans, cestodes and acanthocephalans were absent or nearly absent in farmed hatchery-reared cod. This translated to the mean abundance of these parasites being negatively correlated with Dimension 1 in the MDS analysis, indicating that the origin of the fish explains the occurrence of these parasites. These worms have intermediate stages in fauna which must be consumed by the cod for this to become infected. Farmed cod eat pellets of formulated feed and are prevented from foraging on bottom fauna and most pelagic food organisms by the net pen. Wild-caught cod were most likely infected with such worms before they were stocked in the pens, and were found to have a worm prevalence intermediate between hatchery-reared cod and wild cod (Table 4, Fig. 3). The results are thus congruent with the experimental results of Hemmingsen et al. (1993), where new infections with ascaridoid nematodes in wild-caught cod were not detected after they had been put in cages.

Parasitic Crustacea

The only parasitic copepod found in the present study which has a life cycle involving an obligate intermediate host is *Lernaeocera branchialis*. This copepod has been considered by some to be the most serious metazoan pathogen of cod (Hemmingsen & MacKenzie 2001, Brooker et al. 2007). In the present study only one farmed cod, from the wild-caught group, was infected, but in wild cod from 7 to 15% prevalence was recorded. The larvae and adult males of *L. branchialis* infect the gill filaments of other of teleost species, mainly flatfish such as flounder *Platichthys flesus* L., plaice *Pleuronectes platessa* L. and lemon sole *Microstomus kitt* Walbaum, which serve as intermediate hosts (Kabata 1979). In the north of Norway and in Newfoundland, Canada, the lumpfish *Cyclopterus lumpus* L. has taken the role of intermediate host (Templeman et al. 1976). The lumpfish is not a permanent part of the coastal fauna in Norway, but lives most of its life pelagically in the open ocean (Bjelland & Holst 2004). It is therefore likely that the *L. branchialis* infection pressure from this intermediate host is much lower in the coastal zone in northern Norway than in southern areas, where flounder and plaice are more permanent coastal residents (Froese & Pauly 2009).

Noteworthy absentees and unfulfilled predictions

Among the parasites mentioned in the 'Introduction' as having been predicted to become serious threats to cod mariculture are the copepods *Caligus elongatus*, *C. curtus* and *Lernaeocera branchialis,* and the protozoan *Loma branchialis* (Burt & MacKinnon 1997, Hemmingsen & MacKenzie 2001, MacKenzie & Hemmingsen 2003, Bricknell et al. 2006). Lumpfish *Cyclopterus lumpus* is a major host for *C. elongatus* (Box-

shall 1974, Heuch et al. 2007). It is possible that the very low *C. elongatus* infection and absence of *L. branchialis* on farmed cod is at least partly due to the farm cages being remote from the lumpfish habitat. Lumpfish spawn in kelp forests along the North Atlantic shores (Daborn & Gregory 1983) in spring, and the spent females return to the open ocean before summer to feed on plankton (Bjelland & Holst 2004). Mitamura et al. (2007) tracked female lumpfish spawners caught in the Øksfjord, one of the sampling sites in the present study, and found that these fish do not stay more than a few hours around farm sites but travel quickly out of the fjord after tagging and release in the inner fjord. Adult males guard the eggs until they hatch about 60 d after spawning, and they then leave the coast (Bjelland & Holst 2004). If spawning occurs in the fjord, adult males could therefore be a possible source of *C. elongatus* and *L. branchialis* females in the migration and guarding periods. However, the low prevalence of the former and absence of the latter suggest that the transmission of these to farmed cod from lumpfish is limited.

That *Caligus* larvae were found on only a few percent of hatchery-reared fish is particularly difficult to explain given that such larvae were found on >20% of wild cod caught in the vicinity of the farm sites, and on ca. 25% of the adults (Table 4). Both *C. elongatus* and *C. curtus* can use a range of wild fish species as hosts (Boxshall 1974, Heuch et al. 2007) and should thus be able to seed the waters near the farms with infective stages. Some loss of adults of this species will occur during sampling, but that will be true for all fish groups. This suggests that some aspect of the hatchery-reared cod or their environment may act in a deterrent fashion for *C. elongatus*. Dempster et al. (2011) investigated the copepod parasite abundance of cod sampled at (farmassociated = FA) and distant from (unassociated = UA) salmon farms in Norway. In Øksfjord they found a higher abundance of caligids on FA cod; however, this was not always the case in farms further south. The present data shows the opposite pattern: fewer cod in the cod farm carry lice than do wild cod. Dempster et al. (2011) also found that the abundance of *Loma branchialis* was lower on cod caught at salmon farms, which is congruent with the lack of *L. branchialis* in cod farms in the present survey.

Khan (1988) found that both naturally and experimentally *Loma branchialis*-infected cod are more likely to die when stressed than uninfected fish of the same size. It is plausible, therefore, that the absence of this parasite on wild-caught farmed cod is due to infected fish having succumbed on capture and transport. The presence of infected intermediate hosts in the vicinity of farm cages is necessary for the transmission of the fertilized female *L. branchialis* to farmed cod. Such a situation obviously did not occur at the sites visited during the present study, but under conditions favourable for its transmission, it must still be considered a potential threat to farmed cod.

Thus, *Loma branchialis* is a potential pathogen in both hatchery-reared and net pen-cultured cod in Newfoundland (Khan 2005). *L. morhua* has been identified in up to 100% of Atlantic cod at aquaculture sites in Atlantic Canada and has also been observed in cod at aquaculture sites in Iceland (A. Frenette, Department of Biology, University of New Brunswick, pers. comm.; M. Eydal, Institute for Experimental Pathology, Keldur, Reykjavik, pers. comm.). However, neither were found in wild or farmed cod in the present study. As far as we know, no study has yet examined the geographical range of these 2 *Loma* species. The present study did not include a survey of *Loma* occurrence in cod using molecular tools and it is thus possible that this parasite is present on the Norwegian coast. However, as abnormal outgrowths and cysts within gills and internal organs were examined, it is not likely that heavy *Loma* infections on the sampled fish were overlooked. We conclude that *Loma* sp. is not abundant on Atlantic cod in the sampled areas.

Summing up, the most common parasites in hatchery-reared cod were the digenean *Cryptocotyle lingua*, the monogenean *Gyrodactylus marinus* and the protozoans *Spironucleus torosa* and *Trichodina* spp. The nematode and digenean fauna of the hatchery-reared fish was sparse compared to those of the wild cod (local and migratory) and the wild-caught farmed cod, and caligid copepods were very rare on the hatchery-reared cod. These results support the hypothesis that food-borne parasites such as nematodes and mature stages of digeneans will most likely not become a health problem for hatchery-reared farmed cod, and that parasites with simple life cycles with pelagic transmission stages such as monogeneans and trichodinids may dominate the parasite fauna of farmed cod in the future.

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