

Diseases of gadoid fish in cultivation: a review

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Given the rapid development of intensive culture systems for cold-water marine gadoids such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), hake (*Merluccius* spp.), and ling (*Molva molva*), an urgent need exists to examine likely threats posed by disease in intensive gadoid culture. While little is known about diseases that may affect or be introduced by cold-water marine gadoid fish once the animals are brought into intensive commercial culture systems, certain risks can be inferred both from an examination of disease problems experienced during the introduction of intensive culture systems for other cold-water marine species and from an examination of the existing literature on gadoid pathogens. This paper provides an overview of the potential disease risks associated with the development of intensive gadoid aquaculture and focuses on previously characterized diseases that the authors consider as posing the greatest threat to intensive gadoid culture. In addition to disease risk, this paper discusses risk reduction, including vaccination strategies and the risk of inter-species infection. Specific viral, bacterial, fungal, protozoan, and metazoan pathogens are discussed in light of their previous implication in the causation of disease in cultured gadoids or other cold-water species, their occurrence and pathogenicity in wild gadoids, and with respect to life strategies and biology that may favour their propagation within intensive aquaculture systems.

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Introduction

Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.) are species recently introduced into aquaculture. Other closely related fish, namely hake (*Merluccius* spp.) and ling (*Molva molva*), are currently in the “demonstration” phase of development, whereby the animals’ commercial potential is being evaluated in research institutes. While the former species are common at the fishmonger and popular across northern Europe (Bowden *et al.*, 2003), the data available for these species from the research environment are extremely scarce. Consequently, little is known about the diseases that may affect or be introduced by cold-water marine gadoid fish once the animals are brought into intensive commercial culture systems. Risks, however, can be inferred both from an examination of disease problems experienced during the introduction of intensive culture systems for other cold-water marine species and from an examination of the existing

literature on gadoid pathogens. This paper provides an overview of the potential disease risks associated with the development of intensive gadoid aquaculture.

It is informative to look at the experience of other species. Since both Atlantic cod and haddock are cold-water marine species, the majority of this information will be derived from salmonid culture. The developing gadoid industry can use existing knowledge to avoid problems encountered at the start of commercial salmonid farming. At that time, production rapidly outstripped disease management strategies, allowing some diseases such as furunculosis to seriously impede the development of the industry (Grave and Nafstad, 1995; Grave *et al.*, 1996). This situation led to an effective stalling of the industry, while, throughout the 1980s and early 1990s, antibiotics were increasingly employed to control disease. It was not until the introduction of an effective vaccine in 1994 (Bricknell and Ellis, 1993; Grave *et al.*, 1996) that furunculosis was successfully controlled, leading to a decline in the

use of antibiotics (Grave *et al.*, 1996) and an improvement in fish welfare through reduced disease and clinical interventions. Marine fish also suffer increased risk of disease as a result of prolonged larval development, during which time their immature immune systems leave them more prone to infection than metamorphosed individuals. Early larval death may reflect a variety of factors, including nutritional and environmental conditions, but infectious disease (e.g. Infectious Pancreatic Necrosis Virus (IPNV) and *Vibriosis*) may play a major role. Recent work has suggested that the microbial gut flora is also very important in influencing larval survival (Verner-Jeffreys *et al.*, 2003, 2004), as is good hatchery hygiene and the application of good biosecurity procedures within the hatchery. Currently lacking in the research of gadoid diseases is an investigation of techniques to manage these diseases in culture, including the instatement of effective preventative measures and the development of vaccine strategies to reduce the risk of devastating disease outbreaks, occurring either in the hatchery or in a growing environment.

Disease risks, risk reduction, and species interactions

Many experimental trials have been conducted on cultured cod in an attempt to establish their susceptibility, or resistance, to the common diseases of aquaculture animals in northern Europe and North America. A précis of this research is presented in Table 1.

Atlantic cod have been shown to be susceptible to marine rhabdoviruses such as viral haemorrhagic septicaemia virus (VHSV; Snow *et al.*, 2000). However, susceptibility is only associated with VHSV isolates from Atlantic cod, and only when directly injected into the animal. Elsewhere, work has shown that the bacterium *Vibrio (Listonella) anguillarum* is also a potential pathogen of Atlantic cod (Jones *et al.*, 2000). Variation in serotypes complicates the picture of susceptibility. Work on serotypes 01 and 02 α has shown that vaccines can be very effective in this species (Buchmann *et al.*, 1993; Larsen *et al.*, 1994; Jones *et al.*, 2000). However, 02 β may be the predominant serotype of marine species such as Atlantic cod (Santos *et al.*, 1995). We have unpublished information indicating serious mortalities attributable to this serotype in Atlantic cod hatcheries. Mortalities have continued beyond the hatchery stage, and this bacterium has been indicated as the principal pathogen in animals of about 100 g.

Many *Caligus* spp. have been shown to infect a wide range of gadoid species currently considered for cultivation (Hemmingsen and MacKenzie, 2001; Karlsbakk *et al.*, 2001). Little is known about the likelihood of transfer of *Caligus* spp. between gadoids and salmonids, and between different gadoids under culture conditions. Given that Atlantic cod are now being farmed in association with haddock and Atlantic salmon, experiments currently in

progress in Scotland are studying the question of transfer between species.

Vaccination

There are many effective vaccines available to control diseases of cultivated fish. Vaccines are normally administered early in the production cycle and, under ideal conditions, can provide protection throughout the growing cycle. Revaccination strategies are also possible in marine finfish culture, and may provide a valuable method for reducing disease risk in long-lived, batch-spawning animals. However, it should be noted that there are no vaccines licensed for gadoids and, currently, they are used under the veterinary cascade system. The routine use of vaccines for List I and List II diseases (as defined by the Office International des Epizooties (OIE)) is not permitted in the European Union (EU), as this may adversely interfere with monitoring exercises to detect evidence of the presence of the pathogen. The legal and preferred control strategy is to eradicate these diseases by withdrawal of fish and implementation of strict hygiene and disease control measures on infected farms. However, vaccination may be a useful measure for reducing risk, and could complement effective hygienic measures on farms. This is particularly true for farms in the coastal zone that share waters and, therefore, also have the potential to share disease. Vaccination against Infectious Salmon Anaemia (ISA) may be authorized in accordance with national contingency plans approved by the European Commission. The purpose of such vaccination would be to protect stocks in unaffected cages on an infected farm or to protect farms that are already stocked and are adjacent to an infected farm, i.e. ring vaccination (Anon., 2000).

For diseases that are not covered under EU List I and List II categories, vaccination is permitted in Europe. However, the current suite of vaccines licensed for use in fish is limited to those developed for salmonids, in particular *Vibrio (Listonella) anguillarum* and *Aeromonas salmonicida*. Nevertheless, it should be remembered that these vaccines are specifically formulated for salmonids, and may not be suitable for gadoids. Recent work with *Moritella viscosa* vaccines has highlighted this problem: this vaccine was developed for salmonids but used experimentally in gadoids and turbot (*Scophthalmus maximus*). In this instance, protection was seen in the gadoid challenge, but the vaccinated turbot failed to develop an immune response to the vaccine (Gudmundsdottir *et al.*, 2004a, b).

Failure to develop antibody mediated immune responses may arise because the immune system of Atlantic cod and haddock are unusual in that a measurable, classical antibody response may not be produced against an antigen (Schroder *et al.*, 1992; Magnadottir *et al.*, 1999a, b, 2001, 2002; Lange *et al.*, 2001). As a consequence, it may not be possible to evaluate a gadoid immune response to a vaccine by standard immunological tests such as Enzyme-Linked

Table 1. Major pathogens associated with cultivated gadoids and salmonids in northern Europe.

Pathogen	Species					Source
	Atlantic cod	Haddock	Atlantic salmon	Sea trout	Rainbow trout	
	Susceptible/resistant					
<i>Aeromonas salmonicida</i> (typical)	S	S	S	S	S	Bernoth <i>et al.</i> , 1997
<i>Aeromonas salmonicida</i> (atypical)	S	S	S	S	S	Schroder <i>et al.</i> , 1992; Wiklund and Dalsgaard, 1998
<i>Vibrio salmonicida</i>	?	?	S	S	S	Schroder <i>et al.</i> , 1992; Hjeltnes and Roberts, 1993
<i>Vibrio anguillarum</i>	S	S	S	S	S	Hjeltnes and Roberts, 1993
<i>Renibacterium salmoninarum</i> (BKD)	?	?	S	S	S	Woo <i>et al.</i> , 2002
<i>Morastella viscosa</i>	S	?	S	?	S	Gudmundsdottir <i>et al.</i> , 2004a
<i>Piscirickettsia salmonis</i>	?	?	S	?	S	Mauel and Miller, 2002; Fryer and Hedrick, 2003
<i>Photobacterium damsela</i> var. <i>piscicida</i>	?	?	S	?	?	Kusuda and Kawai, 1998; Kawakami and Sakai, 1999
<i>Yersinia ruckeri</i> (ERM)	?	?	S	S	S	Stevenson, 1997
Sea lice (<i>Lepeophtheirus salmonis</i>)	R	R	S	S	S	Pike and Wadsworth, 2000
Sea lice (<i>Caligus curtis</i>)	S	?	?R	?R	?R	Hemmingsen and MacKenzie, 2001
Sea lice (<i>Caligus elongatus</i>)	S	S	S	S	S	Pike and Wadsworth, 2000; Hemmingsen and MacKenzie, 2001
IHN	?	?	S	S	S	Hemmingsen and MacKenzie, 2001
VHSV* (GT Ia and Ib)	?R	?R	R	?	S	King <i>et al.</i> , 2001a, b; Dixon <i>et al.</i> , 2003
VHSV* (GT II and III)	S	S	R	?R	S	King <i>et al.</i> , 2001a, b; Dixon <i>et al.</i> , 2003
VHSV* (GT IV) (not found in Europe)	?	?	?S*	?	?	Traxler <i>et al.</i> , 1995
ISAV	R	?R	S	S	S	Hastings <i>et al.</i> , 1999
IPNV	?S	S	S	S	S	Lorenzen <i>et al.</i> , 1995; Dixon <i>et al.</i> , 2003; Bruno, 2004
Nodavirus	S	?S	?R	?	?R	Grotmol <i>et al.</i> , 1997; Starkey <i>et al.</i> , 2001
Salmon pancreas disease virus	?	?	S	S	S	Weston <i>et al.</i> , 1999; Lopez-Doriga <i>et al.</i> , 2001; Desvignes <i>et al.</i> , 2002

Susceptible/resistant: ?, no data; ?S, possibly susceptible; ?R, possibly resistant; R, resistant; S, known susceptible. Although it is recognized that there is one publication (Traxler *et al.*, 1995) that suggests the possible infection of Atlantic salmon with GT IV VHSV from the Pacific coast of Canada, the data in this publication do not fulfil Koch's postulates, nor were the affected fish clinically ill, and subsequent virulence challenges failed to induce the disease in Atlantic salmon.

*VHSV classification is based on Snow's genotyping work (Snow *et al.*, 2004). Briefly, VHSV GT Ia and Ib are the typical freshwater continental VHSV strain and Baltic isolated, which can infect rainbow trout. VHSV GT II and GT III are of northwest Atlantic origin and primarily infect marine species, although they have been reported from marine rainbow trout in the Baltic Sea. VHSV GT IV is the Pacific West Coast of the USA isolate, which infects Pacific herring (*Clupea harengus pallasii*) and has been isolated from Atlantic salmon.

Immunoassay (ELISA) or Complement Fixation Test (CFT).

Risks of inter-species infection

As the diversification of aquaculture continues, it becomes more likely that cultivated gadoids will encounter other species that are undergoing serious outbreaks of clinical disease. Conversely, gadoids may develop serious diseases of their own, which act as a point source of infection for other species. Both of these scenarios may create an environment in which a pathogen may jump between species, allowing the emergence of a new disease aetiology.

The known diseases of gadoids and salmonids (at least the most likely pathogens that gadoids will encounter in multispecies fish farms) are listed in Table 1. The limited research and the relative lack of experience with gadoid species in cultivation may mean that many potential pathogens have yet to be identified. Thus, the potential for the emergence of a new disease, or an existing disease crossing the species barrier, is considerable.

The risk that co-culturing a new species (e.g. gadoids) with other species, including salmonids, could result in the emergence of a disease when: (i) a known pathogen of an existing aquaculture species causes disease in the new species; (ii) a known pathogen of the new species

causes disease in an existing species; (iii) a commensal organism, which causes no disease in an existing species, becomes pathogenic in the new species; and (iv) an unknown pathogen, or a commensal organism of the new species, causes disease in an existing species.

Serious diseases can emerge when an infectious agent succeeds in transferring between species. The highest risk is associated with an agent that becomes so pathogenic that it becomes a threat to the industry. However, some of these diseases are extremely virulent when they first emerge, then become attenuated, which can limit their impact. Alternatively, they may be so virulent that they kill everything in close proximity, restricting pathogen spread to the immediate population. Following emergence, the level of virulence may change significantly (increasing or decreasing) as the pathogen co-evolves with the host (Lenski and May, 1994).

It is not advisable to bring established new or emerging cultivated fish species into proximity with one another if one species is showing signs of disease. This would also apply if one species has previously shown symptoms, as a carrier state may have been established. However, if it is apparent that the other species is not carrying a disease, this usually being an unknown factor for gadoid fish, then co-culture may be acceptable.

Pathogens are most likely to spread between siblings of the same species (Haralambous *et al.*, 2003). This risk reduces proportionally if the movement is between non-siblings, different species of the same genus, and unrelated species. For instance, closely related host species may transfer or exchange pathogens, as is seen when Infectious Salmon Anaemia (ISA) and caligid copepodids are transferred between salmonid populations (Nylund and Jakobsen, 1995; Pike and Wadsworth, 2000). During the outbreak of VHSV at Cape Clear in Ireland (J. McArdle, unpublished data), the virus caused significant mortality in turbot, but did not cause mortality in Atlantic halibut (*Hippoglossus hippoglossus*) that were being co-cultured. However, this may have been a result of the strain specificity of the virus (King *et al.*, 2001a). An experiment using an isolate of VHSV from an outbreak in turbot at Gigha in Scotland (Snow and Smail, 1999) indicated low pathogenicity for this isolate when used to challenge Atlantic halibut (Bowden, 2003). Some diseases, however, have a wide host range. For example, *Aeromonas salmonicida* subsp. *achromogenes* infects many species of fish, including gadoids (Cornick *et al.*, 1984; Bernoth *et al.*, 1997; Wiklund and Dalsgaard, 1998), as does the parasitic copepod *Caligus elongatus* (Kabata, 1979).

It is not possible to rule out the risk of disease emergence when new species are cultured in close proximity, although some specific pathogens are known to have limited host ranges (Table 1), and known pathogens' host ranges can be investigated experimentally in the emerging aquaculture species.

Priority diseases

The following discussion focuses on previously characterized diseases, which the authors consider to pose the greatest threats to intensive gadoid culture. Pathogens are included here through their previous implication in the causation of disease in cultured gadoids or other cold-water species, through their occurrence and pathogenicity in wild gadoids and through evidence of life strategies and biology that may favour their propagation within intensive aquaculture systems.

Bacterial diseases

Vibrio anguillarum serotype 02 β is emerging as the major pathogenic *Vibrio* of Atlantic cod and haddock in culture, and there is strong evidence that current salmonid vaccines, which contain serotypes 01 and 02 α and *V. ordalii*, are not effective in protecting against infection with the 02 β serotypes. There is also unpublished evidence, from Scotland at least, that early-cultured Atlantic cod were infected with *Vibrio anguillarum* serotype 02 α , and that the "standard" salmonid vaccine was very effective (K. Agnew, personal communication). However, as culture of Atlantic cod has become more common, the 02 β serotype appears to have become the dominant isolate (Santos *et al.*, 1995).

Atypical *Aeromonas salmonicida* subsp. *Achromogenes* has been found in wild and farmed Atlantic cod (Wiklund and Dalsgaard, 1998; Magnadottir *et al.*, 2002). This strain seems to be emerging in Scandinavian countries and Canada, although as yet there has not been a report of *Aeromonas salmonicida* in cultured Atlantic cod in Scotland. Simply, this may reflect the lack of experience with this species in Scottish culture, coupled with a lack of appropriate conditions for an outbreak to occur. It is a concern that there is, as yet, no commercial vaccine licensed for Atlantic cod against atypical *Aeromonas salmonicida*, despite its potential as a highly problematic pathogen for this species. The need to formulate a vaccine against atypical *Aeromonas salmonicida* is clear.

Vibrio anguillarum serotype 02 β and atypical *Aeromonas salmonicida* are currently the two bacterial pathogens posing the greatest risk to gadoid culture. However, there are other potential bacterial pathogens of concern. Of these, the mycobacteria, in particular *Mycobacterium chelonae* and *M. fortuitum*, are potentially serious pathogens for this group of fish. Evidence of this group of pathogens infecting gadoids in the wild and in culture is currently limited, although it has been found in wild fish (Mediel *et al.*, 2000). However, the increase in public-display aquariums has placed many large gadoids on display, and mycobacterium infection, characterized by tubercle-like lesions in the viscera, and to a lesser extent, elsewhere (Lansdell *et al.*, 1993) is one of the major health problems encountered by these fish in captivity. These fish often show a loss of condition and, characteristically, appear to be "wasting" away.

How Mycobacteriaceae will affect intensively cultured gadoids is unclear. However, given their apparent susceptibility to this disease in captivity, it is recommended that a watching brief be maintained.

Viral diseases

Currently, Infectious Pancreatic Necrosis Virus (IPNV), Nodavirus, and Viral Haemorrhagic Septicaemia Virus (VHSV) are the major viral diseases of the developing gadoid industry. The risk posed by these diseases to the developing gadoid aquaculture industry has yet to be established.

IPNV

Compared with the situation for halibut (Biering *et al.*, 1994; Ness *et al.*, 1994; Biering and Bergh, 1996; Wood *et al.*, 1996; Biering, 1997), there are very few reports of IPNV in Atlantic cod. While there has been a report of isolation of the virus from wild fish (Dixon *et al.*, 2003), it is not clear if this fish was truly infected, there being no evidence of pathology. Clearly, it would be useful to fulfil Koch's postulates for this isolate, and to determine if it is truly pathogenic. In addition, there is a single report of IPNV causing high mortality in larval Atlantic cod in Denmark (Lorenzen *et al.*, 1995). Provisional trials at FRS have indicated that post-metamorphosis Atlantic cod are not susceptible to IPNV, but further work is needed to confirm this finding (T. Bowden, unpublished data).

VHSV

This disease is of particular concern to the gadoid farmer, as it is covered under LIST II of Schedule 1 of Council Directive 91/67/EEC. Thus in some EU countries (including the UK), an eradication policy may be implemented following an outbreak of disease. This was the case after the outbreaks of VHSV on turbot farms in Scotland and Ireland in the 1990s (J. MacArdle, unpublished data).

VHSV has been isolated from many gadoids in the wild including Atlantic cod, haddock, whiting (*Merlangius merlangus*), Norway pout (*Trisopterus esmarkii*), and bearded rockling (*Ciliata mustela*). In experimental challenges (Snow *et al.*, 2000; King *et al.*, 2001b), it proved to be very difficult to infect Atlantic cod even though the strains of VHSV used included isolates from wild Atlantic cod. In this work, Atlantic cod only became extensively infected when intraperitoneal injection was used to introduce the virus. The experimental animals were resistant to infection by bath and cohabitation routes of infection. This suggests that, although Atlantic cod are susceptible to VHSV, the disease is difficult to establish in them. Unfortunately, the full answer to the question of how susceptible gadoids are to VHSV will not be fully answered until they have been cultured commercially for a considerable period, or until more strains from gadoids have been tested under research conditions.

Nodavirus

Nodavirus is possibly the earliest virus to be isolated from gadoids in culture (Starkey *et al.*, 2001; Johnson *et al.*, 2002; Olivier, 2002). It is normally associated with a mass mortality in larvae, which display lesions in the neural tissue and retina, with associated pathological changes in the liver. Often, there are major changes to the behaviour of larval fish, with the animals changing their schooling behaviour and position in the water column before showing a spiralling swimming behaviour, followed by loss of orientation and death. This is usually associated with inappetence in infected animals, and may be reflected by a lack of food in the larva's digestive tract or by the presence of uneaten prey items. Where the affected animals were larger, around 100 g, there was a significant mortality in Atlantic cod, with about 10% of the animals dying (Starkey *et al.*, 2001). In this instance, the virus was isolated from the brain and eyes, and there were significant changes in the infected animal's behaviour and appearance, most notably, a darkening of the skin, which lasted throughout the infection in the clinically ill animals. In addition, the virus seems to enter a carrier state in other susceptible species, such as sea bass and gilthead bream (Rodgers and Furones, 1998; Le Breton, 1999; Breuil *et al.*, 2001; Dalla Valle *et al.*, 2001), which may be problematic if the establishment of disease-free breeding programmes is desirable.

Vertical transmission of Nodavirus is known for other marine species (Muroga, 1995; Munday and Nakai, 1997; Breuil *et al.*, 2002; Johansen *et al.*, 2002), although this has yet to be shown in gadoids. Thus, the screening of broodstock and potential broodstock recruited from the wild for the presence of the virus by reliable, non-destructive tests needs to be developed rapidly to ensure a constant, healthy supply of larvae to the industry.

Given that Nodaviruses are globally distributed, this group of viruses poses a significant risk to both adult and larval fish. There has been much effort by vaccine companies to develop effective Nodavirus vaccines for gadoids, but at the time of writing, they have only just completed the research phase and entered field trials, although they seem to offer very high levels of protection with long duration. While there is hope for the application of vaccines to fish over 5 g, the virus remains a major problem for hatcheries. Investment in good biosecurity, including disinfection of incoming water and health screening of broodstock, is something that producers may wish to consider in order to reduce the risk of Nodavirus infection.

Other viruses

Although Table 1 shows an extensive list of viruses, virtually none have been researched in gadoids, with the exception of ISAV, which was extensively tested in saithe (*Pollachius virens*) and Atlantic cod, following the outbreak of ISAV in Scotland in 1998–1999, and these species were found to be resistant to infection. The list in Table 1

cannot be considered complete at this stage, because it is likely that other gadoid-specific viruses, with a range of impact on cultured gadoids, will be isolated in future.

Fungal diseases

The biggest potential risk to gadoids from fungi is from saprolegniaceous fungi, particularly in the case of larval gadoids kept under poor hygienic conditions. Saprolegniaciae have been recorded from moribund Baltic cod larvae (Buchmann *et al.*, 1993), but have yet to be reported from adults.

Currently, the microsporidia are considered to be closely related to fungi as well (Hirt *et al.*, 2002), and a number of species have been recorded from gadoids, some of which may pose a threat under farm conditions. Species recorded include *Loma branchialis* (syn. *L. morhua*), described from the gills of Atlantic cod (Morrison and Sprague, 1981), and *Pleistophora gadi*. The salmonid microsporidian *Loma salmonae* has been responsible for severe gill lesions in marine cage-reared coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) (Kent *et al.*, 1989; Shaw *et al.*, 1998) and, since the two parasites produce similar lesions (Shaw *et al.*, 1998; Kent and Poppe, 2002), there may be reason to consider *Loma* spp. as potential pathogens of farmed gadoids. *Loma* may be transmitted through various routes, with cohabitation and ingestion of spores both leading to infection (Shaw *et al.*, 1998). There is, nevertheless, some discussion of the role of vertical transmission of *Loma*, with vertical transmission possibly occurring via ova or ovarian fluid (Kent and Poppe, 2002). More recently, Rodriguez-Tovar *et al.* (2003) have suggested that auto-infection processes occur when *Loma* sp. infects the gills of Atlantic cod. This leads to secondary infections, and may give rise to persistence of the infection in the population and, thus, the maintenance of a pool of infective hosts. Ramsay *et al.* (2002) suggested that there may be some differential resistance in experimentally infected salmonids and, thus, there might also be differences in susceptibility of farmed gadoids to infection. While little is known about the *Pleistophora* species of gadoids, fish microsporidia are generally transmitted orally or directly between fish (Dykova, 1995). Since other *Pleistophora* species show large amplification of numbers within the host and, where muscle-associated (e.g. *Pleistophora hippoglossoides*), may render heavily infected individuals unfit for human consumption (Dykova, 1995), there is reason to be concerned about possible infection of farmed gadoids by wild gadoid hosts in the environment of marine cages.

Protoctistan and macroparasitic diseases

Because gadoids occupy such a wide range of habitats and niches, they display varied and taxonomically diverse protoctistan and macroparasitic parasites. This fauna varies by locality, season, and age/size of fish (Hemmingsen and

MacKenzie, 2001). Our knowledge of gadoid parasites is extensive, partly as a result of the large amount of material from commercial fisheries that has been available to the classical parasitologist over the last century. The broad nature of the gadoid parasite fauna is well illustrated by the specific case of Atlantic cod, for which Hemmingsen and MacKenzie (2001) list 107 named parasite species from ten separate phyla. Of those parasites, seven were suggested to be specific to Atlantic cod, 17 to gadoids generally, and the remaining 83 were non-specific generalists. The final observation suggests that farmed gadoids are likely to be exposed to potential infection from a wide range of parasites. The set of possible infecting species, however, will be largely determined by such aspects of culture as feed source, tank/cage regime, and farm locality. The local mammalian, bird, fish, and invertebrate populations will also determine the parasite pool to which farmed fish will be exposed. A further important consideration in the prediction of which parasites are likely to infect cultured gadoids is their life cycle strategy. Those with a direct life cycle require no additional hosts and, therefore, are theoretically able to form a self-sustaining and amplifying population within the farmed stock. Those with an indirect life cycle, requiring additional vertebrate or invertebrate hosts, rely upon one or more intermediaries to provide large numbers of infective stages. There may also be some distinction between more opportunistic species such as trichodinids, which might cause problems for cultured fish under conditions of poor water quality, high temperature, etc., but which do not necessarily pose a problem for healthy fish. Here we present an overview of the parasites that gadoids may encounter in culture.

Protoctistan parasites

Phylum Mastigophora. Systemic spironucleosis, resulting from infection by the diplomonad flagellate *Spiroucleus* (family Hexamitidae), has caused high mortality in marine-farmed salmonids (Kent *et al.*, 1992; Poppe *et al.*, 1992; Sterud, 1998; Sterud *et al.*, 1998, 2003). There is also evidence that farmed salmon were infected by wild fish (Sterud, 1998; Sterud *et al.*, 1998). Given that, in recent years, the species *S. torosa* has been described from a number of gadoids including Atlantic cod, haddock, and saithe (Poynton and Lom, 1989; Sterud, 1998; Sterud *et al.*, 1998), it has been suggested that infection of farmed gadoids by wild hosts could also prove to be a threat.

Ichthyobodo (previously *Costia*) is a parasitic flagellate living on gill and skin that has been widely responsible for disease and mortality of farmed and ornamental fish (Woo, 1994). *Ichthyobodo necator* was previously considered to be a single, widely dispersed species. Recent work by Todal *et al.* (2004) suggests that the genus comprises several sibling species or strains. These strains display differing host and environmental (freshwater/seawater) preferences, with the marine strain, isolated

from Atlantic cod, separate from that which infects salmonids. The occurrence of a species-specific strain in Atlantic cod suggests that this parasite might pose a threat to fish health under culture conditions, although the risk of cross-infection between salmon and Atlantic cod may be low.

Trypanosoma murmanensis has been reported from the blood of gadoids, and in experimental infections, has been demonstrated to cause high mortality (65%) in Atlantic cod less than 1-year-old (Khan, 1985). The requirement for a leech vector to transmit the parasite between fish, however, may reduce possibilities for problematic infections under farm conditions. Specifically, this is true for the normal leech vector *Johanssonia arctica*, a benthic oceanic species with preferred water temperatures of 0–2°C (Khan, 1985), although other vectors might exist.

Phylum Ciliophora. More than eight species of *Trichodina* are listed as having been isolated from the skin and fins of wild Atlantic cod (Hemmingsen and MacKenzie, 2001). This parasite is generally recorded as a problem for freshwater fish hatcheries rather than for marine hatcheries. A recent report (Khan, 2004) attributed recurring incidences of mortality of cultured Atlantic cod in Newfoundland to *T. murmanica*. This study found, in experimental infections, that cultured Atlantic cod were more susceptible to the parasite than wild fish. It was suggested that outbreaks might be associated with temperature extremes and poor water quality. It has also been noted by Poynton and Lom (1989) that captured Atlantic cod held in captivity showed increased burdens of *T. murmanica* and *T. cooperi*. While Khan (2004) reported that no mortalities were experienced in fish larger than 20 cm, mass mortality of smaller and, in particular, fingerling Atlantic cod were experienced, with parasite numbers up to 260 mm⁻² being recorded.

Phylum Apicomplexa. A number of parasitic protozoa from the phylum Apicomplexa have been recorded from Atlantic cod, including *Eimeria* sp., *Goussia gadi*, *G. spraguei*, and *Haemogregarina aeglefinus*, although the potential of these species to pose a threat to farmed gadoids is hard to assess. While Molnár and Ogawa (2000) have suggested that the majority of fish coccidians show relatively low pathogenicity, Odense and Logan (1976) have reported mortality of haddock infected with *G. gadi*, and MacKenzie (1981) indicates reduced growth in blue whiting (*Micromesistius poutassou*) infected with *Eimeria* sp. In terms of the presence of haemogregarines in cultured fish, muscle and visceral tumours have been noted in farmed turbot caused by *Haemogregarina sachai* (Kirmse, 1980). Although haemogregarines infecting gadoids also exist, haemogregarines are suggested to require leeches as vectors, which may make infection within a cage farm environment less likely for gadoids. That having been said, Davies (1982) has suggested that *H. bigemina* might develop in both the leech

Oceanobdella blenii and the isopod *Gnathia maxillaris*, also suggesting a wider intermediate host/vector range for *H. aeglefinus*.

Metazoan parasites

Animals of the phylum Myxozoa were originally considered to be protozoa, but are now believed to be related to coelenterates (Petrov and Aleshin, 1999). The phylum is divided into two classes, the Myxosporaea and the Malacosporea, both of which contain major farmed fish pathogens. In addition to the fish host, an intermediate invertebrate host is also required to complete the life cycle. This is usually an annelid worm, e.g. *Tubifex* or a bryozoan. For most species identified from fish hosts, however, the intermediate host is unknown. The myxosporean *Kudoa thyrsites* infects the muscle of a wide range of marine fish species including Atlantic cod (Hemmingsen and MacKenzie, 2001) and Pacific hake *Merluccius productus* (Adlerstein and Dorn, 1998; Moran *et al.*, 1999). Although the parasite is rarely associated with host mortality, at high infection levels, it causes softening of muscle tissue after death, making it unsuitable for human consumption. This has caused a considerable problem for a number of cultured species including Atlantic salmon, coho salmon (*Oncorhynchus kisutch*), and brown trout (*Salmo trutta*) (Kent and Poppe, 2002). Little is known about the transmission of this parasite, including the intermediate host, so it is difficult to gauge the risk to gadoid culture. However, the broad host specificity of the species suggests that, at sites where salmon have become infected, conditions are also likely to be unfavourable for gadoid culture.

A number of *Myxidium* and *Zschokkella* species are recorded from the gall and urinary bladders of Atlantic cod (Hemmingsen and MacKenzie, 2001), although Lom and Dykova (1995) suggest that species infecting these organs tend to be innocuous and, therefore, less likely to cause problems for farmed gadoids. Similarly, there is little evidence that *Myxobolus aeglefini*, a parasite with relatively low host specificity recorded from the cranial cartilage of a number of gadoids, is likely to pose a major problem for cultured gadoids.

Phylum Platyhelminthes. The phylum Platyhelminthes is considered to be a polyphyletic assembly of parasitic worms, and includes the major parasitic classes Monogenea, Trematoda, and Cestoda. All these classes are represented in the parasites of gadoids, and many are likely to prove pathogenic to cultured species.

Class Monogenea. The Monogenea of gadoids are represented principally by the genus *Gyrodactylus*, of which seven named and three unclassified species are listed by Hemmingsen and MacKenzie (2001) as having been isolated from wild Atlantic cod. These species all inhabit the gills, skin, or pharynx, except for *G. cryptarum*, which was isolated from pre-opercular sensory canals. The

propensity of the genus *Gyrodactylus* to cause problems for all types of fish culture (Cone, 1995), particularly in cases of poor husbandry, suggests that they are likely to pose a constant threat to farmed gadoids. A root cause of this threat is the rapid amplification in numbers that follows attachment of a single individual to a host. This ability to colonize a host rapidly results from the presence of nested embryos within the parental uterus, so that the colonizing individual contains the next two generations (Cable and Harris, 2002). This rapid reproduction provides a particular problem for hatcheries and re-circulating systems where numbers may build-up exponentially over a short period.

Class Trematoda. Digenean worms (flukes) are characterized by a heteroxenous life strategy, requiring more than one host to complete their life cycle. For cultured fish, the requirement for intermediate hosts reduces the likelihood that the life cycle can be completed in the vicinity of the farm and, thus, that a continuous cycle can proceed. Digenean worms may be present in fish either as larval metacercariae or as adult worms. Because of the wide range of habitats and foods exploited by the gadoids, a large number of digenean species have been isolated from the group. For Atlantic cod, Hemmingsen and MacKenzie (2001) list eight metacercarial species inhabiting a range of sites including skin, gills, eye, and gut that are penetrating infective stages. They also list 30 adult species, all from regions of the gut. Some of these species may not be considered true parasites of Atlantic cod owing to their accidental ingestion with food or transfer from true hosts. For many of these species, it is difficult to assess the risk to cultured gadoids, since they may not occur in the usual culture environments, or might show no discernible pathogenicity.

One species, *Cryptocotyle lingua*, however, is widespread in the coastal environment and capable of displaying pathogenic effects in cultured gadoid species (Lysne et al., 1998). The definitive hosts for *Cryptocotyle lingua* are piscivorous birds and mammals, the former carrying adult fluke in the small intestine. Eggs from infected bird faeces undergo embryogenesis in seawater and hatch following ingestion by a gastropod host, usually the littoral periwinkle species *Littorina littorea*. Within this host, they pass through sporocyst and redial stages, finally re-entering the water column as cercarial stages. These are capable of infecting a wide variety of fish hosts, including all the cultured gadoid species, and penetrate the skin, fins, cornea, and gills. The metacercaria is encysted in the host tissue, the cyst comprising a thin parasite-derived wall surrounded by a substantial host reaction in the form of a melanized connective tissue sheath, which suggests the common term “black spot” for the disease. Lysne et al. (1994, 1997) described the presence of *Cryptocotyle* on cage-reared Atlantic cod and found that, during natural infections of caged Atlantic cod, the prevalence of encysted metacercariae increased within 3 months following introduction to cages, and had reached 100% prevalence after 12 months

(Lysne et al., 1994, 1997). Lysne et al. (1998) also found that Atlantic cod, at shallower depths, accumulated more metacercariae than those kept at greater depths. Distance from shore up to 200 m had no effect on prevalence. Despite the fact that fish may be clinically affected only at very high infection levels (Kent and Poppe, 2002), heavily infected fillets might show brown discoloration (Buchmann, 1986), and may not be deemed suitable for sale or consumption. A second parasitic digenean, the “eye fluke” *Diplostomum spathaceum*, whose metacercariae live within the lens of infected fish, have also been recorded from Atlantic cod (Buchmann, 1986). While eye fluke have been a major problem for cultured freshwater salmonids, they may not prove so problematic in cultured gadoids, since only minor opaque spots have been observed in affected gadoid lenses.

Class Cestoda. As with the digenea, gadoids have been shown to be hosts to a wide assortment of cestode species, mostly occurring as larval metacestodes. Hemmingsen and MacKenzie (2001) list 26 species of metacestode and four species occurring as adult worms for Atlantic cod. As with the digenean worms, it is hard to predict whether these worms will be a threat to gadoid culture, since relatively high worm burdens may be sustained by hosts for many species with little clinical effect, although growth might be reduced.

Phylum Nematoda. Nematodes parasitizing fish may use them as definitive, intermediate, or paratenic hosts. In many cases, a number of hosts may be needed to complete the life cycle, thus reducing possibilities for successful completion in the vicinity of the culture environment. The gadoids harbour a wide range of nematode species, including both juvenile and adult stages. Hemmingsen and MacKenzie (2001) list 16 juvenile worm species and 12 adult worm species for Atlantic cod, but as with the Cestoda, it is difficult to determine which, if any, of these species are likely to be a problem for cultured gadoids. Because gadoids would normally become infected through ingestion of either copepod intermediate hosts or previously infected fish, these worms will be less of a threat to fish fed cultured (e.g. *Artemia*/rotifer) or pelleted diets. This view is supported by observations of marine cultured salmonids, which, while prone to heavy nematode infection in the wild, rarely display nematode infections in marine culture systems. Nevertheless, such infections do occur, as reported by Berland (1987), who attributed mortality in farmed rainbow trout (*Oncorhynchus mykiss*) to the presence of the nematode *Hysterothylacium aduncum*, which also infects gadoids, possibly introduced through a wet fish diet. The main threat to gadoid culture, aside from feeding fresh fish, is the use of wild plankton for larval feeding. The possible dangers of this practice are supported by evidence from Karlsbakk et al. (2001) who found larval *H. aduncum* in the visceral cavity of Atlantic cod larvae fed wild plankton.

Phylum Acanthocephala. Fish provide definitive hosts for acanthocephalan worms, with a range of arthropods acting as intermediaries. The worms attach by embedding a spiny proboscis into the mucosal epithelium of the fish gut with attendant damage to tissue (Nickol, 1995). As with the Nematoda and Cestoda, the possibility of infection through ingestion of parasitized prey organisms is reduced in the farm environment. Hemmingsen and MacKenzie (2001) list four species of juvenile, all from the genus *Corynosoma*, and eight species of adult from Atlantic cod. Often these worms may be present in large numbers without significant pathology, although Buchmann (1986) noted a negative correlation between energy reserves and the number of acanthocephalan *Echinorhynchus gadi* infecting wild Baltic cod.

Arthropodan parasites. The arthropods, and particularly the class Copepoda and the order Isopoda, are likely to cause major problems for the marine culture of gadoids. Previously, they have been the source of considerable difficulty for salmonid culture as well as a wide range of other marine fish groups. A broad range of parasitic copepods may be found in gadoids. For Atlantic cod alone, Hemmingsen and MacKenzie (2001) list five species of siphonostomatoid (*Caligus curtus*, *C. diaphanus*, *C. elongatus*, *C. minimus*, and *Lepeophtheirus pectoralis*), one lernaecopodid (*Clavella adunca*), one poecilostomatoid (*Holobomolochus confusus*), and one penellid (*Lernaecocera branchialis*), representing a cross-section of the major families parasitizing fish. Haddock and ling share the same genera of parasitizing copepods as Atlantic cod (Kabata, 1979, 2003), while hake are additionally parasitized by members of the genera *Chondracanthus* and *Neobrachiella*. The most serious threat to cultured gadoids is likely to come from the various *Caligus* species, which show a direct life cycle (Piasecki and MacKinnon, 1995). These species often demonstrate broad host specificity, allowing the introduction of parasites to cultured fish from wild hosts living in the vicinity of the farms. All *Caligus* species noted to parasitize gadoids have been cited already as pathogens of farmed fish: *C. curtus*: (Hogans and Trudeau, 1989b); *C. elongatus inter alia* (Wootten *et al.*, 1982; Wootten, 1985; Tully, 1989; Hogans and Trudeau, 1989a, b; Landsberg *et al.*, 1991; Mustafa and MacKinnon, 1993; Shaw and Opitz, 1993; Karlsbakk *et al.*, 2001), *C. minimus* (Paperna, 1980; Papoutsoglou *et al.*, 1996) save for *C. diaphanus*. Of these species, *C. elongatus* probably poses the greatest threat, a fact supported by its current tally of cultured fish hosts, given that it is known to parasitize more than 80 species of fish (including Atlantic cod, haddock, hake, and ling) comprising 17 orders and 43 families and furthermore, is distributed through most of the world's oceans (Kabata, 1979, 2003). One of the main features of *C. elongatus* epizootics in Atlantic salmon aquaculture is that outbreaks are a summer phenomenon, and it has been suggested (Bron *et al.*, 1993; Revie *et al.*, 2002) that this is a consequence of inshore migration of infected

wild fish over the summer months. A further feature of *C. elongatus*, and possibly other *Caligus* species, is the ability of adult stages to enter the water column and infect new hosts. This has been observed for tankreared salmonids (Wootten *et al.*, 1977), and in addition, the adult stages are frequently captured in plankton trawls (Pearson, 1904; Hardy, 1956; Neilson *et al.*, 1987). While severe epizootics on cultured Atlantic cod have not been reported in the literature, *C. elongatus* infections have already been reported from cultured Atlantic cod larvae fed with wild plankton assemblages (Karlsbakk *et al.*, 2001), and from broodstock Atlantic cod in Canada (Stewart Johnson, personal communication). *C. curtus* has an arctic-boreal distribution, and is regarded by Kabata (1979, 2003) as a gadoid specialist, infecting Atlantic cod, haddock, hake, and ling among other gadoids but nevertheless, it infects a range of fish, having 23 recorded hosts. Although *C. diaphanus* is regarded as a triglid specialist (Kabata, 1979, 2003), it similarly displays a broad distribution from Spain to Norway and a wide host range including hake, Atlantic cod, and ling. In some respects, *C. minimus* is the odd species out in this group because it has been regarded as a percid specialist with few hosts (Kabata, 1979, 2003). Despite this, the occurrence of this species in British waters, including the North Sea, and records of Atlantic cod infection (Hemmingsen and MacKenzie, 2001) coupled with reports of infestation of Mediterranean cultured fish species (Paperna, 1980), suggest that it may pose a threat to cultured gadoids.

The lernaecopodid copepod *Clavella adunca* is a common gadoid parasite, frequently recorded in the North Atlantic and Mediterranean, and shows infections of Atlantic cod, haddock, whiting, and hake (Kabata, 1979, 2003). In most hosts, the parasite elicits little host response, and is apparently well tolerated, although Nunes-Ruivo (1957) notes that it produces a prominent tumour at the site of attachment in haddock. Because of its limited pathology, it is hard to determine if this parasite will be a problem for cultured gadoids, although it is likely that future infection of gadoid larvae fed with wild caught plankton, as observed by Karlsbakk *et al.* (2001), would have serious consequences. Another copepod, the poecilostomatoid *Holobomolochus confusus*, which was found to infect Atlantic cod larvae under the same circumstances and which inhabits the nares of gadoids, is extremely common in the European part of the Atlantic and the North Sea. This species was observed to have infected 94% of sampled Atlantic cod, although the pathological and host-sensory effects have yet to be established (Boxshall, 1974).

The parasite genus *Lernaecocera*, a penellid copepod, differs from the previously described species by its requirement of an intermediate fish host in the life cycle. While the definitive host is normally a gadoid, the intermediate host is non-gadoid, and is usually a pleuronectid, although a number of other groups may be parasitized. After settlement on the gills of the intermediate host, the copepodids develop into adult stages, and mate on the host. This is

followed by re-entry of the fertilized female into the water column, and subsequent attachment to a definitive host. Once attached to a gill arch, the majority of females migrate to the base of the arch and penetrate towards the ventral aorta, bulbus arteriosus, or ventricle of the fish heart, at which point they become obligate blood feeders with major consequences for the gadoid host (Kabata, 1979, 2003). As suggested by Khan *et al.* (1990) this genus represents a potentially major threat to cultured gadoids. Of particular importance are two species, *L. branchialis*, which infects Atlantic cod, and haddock as well as a range of other gadoids (Kabata, 1979, 2003) and *L. lusci*, which has been shown to infect hake. Consequences of infection vary according to host species, age, and number of parasites present, but may include abnormal behaviour, reduced growth, reduction in fat content and liver weight, low haemoglobin and haematocrit, emaciation, lethargy, decreased reproductive potential, and may result in death of the fish, particularly where the infected host is young and in cases of multiple parasite infection (Khan, 1988; Khan and Lee, 1989; Khan *et al.*, 1990; Knudsen and Sundnes, 1998; Megan *et al.*, 1998). In terms of host mortality, Megan *et al.* (1998) estimated that infected wild Atlantic cod could suffer an increased mortality of up to 8%, while Sundnes (1970) estimated mortality of up to 20% in 4–5-year-old Norwegian cod. In experimental infections, Khan (1988) measured peak mortality of 30% within 4 months of infection, with multiple infections in young fish responsible for most mortalities. Given that various aspects of fish culture may lead to increased stress in farmed gadoid populations, it is also important to note that infected fish suffered higher mortality levels when subject to stressful handling events, simultaneous infections with other pathogens, or pollution exposure (Khan, 1988; Khan *et al.*, 1990). In experimental Atlantic cod infections, Lysne and Skorpung (2002) found that previously infected hosts, which had lost the initial infection, had a significantly higher rate of (re)infection than previously uninfected animals. The authors took this to indicate that a proportion of the Atlantic cod in a population had a higher inherent susceptibility to infection. These authors also observed a decrease in infection rate with time, which was interpreted to indicate that the susceptible fish in the population had already been infected. Certain environments are likely to reduce the possibility of infection with *L. branchialis*, including those with salinities below 20 (Knudsen and Sundnes, 1998). Khan and Lee (1989) found that larger Atlantic cod compensated for infection by increased food consumption, while younger Atlantic cod did not.

A number of isopods of the suborder Flabellifera have been isolated from the body surface of gadoids, with four species of *Aega* (*A. monophthalma*, *A. psora*, *A. stromii*, and *A. tridens*) and one of *Rocinela* (*R. danmoniensis*) listed as parasites of Atlantic cod by Hemmingsen and MacKenzie (2001). It is possible that under certain conditions, and particularly for juvenile fish, flabelliferid isopods are a potential threat for gadoid culture. While Hemmingsen and

MacKenzie (2001) report that isopods of the suborder Gnathiidae have been recorded from gadoids (*Gnathia elongata*), these praniza larvae, which migrate from the substrate to take blood meals and then return, have rarely been problematic for fish culture.

Conclusion

Aquaculture has facilitated the study of fish disease, not least because of the possibility of closely observing these animals and calling in veterinary support or the appropriate authorities when disease episodes occur. While modern production techniques, improved husbandry, and an awareness of the hazards associated with intensive cultivation have reduced the risk of disease outbreak, those risks still remain. The introduction of new species to commercial cultivation could expand the host range for existing pathogens, and may generate new diseases and pathogens, as yet unknown. The former case can be studied, and measures, such as vaccination or altered husbandry routines, can be taken to reduce their impact. The latter case requires contingency plans that will allow rapid identification of new pathogens and the subsequent, timely development of prophylaxis and treatment.

Gadoids have the potential to make a significant impact on global aquaculture. Their natural distribution is global, thus broadening the range of potential pathogens to which they may be susceptible. Given the diversity of pathogens likely to impact gadoid cultivation, every effort should be made to ameliorate the risks.

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