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Seals, fish, humans and parasites in the Baltic: ecology, evolution and history

Kurt Buchmann

Department of Veterinary and Animal Sciences, Faculty of Health and Medical Sciences, University of Copenhagen, Frederiksberg C., Denmark

Abstract: Evolutionary and ecological processes affecting the interactions between hosts and parasites in the aquatic environment are at display in the Baltic Sea, a young and ecologically unstable marine ecosystem, where fluctuating abiotic and biotic factors affect the parasitofauna in fish. The dynamic infections of Baltic cod, a subpopulation of the Atlantic cod (*Gadus morhua* Linnaeus), with third stage anisakid nematode larvae of *Pseudoterranova decipiens* (Krabbe, 1878) and *Contracaecum osculatum* (Rudolphi, 1802) have increased following a significant increase of the Baltic grey seal *Halichoerus grypus* (Fabricius) population in the region. Cod serves as a paratenic host and marine mammals, pinnipeds, are definitive hosts releasing parasite eggs, with faeces, to the marine environment, where embryonation and hatching of the third stage larva take place. The parasite has no obligate intermediate hosts, but various invertebrates, smaller fish and cod act as paratenic hosts transmitting the infection to the seal. *Contracaecum osculatum* has an impact on the physiological performance of the cod, which optimises transmission of the larva from fish to seal. Thus, a muscle mass decrease of nearly 50% may result from heavy *C. osculatum* infections, probably amplified by a restricted food availability. The muscle atrophy is likely to reduce the escape reactions of the fish when meeting a foraging seal. In certain regions, where fish and seals are restricted in their migration patterns, such as the semi-enclosed Baltic Sea, the predation may contribute to a severe cod stock depletion. The parasites are zoonotic and represent a human health risk, when consumers ingest insufficiently heat- or freeze-treated infected products. Marked infections of the cod were previously reported during periods with elevated seal populations (late 19th and middle 20th century) and various scenarios for management of risk factors are evaluated in an evolutionary context.

Keywords: *Gadus morhua*, *Contracaecum*, *Pseudoterranova*, Baltic Sea, fish stocks, zoonosis

Gastrointestinal nematodes in seals are related to a range of large roundworm species within the superfamily Ascaridoidea parasitising different vertebrate hosts (Nadler and Hudspeth 2000). Well-known representatives are *Ascaris lumbricoides* Linnaeus, 1758 in humans, *Ascaris suum* Goeze, 1782 in pigs, *Parascaris equorum* (Goeze, 1782) in horses, *Toxocara canis* (Werner, 1782) in dogs, *T. cati* (Schrank, 1788) in cats, *Anisakis simplex* (Rudolphi, 1809) in whales, *Pseudoterranova decipiens* (Krabbe, 1878), *Contracaecum osculatum* (Rudolphi, 1802) in seals and *Contracaecum rudolphii* Hartwich, 1964 in birds. Although nematodes are believed to have an early marine origin they later developed various terrestrial lines (Blaxter and Koutsovoulos 2015).

The mammalian hosts of these large roundworms may have a common ancestor, probably parasitised with one or more of the ancestral roundworms in the terrestrial and aquatic mammals seen today. However, due to host switch some of the ascaridoids in mammals may have a later origin from other invertebrate and vertebrate groups (Li et al. 2018). The nematodes in the terrestrial hosts, such as *A. suum*, perform their life cycles without intermediate or paratenic hosts, because they rather easily can obtain infection by contact with and ingestion of embryonated parasite eggs in the soil. When the terrestrial mustelid ancestors of seals (carrying ascaridoids) re-colonised the aquatic environment 20–24 Mya (Rybczynski et al. 2009), these terrestrial nematodes faced new environmental challenges and a selective pressure for an alternative closure of the life cycle occurred.

Terrestrial mammalian hosts are in close contact with the soil, from where they obtain embryonated eggs. In contrast, freely swimming aquatic hosts are not in direct contact with the sediment, which prevents egg ingestion. Other transmission routes are therefore needed for closure of a life-cycle. When seals move freely in the pelagic zones of the seas the use of paratenic hosts therefore became an indispensable part of the life cycle. Early egg development of the marine anisakid nematodes involves two larval moults within the egg, which leads to subsequent hatching

Address for correspondence: Kurt Buchmann, Department of Veterinary and Animal Sciences, Faculty of Health and Medical Sciences, University of Copenhagen, Stigbøjlen 7, DK-1870, Frederiksberg C., Denmark. E-mail: kub@sund.ku.dk

Fig. 1. Subsamples of adult and larval nematodes *Contracaecum osculatum* (Rudolphi, 1802) (ethanol conserved) recovered from the stomach of a Baltic grey seal, *Halichoerus grypus* (Fabricius), and the liver of a Baltic cod, *Gadus morhua* Linnaeus, respectively.

with release of the infective third stage nematode larva to the water column (Køie and Fagerholm 1995, Køie et al. 1995). This was a beneficial trait for survival of the parasite in the aquatic environment and opened the possibility that various invertebrates including crustaceans (pelagic, semipelagic and benthic) could ingest larvae and transmit these to fish.

When the aquatic predatory mammals, including ancestral seals, ingested the third-stage larvae, these could moult twice in the stomach of the predator. Then copulation could occur, fertilised nematode eggs could be released with faeces and the life cycle closed. During this process an evolutionary pressure for selection of parasites with virulence genes leading to a physiological depression of the paratenic host would benefit transmission. Thus, the likelihood to end as prey for an aquatic mammal is higher if the swimming and escape performance of the infected fish become depressed. On the other hand, the level of virulence should be balanced, as the infection should not be instantly lethal to the paratenic host, because it would prevent further transmission to the definitive host.

In addition, a selective pressure exists for modulation of the host immune reaction to an extent that secures extended survival of the worm until transmission. The cod immune system (Star et al. 2011), lacking a series of central elements (e.g., MHCII and CD4), was well suited for this process. Marked attraction of cod leukocytes to the invading worm larvae ending with an encapsulation process involving fibroblasts (Buchmann 2012, Zuo et al. 2017) will arrest further migration of the worm but not kill it. Recent developments in the Baltic Sea have provided us with a showcase for these basic ecological and evolutionary interactions between hosts, parasites and environmental factors.

The Baltic Sea

The Baltic Sea is a relatively young and unstable brackish ecosystem, merely a few thousand years old, which contains a limited number of species. Today it is considered the largest brackish water sea in the World but, and due to its short history and brackish water, it exhibits a low biodiversity. It was formed after the last glacial period when the ice cap, covering large parts of Northern Europe, melted away more than 10,000 years ago (Berglund et al. 2005). A freshwater lake (termed the *Ancylus* lake due to presence of the freshwater snail carrying this name) was the first aquatic system to occur in the region, but it was – due to the limnic conditions – not able to sustain stocks of marine fish, including *Gadus morhua* Linnaeus (termed the Atlantic cod). However, due to later inflows of Atlantic saltwater to the basin, via depressed land areas (today a part of Southern Sweden), a marine ecosystem was established.

The inflow of marine water facilitated the immigration of various marine species (invertebrates and vertebrates) and the system was then termed the *Littorina* sea (due to presence of the periwinkle *Littorina*) (Berglund et al. 2005). After the depressed areas in Sweden were elevated, whereby the inflow ended, a new connection to the Atlantic was established through the so-called Dana Älv, located in the region where the major inflow of marine water occurs today. Today the inflow of Atlantic high salinity water occurs through two main inlets, the Danish straits, named the Belt Sea and Øresund (The Sound), whereas the freshwater arrives from the drainage areas in countries surrounding the sea (Denmark, Sweden, Finland, Russia, Latvia, Estonia, Lithuania, Poland, Germany).

The Baltic fishes

The immigration of fish to the semi-enclosed young Baltic Sea included Atlantic cod (*G. morhua*), herring *Clupea harengus* Linnaeus, sprat *Sprattus sprattus* (Linnaeus), flounder *Platichthys flesus* (Linnaeus), Atlantic salmon *Salmo salar* Linnaeus and a limited number of other teleost species. The new environment allowed the establishment of semi-isolated sub stocks with special adaptation to the harsh hydrographic conditions in the Baltic Sea. Especially the fluctuating salinity and oxygen conditions have been the main challenges after immigration. The continuous inflow of freshwater to the sea is counteracted by a discontinuous inflow of high salinity North Sea water through the straits, and this creates a salinity gradient from less than 2 ppt in the Northern Baltic Sea to sometimes more than 30 ppt in the western part. These fish species were all limited to the enclosed marine area with limited contact with the Atlantic populations.

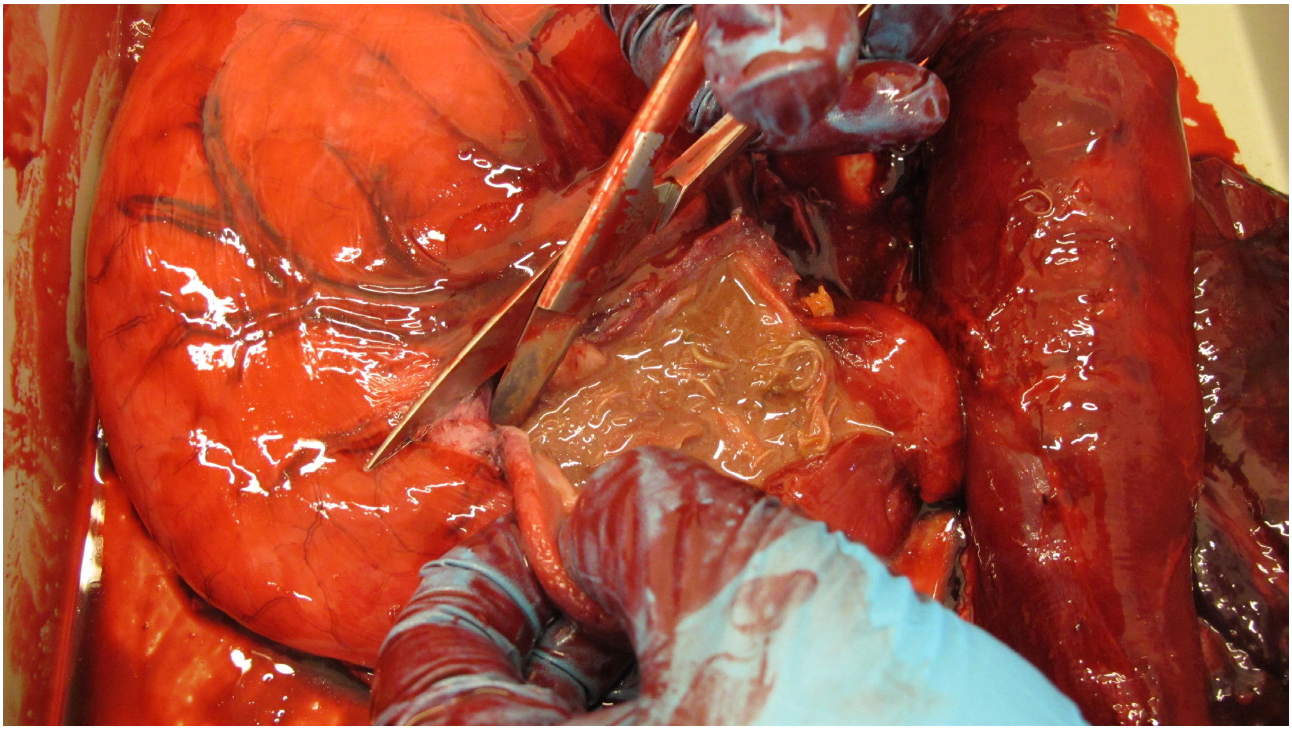

Fig. 2. Dissection of the stomach of a Baltic grey seal, *Halichoerus grypus* (Fabricius), showing high intensity of adult *Contracaecum osculatum* (Rudolphi, 1802) nematodes.

An extraordinary high selection pressure was placed on the newly immigrated cod in the Baltic, because the spawning, egg fertilisation, egg flotation in the pelagic zone, subsequent hatching and survival of yolksac larvae are all processes dependent on high salinity water. However, the inflow of high salinity water is highly dependent on meteorological conditions (storms, differential air pressures) moving the high density and high salinity water through the narrow straits. A halocline is created in the deeper basins (cold high salinity water in deeper layers with low salinity water in the surface water column), which are serving as spawning grounds for the Baltic cod. This stock is subdivided into two populations, one east of the island of Bornholm and another west of the island (Sick 1965, Jamieson and Otterlind 1971, Hemmer-Hansen et al. 2019). The interactions between the Baltic cod and the seal population were initially recognised in the Bornholm Basin (Buchmann and Kania 2012, Haarder et al. 2014), although the Western stock recently became affected (Sokolova et al. 2018).

The Baltic seals

Molecular evidence suggests that grey seals *Halichoerus grypus* (Fabricius) immigrated to the Baltic Sea already 9,000 years ago, but it also indicates that the species later succumbed due to unknown factors. Recolonisation was then believed to occur during the Bronze and Iron Ages or even later by immigration of grey seals from the North Sea (Ahlgren et al. 2022). Scattered historical evidence indicates that the seal population also later has shown marked fluctuations, at least with peaks in the 17th and 18th century (Olsen et al. 2018). The seal is the top predator in the Baltic Sea, because their natural enemies such as killer whales, sharks and other top predators, known from the North Atlantic, are absent in this semi-enclosed brackish sea with a low diversity. The only top-predators during historical times were humans.

The latest well described population peak occurred in the last part of the 19th century (Olsen et al. 2018). At that time salmon and herring were the main species in the fisheries, with cod as a less important species. Already in the 1840s local fishermen from the island of Bornholm complained about seals and their severe emaciation of their salmon catches (Krøyer 1845), and when organising in the Fisheries Association for Bornholm and Christiansø the control and regulation of the seal population was a main issue at the inauguration meeting in February 1883 (Pedersen 1933). At that time 150 fishing vessels (130 using hooks and lines, 20 with nets) were engaged in the salmon fishery around the Bornholm Island, and it was estimated that 66 % of all catches were eaten (partly or entirely) by seals. The association contacted the Danish Government (Ministry of War) and requested a canon and ammunition to shoot off and eradicate grey seals from the rocky islets, Christiansø, east of Bornholm, where the seals had an important haul-out area. At that time approximately 100 seals were recorded on the islets (Pedersen 1933), which is comparatively less than today, where 400–500 individual seals may gather in this specific area. This suggests a much higher occurrence of seals today compared to the situation in the late 19th century.

The main problem with seals was considered to be predation on hooked or netted Baltic salmon and destruction of fishing gear. The limited salmon fishery around Born-

Fig. 3. Livers of Baltic cod showing presence of numerous *in situ* third-stage larvae of *Contracaecum osculatum* (Rudolphi, 1802).

holm is similarly affected today (Zuo et al. 2018), but since the 1940s the Baltic cod has been of increasing importance (Thurow 1997), and the predation on the cod stock is presently significant, at least locally. Thus, the proportion of cod in the seal diet may reach 83% as judged from DNA measurements and otolith identification (Behrens et al. 2018). This suggests that cod is a preferred food item of seals. In the 1880s the fishermen also suggested to establish a targeted fishery after seals by use of net-traps (Pedersen 1933), but it was never implemented, because a culling program was installed by the government. Free rifles and ammunition were delivered to fishermen and hunters, which were paid bounties per culled seal (mainly harbour and grey seals). The program operated from 1889 until 1927, with more than 37,000 bounties paid, and resulted in a marked reduction of the seal population (Olsen et al. 2018).

The parasites in the Baltic fishes and seals

When immigrating into the newly established Baltic Sea area a few thousand years ago the different teleosts must have carried their characteristic Atlantic parasites with them (for a list of cod parasites see Hemmingsen and MacKenzie 2001). Several of these (especially stenohaline ectoparasites) succumbed due to the low salinity in the region, but a few succeeded to establish their life cycles in the Baltic Sea using available invertebrates and vertebrates as intermediate and paratenic hosts. The metazoan parasitofauna of Baltic cod, as known today, comprises mainly nematodes, trematodes and acanthocephalans. Nematode genera listed are *Capillaria* Zeder, 1800, *Hysterothylacium* Ward et Magath, 1917, *Anisakis* Dujardin, 1845, *Pseudoterranova* Mozgovoi, 1951, and *Contracaecum* Raillet et Henry, 1912 (Perdiguero-Alonso et al. 2008, Buchmann and Kania 2012, Mehrdana et al. 2014, Setyawan et al. 2020).

It is generally accepted that the life cycle of *A. simplex* does not occur in the Baltic Sea, despite the finding of a larva in *Crangon crangon* (Linnaeus) in the southern Baltic (Pawlak et al. 2019). This explains the absence of *Anisakis* larvae in the local clupeid populations, which merely perform limited migrations in the eastern Baltic Sea. The presence of the parasite in the Baltic cod depends on import with seasonal migrations of infected North Sea herring, through the Danish straits to the western part of the Baltic Sea, where local cod can obtain infection by feeding on the so-called Rügen herring (Grabda 1976).

Species of *Pseudoterranova* may conduct its life cycle in the western part of the Baltic, as the salinity conditions support development of eggs and larvae (Measures 1996), but it has generally been quite rare in the musculature of Baltic cod after the culling program (Kahl 1939). Along with an increasing grey seal population a surprisingly high occurrence of *P. decipiens* infected cod, captured in the Bornholm basin (the main spawning ground of the Baltic cod), was reported (Buchmann and Kania 2012, Mehrdana et al. 2014).

Another anisakid nematode, *C. osculatum*, which had been rare for decades, became highly prevalent in cod in the same area in the first part of the 21st century (Haarder et al. 2014, Mehrdana et al. 2014, Nadolna and Podolska 2014, Sokolova et al. 2018, Zuo et al. 2018). This species (Fig. 1) was originally isolated from harbor seal *Phoca vitulina* Linnaeus, caught in the Baltic Sea near the German city of Greifswald, and described, as *Ascaris osculata* Rudolphi, in its adult stage by Rudolphi (1802). The species was later transferred to the genus *Contracaecum* by Raillet and Henry (1912). Recent studies have confirmed the original investigations by Rudolphi (1802) by documenting the dominating position of *C. osculatum* among adult worms in the stomach (Fig. 2) of Baltic grey seal (*H. grypus*) (Szostakowska et al. 2002, Skrzypczak et al. 2014, Lunneryd et al. 2015, Zuo et al. 2018).

In the 19th and early 20th century the life cycle was unknown and the adult parasite was far later connected to the infections in cod (Fig. 3). Thus, the connection between cod and *C. osculatum* seal parasites was pointed out by Fagerholm (1982, 1989) and further documented experimentally (Køie and Fagerholm 1995). We now know that cod obtain infection through feeding on invertebrates, such as copepods and the amphipod *Gammarus* sp. (Pawlak et al. 2019), or by feeding on fish (herring, sprat, sand eel) acting as paratenic hosts (Rodyuk 2014, Zuo et al. 2016, Nadolna-Altyn et al. 2017) (Fig. 4). The third-stage larva of *C. osculatum* has been recorded in numerous ichthyoparasitological investigations of cod in the North Atlantic conducted through decades (Perdiguero-Alonso et al. 2008, Severin et al. 2020).

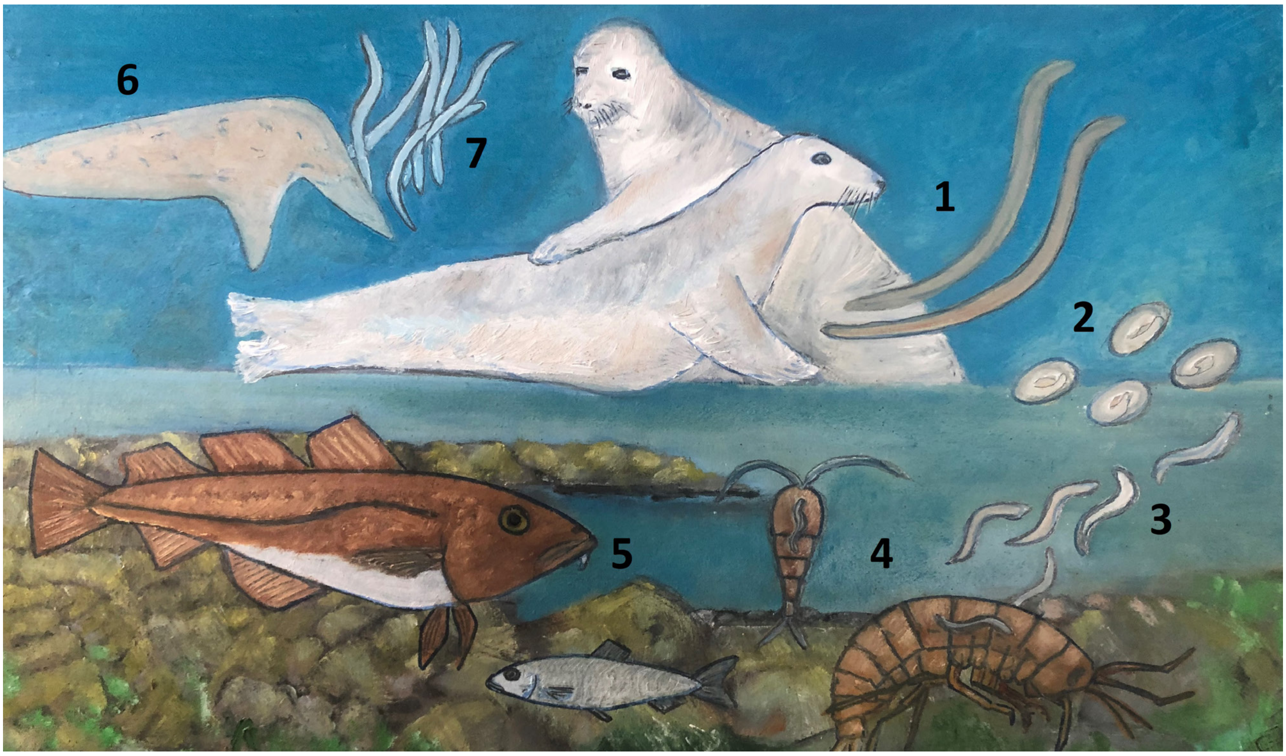

Fig. 4. Life cycle of *Contracaecum osculatum* (Rudolphi, 1802) in the Baltic Sea. 1 – adult parasites in the stomach of grey seal, *Halichoerus grypus* (Fabricius); 2 – parasite eggs released with seal faeces; 3 – third-stage larvae hatched from parasite eggs; 4 – paratenic invertebrate hosts (copepods and amphipods); 5 – paratenic piscine hosts (clupeids and cod); 6 – liver of cod showing encapsulated larvae; 7 – the third-stage larvae released in the seal stomach following ingestion.

However, biochemical and molecular studies have shown that *C. osculatum* sensu lato comprises a species complex (Mattiucci and Nascetti 2008), and that the different species differ biologically. Thus, whereas the North Atlantic *C. osculatum* larvae are found in various organs, the parasite larvae in Baltic cod are almost without exceptions located in the liver of cod. It can therefore be speculated that the grey seals immigrating to the Baltic Sea during the Bronze and Iron Ages may have carried an ancestral *C. osculatum* form with them. After an evolutionary selective process one form survived in Baltic seals and fishes, whereas their ancestral forms remained in the North Atlantic. However, because the first and original description of the type specimen of *C. osculatum* (isolated from a seal recovered from the Baltic Sea in the year 1800) was presented by Rudolphi (1802), the parasite larva in cod should be termed *C. osculatum* sensu stricto (Zuo et al. 2018).

Developments in the 19th, 20th and 21st century

The large seal population found during the last part of the 19th century may explain the background for early papers from the period reporting that cod were heavily infected with this (or related) anisakid larvae (Schneider 1862). The author stated that it was impossible to present and sell Baltic cod on the market in Copenhagen due to heavy nematode burdens in their internal organs. Although a precise diagnosis of the worms was not provided by this author, the resemblance to the situation today (Zuo et al. 2018, Mohamed et al. 2020, Ryberg et al. 2020, 2021) is compelling, and suggests that the parasite problem of cod was associated with the impressive seal population present at that time.

In the years after the culling program (active during the period 1889 to 1927) the parasite infection intensity, at least in the musculature, was low (Kahl 1939). We have no valid reports on the infection of Baltic cod livers from this decade, but evidence obtained during the 1940s and 1950s indicated that at least *C. osculatum* third-stage larvae again became prevalent and abundant in livers of Baltic cod (Getsevitjute 1955, Petrushevski and Shulmann 1955). Reports from the islet Christiansø (the seal haul out area east of the island of Bornholm) from 1944 stated that the seals were less numerous than previously, but still present, and that seals again harvested salmon from the fishing gear (Mejndor 1944). This indicates that the seal population in those years was increasing after a depression resulting from the culling program ending in 1927. This is further supported by the seal hunting statistics in the Baltic, showing often more than 600 seals killed per year during the period from 1940 to 1960 (Olsen et al. 2018).

It is unknown if the reported hunting efforts can explain a subsequent decrease of the seal population, but the lower infection level of cod examined in the 1970s and 1980s suggests such a decrease. Thus, the abundance of *C. osculatum* infection in cod was limited from the 1970s to 1990s as judged from a series of ichthyoparasitological reports (Grabda 1976, Myjak et al. 1994, Haarder et al. 2014, Setyawan et al. 2020). The grey seal population was considered critically low in the 1960s, which led to implementation of protective measures in 1967 (Olsen et al.

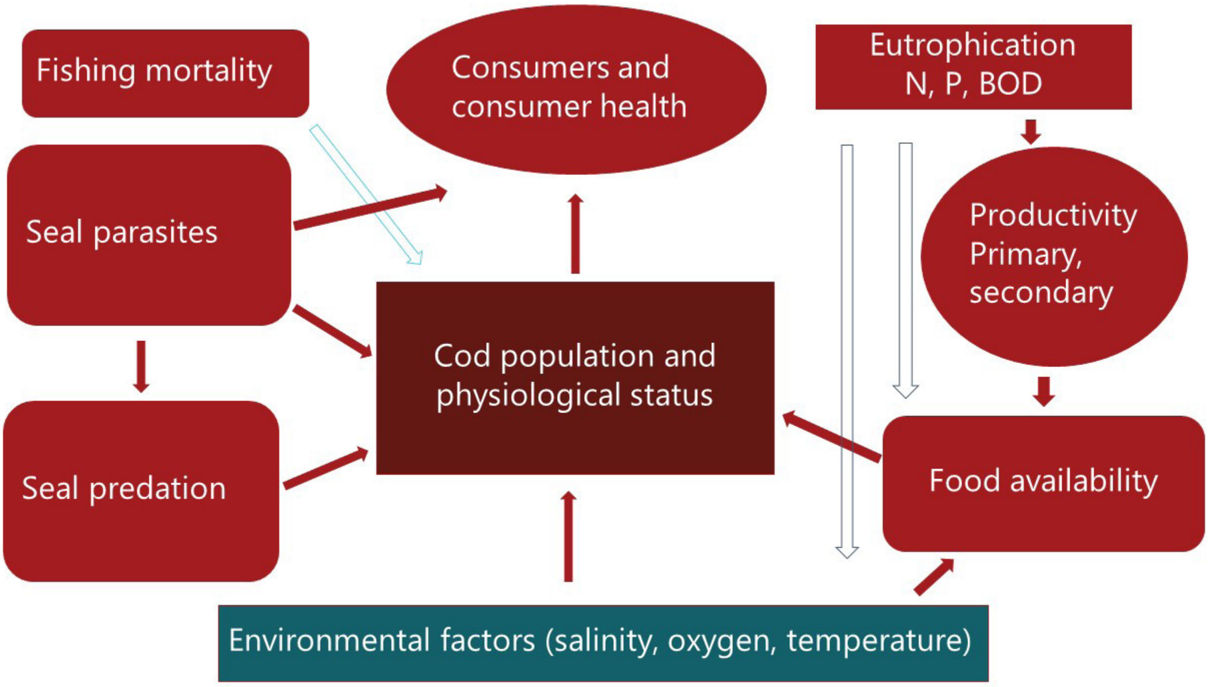

Fig. 5. Diagrammatic visualisation of ecological interactions in the *Contracaecum osculatum* (Rudolphi, 1802) host-parasite relation.

2018). From the year 2000 the protected grey seal population in the Baltic Sea increased dramatically (Harding et al. 2007, Haarder et al. 2014), and subsequent cod investigations then showed increasing *C. osculatum* infections again (Perdiguero-Alonso et al. 2008, Haarder et al. 2014, Nadolna and Podolska 2014, Horbowy et al. 2016, Sokolova et al. 2018, Zuo et al. 2018). This indicates that the infection in cod reflects the size of the seal population in the Baltic Sea, whereby it is relevant to use the nematode infections as an ecological indicator (Setyawan et al. 2020).

Biological indicators

The *Pseudoterranova* and *Contracaecum* infections of cod in the Baltic Sea are positively associated with occurrence of seals. Our knowledge on the life cycles, and their involvement of invertebrates and vertebrates at different ecological and trophic levels, makes the parasites in fish suitable as bioindicators or so-called parasitological tags (MacKenzie 2002, Timi and Buchmann 2023). Therefore, the presence of a certain parasite species in the ecosystem reflects the occurrence of hosts (intermediate, paratenic or definitive) or migration/drift of infected hosts. The ecological information gained from the parasitological investigations may supplement classical surveys on fish stocks and be a valuable tool for stock assessments and historical changes (Timi and Poulin 2020).

The recent investigations in the Baltic has provided evidence for the suitability of *Pseudoterranova* and *Contracaecum* infections as bioindicators, because they clearly indicate the association between occurrence of seals and severe nematode infections of cod. Thus, large populations of grey seals and severe cod infections co-occurred in the late 19 century (Schneider 1862, Pedersen 1933), the middle 20th century (Mejndor 1944, Getsevitjute 1955, Petrushevski and Shulmann 1955) and the early 21st century (Harding et al. 2007, Haarder et al. 2014, Mehrdana et al. 2014, Setyawan et al. 2020).

Effect of parasites on the fish

Different parasites have different life cycle strategies, and thereby pathogenicity, and will affect the host in different ways. Intestinal parasites such as the acanthocephalan *Echinorhynchus gadi* Müller, 1776 may occur in large quantities in the intestine of Baltic cod, where it obtains host nutrients by tegumental absorption. It exerts a limited pathogenic effect on the host as it is attached superficially to the intestinal mucosa. The worm should merely be regarded as a nutritional competitor. This is indicated by the finding that the number of worms per host is negatively correlated to the liver size (indicator of even small changes in the nutritional status) but not the body condition factor reflecting the muscle mass (Buchmann 1986).

The anisakid nematodes use another strategy, penetrate host organs and occur in host tissues as encapsulated third-stage larvae in the piscine host (Buchmann 2012). These larvae may survive for years in the host, as an expanded survival time increases the chance of reaching the final host, the seal. The survivability of the *C. osculatum* larvae in the host liver is enhanced by production of immunomodulatory compounds, which affect local immunological responses in the cod (Mehrdana et al. 2017, Marnis et al. 2019, 2020).

Transmission to the final host will be elevated by release of compounds decreasing muscle function by down-regulation of growth associated genes (Marnis et al. 2020). These effects may lead to a significant loss of muscle mass and condition factor (Mohamed et al. 2020, Ryberg et al. 2020, 2021), whereby the ability to escape attacks from predators, such as seals, is depressed. Additional factors, including food availability, may influence the parasite-induced depression of the cod. Controlled pig studies have not only shown that nematode infections depress growth of the host (Knecht et al. 2011), but also that the combination of protein deprivation and nematode infections depresses growth to an even higher degree than the two isolated factors alone (Pedersen et al. 2002). Therefore easy access to food may counteract the parasite induced physiological depression but only to a certain level. When the *C. osculatum* burden gets too high, the growth of Baltic cod is depressed despite high food availability (Ovegård et al. 2022).

Effects of anisakid parasites on humans

It has been known since the 1950s that anisakid nematodes can infect humans ingesting insufficiently processed fish products carrying infective larvae (Ishikura 2003). Following ingestion of the infected fish the third stage larvae become activated in the stomach of the human consumer due to the exposure to high temperature, pepsin and acid, conditions corresponding to stomach contents in marine mammals. It may subsequently invade the stomach or intestinal mucosa and elicit severe inflammatory reactions producing symptoms in the patient. Clinical signs differ considerably. The most prevalent infections reported are caused by species within the genus *Anisakis* (see Ishikura 2003) but also species of the genera *Pseudoterranova* and *Contracaecum* are associated with numerous cases.

Human cases caused by species within the genus *Pseudoterranova* comprise stomach infections (Margolis 1977, Pinel et al. 1996, Koh et al. 1999), infections of the oesophagus (Torres et al. 2007), infections of the throat (Little and Most 1973, Chitwood 1975, Juels et al. 1975, Lichtenfels and Brancato 1976, Skirnisson 2006, 2022). The parasite larvae may also penetrate the mucosa or wall of the stomach or intestine (Little and McPhail 1972, Sawada et al. 1983, Amin et al. 2000, Mercado et al. 2001, Yu et al. 2001, Na et al. 2013, Cavallero et al. 2016). *Pseudoterranova* larvae may also leave the human patient through the mouth (Kliks 1983, Arizono et al. 2011, Dupouy-Camet et al. 2014) or anal opening (Skirnisson 2006, 2022). More rare cases described infections of the nasal cavity (Brunet et al. 2017, Nordholm et al. 2020).

Human infections involving *C. osculatum* have been reported from the Baltic area (Schaum and Müller 1967), from Australia (Shamsi and Butcher 2011) and from Japan (Nagasawa 2012). Further experimental studies using pigs have documented the zoonotic potential of the third-stage *C. osculatum* larvae from Baltic cod liver (Strøm et al. 2015). With the increasing seal populations in the Baltic area, which has resulted in an increase of *P. decipiens* and *C. osculatum* infections of fish, the risk of transmission to humans is increased unless strict food safety measures are followed. This means that recommended preventive treatments (European Union (EU) regulation 853/2004) with heat, freezing or salt/acid should be followed.

Mitigation of the problems

The infection of seals and cod in the Baltic, and the effects derived from this association (Horbowy et al. 2016, Zuo et al. 2018), can be regarded as natural fluctuations occurring in an unstable and young ecosystem highly influenced by meteorological factors. A political aim could be to increase wildlife and ecotourism (seal-safari) based on the abundance and visibility of seals (Olsen et al. 2018). Another view, with focus on the fishing industry, would express concerns over the abundance of seals. The documented effects on fish quality (condition factor, fillet recovery) and survival (elevated predation and stock decrease), may suggest a control of the seal population, if this is considered a political aim and can find social acceptance. The governmental culling program, running during the period from 1889 to 1927, seemed effective over a time span of almost 40 years, but it was based on an extensive payment of bounties to hunters and fishermen per culled seal (Olsen et al. 2018). The protected status of grey seals from 1967 limits the possibilities for seal control, but if the needed dispensations can be obtained, it may be possible to control the seal population locally by targeted culling. Various types of seal nets and traps may be applied for the purpose, a solution already suggested by local fishermen at Bornholm during the 1880s (Pedersen 1933). Limited dispensations for elimination have already been provided with regard to specific seals attacking fish gear (Olsen et al. 2018), but it is very difficult to identify an individual seal as problematic and even harder to eliminate it. When selecting the culling method welfare concerns should be observed and equipment evaluated before use.

If disregarding predation and its impact on the fish stocks, and placing focus on the parasite infections only, anthelmintic treatments of seals could be suggested. However, treatments of a huge seal population seem practically impossible and, in addition, ethical and environmental concerns may exclude this possibility.

Discussion and perspectives

The Baltic Sea has a low biodiversity, and abiotic and biotic factors are highly variable due to varying inflows of oxygen rich saline North Sea water. This makes the entire ecosystem unstable, vulnerable and sensitive. During the latest decades several factors (Fig. 5) have changed and may influence the cod population in the Baltic Sea through their possible impact on chemical and biological processes (Eero et al. 2015). Focus has been placed on climate changes (Hinrichsen et al. 2011), and on oxygen conditions, as they may exert a strong influence on the available food elements for the cod (Casini et al. 2016). Also the local seal population, carrying an important parasite burden, has increased with notable implications for the ecosystem (Haarder et al. 2014). A notable effect is the parasite-induced growth stagnation, aggravated by starvation, which may lead to increased predation by seals.

An additional factor, with implications for the cod food availability, may be the lowered nutrient input to the Baltic ecosystem. This may have reduced the primary and secondary production, seen during the latest decades. According to Thurow (1997), the increasing cod population, seen in the Baltic since the 1940s and until the 1980s, was not only based on culling of seals but also based on eutrophication. The increased nutrient input to the Baltic Sea during that period was suggested to increase productivity (primary and secondary production), and thereby abundance of various prey species. Similar reflections, but based on marine bird fecundity in the same area, were presented by Laursen and Møller (2014). The authors documented a positive correlation between eutrophication and the breeding eider duck population on the islet Christiansø, located next to the spawning ground of the Baltic cod, from the 1920s to 1990. The marked decrease of breeding eiders seen from 1990 to 2010 was accordingly explained by the decreased food availability for eiders in this marine area, associated with a decreased nutrient input to the Baltic since 1990. This would imply that the food availability in this brackish water region balances on an edge between oxygen depletion (reducing available prey for fish) and sufficient nutrient input to sustain sufficient food elements for cod (e.g., crustaceans, mussels, fish).

The Baltic Sea covers a limited geographic area, and it can serve as a centre for ecological, historical and short term evolutionary studies. Changes of one or more factors may be reflected by large variations in living conditions for local fish populations, which thereby are subjected to a strong evolutionary selection pressure in this brackish water zone. The pressure is probably much stronger when compared to other marine areas. Seal populations carrying corresponding worm burdens are also known from the Northern Seas (Aspholm et al. 1995, Johansen 2010), the Atlantic Ocean (Olafsdottir and Hauksson 1997, 1998) and adjacent marine areas (Marcogliese et al. 1996, McClelland 2002). Accordingly, the cod parasitofaunas in those marine areas are also exhibiting a higher biodiversity (Heuch et al. 2011, Münster et al. 2015) including common occurrence of nematode larvae (Hafsteinsson and Rizvi 1987, Jensen et al. 1994, McClelland and Martell 2001, Kuhn et al. 2013, Gay et al. 2018, Severin et al. 2020).

However, where complex ecosystems, such as the North Atlantic and adjacent waters, are exposed for example to meteorological changes, the effects on the populations of invertebrate and vertebrate species are limited. When a seal population increases, it may affect the infection level of local fish populations (Jensen and Idås 1992, Hauksson 2002), even in the North Atlantic, but the extended migration possibilities of both fish stocks and predatory mammals will limit the overall impact on the stock. In the Baltic Sea both fish stocks and seals remain in a limited area without possibilities for extensive migration to areas with better food supply and lower infection pressures.

Investigations on seals, cod and their parasites have in the past increased our knowledge on the Baltic Sea ecology. This brackish water zone is a few thousand years old but dramatic changes have occurred over this (on an evolutionary time-scale) limited time span. The recent grey seal population increase has provided new insight into the evolution of parasites, their hosts and the interactions between them. Thus, the isolation of *C. osculatum* in the Baltic seals and cod has resulted in the establishment of a species, separated from its sister species in the North Atlantic (Mattiucci and Nascetti 2008). In addition, the high infection level in cod has also elucidated how nematode larvae may contribute to physiological/immunological dysfunction in a fish. Future and continued efforts addressing interactions between the different trophic levels may therefore improve our understanding of ecological parasitology in a simple system.

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