JOANNA PAWLAK

TRANSMISSION OF PARASITES BY MARINE CRUSTACEANS WHICH CONSTITUTE FOOD OF COD, *GADUS MORHUA* FROM THE SOUTHERN BALTIC

SUMMARY

Cod (*Gadus morhua*) Linnaeus, 1758, is an important fish species due to its commercial exploitation in many parts of the world, for example, in the fisheries of northern Europe. In the Baltic Sea there are two biologically distinct stocks: western Baltic cod and eastern Baltic cod (ICES, 2021a). For many years, the eastern Baltic cod stock was a very important part of the fishing industry in Poland, but over the last four decades there has been a massive drop in biomass and a contraction of its distribution to the southern areas (Orio *et al*., 2019). The poor status of eastern Baltic cod is characterised by biological changes in the fish: growth, condition (weight-at-length), size-at-maturation and recruitment have all substantially declined (ICES, 2021b). Changes in the ecosystem, such as poor oxygenation conditions, can affect cod both directly by altering their metabolism and indirectly by resulting in a shortage of benthic prey (Conley *et al*., 2009; Carstensen *et al*., 2014; Haase *et al*., 2020). In addition, the reduced availability of food in the main distribution area of cod may have a negative impact on fish (Eero *et al*., 2012). Indeed, the feeding levels of small cod in recent years are consistent with severe growth limitation and increased starvation-related mortality (Neuenfeldt *et al*., 2020). In the same time period, sprat and herring, major prey species of adult cod, have developed a more northerly distribution, and there is less overlap with the distribution of the cod stock. It is, however, unclear whether the limited remaining cod stock would be impacted by this shift in distribution (ICES, 2021b). Importantly, increasing infection with parasites likely also affects the health and condition of fish (Haarder *et al*., 2014; Mehrdana *et al*., 2014; Horbowy *et al*., 2016), while intensive exploitation of marine resources probably also has a negative impact (Lindegren *et al*., 2009). All these factors contribute to the fact that the population of eastern Baltic cod stock has decreased dramatically over the years and the European Commission decided to close the cod stock fishery from July 2019 (EC, 2019; COM, 2019). The International Council for the Exploration of the Sea (ICES) has advised fisheries focused on cod in the Baltic Sea (in subdivisions 24-32) to cease fishing in 2020, 2021 and 2022 (ICES, 2019; ICES, 2020; ICES, 2021b).

In ecological terms, cod is a predator at the top of the trophic pyramid, alongside the salmonids and marine mammals. During spawning, cod concentrate in offshore waters and migrate to coastal waters for feeding (Bagge *et al*., 1994). Young individuals mainly occupy the shallow water of coastal zones, which provide optimal conditions for growth, such that cannibalism does not occur. Older individuals migrate to deeper, offshore areas. Feeding preferences differ between small and larger fish and depend on their ability to catch and eat specific prey species. Cod is predator during almost its whole lifetime. Young fish prey on invertebrates, for example *Bylgides sarsi*, *Pontoporeia femorata*, *Gammarus* sp., *Mysis mixta*, *Crangon crangon*, *Saduria entomon* and also on small fish e.g. Gobiidae (Załachowski *et al*., 1975; Załachowski, 1977; Pachur and Horbowy, 2013; Haase *et al*., 2020). Adult fish feed on Clupeidae fish (sprat *Sprattus sprattus*, herring *Clupea harengus*), but also on larger crustaceans (Załachowski *et al*., 1975; Załachowski, 1977; Pachur and Horbowy, 2013; Haase *et al*., 2020). These changes in cod diet therefore reflect both fish age and the biodiversity of prey species in the specific areas where fish are feeding.

Diet is not only a source of nutrients, but may also be a source of infection by parasites. The type of parasite species a fish might contain depends on its age and developmental stage. Different parasite species occur in small/young versus larger/older cod. The phenomenon of organ specificity (topospecificity) appears to limit the occurrence of parasites to specific organs. In young fish, the acanthocephalan parasite *Echinorhynchus gadi* (Pilecka-Rapacz and Sobecka, 2004), which resides in the digestive tract, is often recorded. Acanthocephalans also occur in older fish (Studnicka, 1965; Sobecka, 2007), but the dominant parasitic fauna are the nematodes *Anisakis simplex, Contracaecum osculatum, Pseudoterranova decipiens* and *Hysterothylacium aduncum* (Szostakowska *et al*., 2005; Buchmann and Kania, 2012; Nadolna and Podolska, 2014). *H. aduncum* is an intestinal parasite, while *C. osculatum* prefers liver, and *A. simplex* and *P. decipiens* are most often located in muscle tissue. Cod may play various roles in parasite life cycles. For example, cod might be an intermediate host in which the transformation of the parasite to the next developmental stage occurs. Fish may also act as a paratenic host, i.e. it hosts the larval stage, but this role is not necessary for completion of the parasite life cycle because there is no transformation of the parasite to the next developmental stage (Pojmańska *et al*., 2016). Lastly, fish may be the final host, in which transformation from the larval stage to the adult form takes place.

The life cycles of *A. simplex*, *C. osculatum* and *P. decipiens* are very similar: marine mammals are the final hosts for these parasites (McClelland *et al*., 1990; Klimpel and Palm, 2011) and there is a clear host specificity, with particular species of marine mammal being responsible for closing the life cycle of a particular parasite species. Thus, the final hosts for *A. simplex* are cetaceans, which in the Baltic Sea are represented by the harbor porpoise, *Phocoena phocoena* (Herreras *et al*., 2004); for *C. osculatum*, the grey seal, *Halichoerus grypus* (Fagerholm, 1990); and for *P. decipiens*, the harbor seal, *Phoca vitulina* (Aspholm *et al*., 1995) and the grey seal (Hauksson, 2011). In the final host, larval stage L4 transforms to the dioecious mature stage, which is capable of producing fertilized eggs. Parasite eggs enter the water environment via the feces of their final hosts, i.e. marine mammals. Transformation to the larval stages L1, L2 or even L3 occurs within the egg (Køie and Fagerholm, 1995). L2 or L3 larvae are eaten by crustaceans, which then play the role of intermediate host where transformation from L2 to L3 can take place. Such infected crustaceans are eaten by pelagic fish (e.g. sprat, herring), which in turn are eaten by predatory fish (e.g. cod). Marine mammals represent the last link in the trophic chain: they feed on infected fish and thus become the definitive, i.e. final host and subsequently the life cycle is complete (Køie and Fagerholm, 1995; Klimpel *et al*., 2004; Mouritsen *et al*., 2010). The life cycle of *H. aduncum* is similar to that described above, but the final hosts are fish, e.g. eepout (*Zoarces viviparous*) or cod (Jackson *et al*., 1997), where sexually mature individuals develop in the digestive tract.

Marine crustaceans - Amphipoda, Cirripedia, Copepoda, Decapoda, Euphausiacea, Isopoda and Mysidacea - very commonly act as intermediate or paratenic hosts of parasites. Studies on this issue have been conducted in Canada, Norway and Scotland. However, until now, research on the detection of intermediate hosts for nematode and acanthocephalan parasites in the Baltic Sea has been limited to western areas (e.g. Kiel Bay and Lübeck Bay in Germany) or has focused on experimental approaches.

Examples of Baltic Sea crustaceans infected with nematodes and acanthocephalans are listed below:

- *Acartia bifilosa* - *Hysterothylacium* sp. (Lick, 1991; Zander *et al*., 1994);
- *Acartia tonsa* - *H. aduncum, A. simplex, C. osculatum* (Køie, 1993, 2001; Køie and Fagerholm, 1995);
- *Temora longicornis* - *C. osculatum* (Køie and Fagerholm, 1995);
- *Oithona similis* - *A. simplex* (Køie, 2001);
- *Balanus* sp. - *A. simplex, C. osculatum* (Køie, 2001; Køie and Fagerholm, 1995);
- *Neomysis integer* - *H. aduncum, P. decipiens, C. osculatum* (Gibson, 1972; Lick, 1991; Køie and Fagerholm, 1995);
- *Gammarus salinus* - *Hysterothylacium* sp., *E. gadi* (Zander *et al*., 1994, 2000, 2002);
- *Gammarus zaddachi* - *Hysterothylacium* sp., *E. gadi* (Zander *et al*., 1994, 2002);
- *Gammarus oceanicus* - *E. gadi, H. aduncum* (Zander *et al*., 1994; Fagerholm, 1987; Zander *et al*., 2002);
- *Gammarus locusta* - *Hysterothylacium* sp. (Zander *et al*., 2000);
- *Crangon vulgaris* (*C. crangon*) - *H. aduncum* (Gibson, 1972);
- *Hyperia galba* - *H. aduncum* (Klimpel and Rückrt, 2005);
- *Idotea* sp. - *H. aduncum* (Køie, 1993).

In addition, the last studies in the Baltic area were performed almost 20 years ago, and therefore it is timely to check for, and determine the nature of any changes that have occurred in the marine environment. To the best of my knowledge there have been no reports on the details of the life cycle of the above parasites, except in the western part of the Baltic Sea. For these parasites, intermediate hosts in the southern and central Baltic sea are unknown.

The presence of the nematodes *H. aduncum, A. simplex, C. osculatum,* and the acanthocephalan *E. gadi*, has been noticed in a variety of crustaceans, many of which also occur in the Baltic Sea, but to date there are no reports of individual crustaceans from the Baltic Sea containing these parasites. Indeed, the life cycles of the above parasites are only described in a general way for the Baltic Sea and there is no information on which specific crustacean species are potentially intermediate hosts.

The only studies performed are those for areas bordering the western part of the Baltic Sea, i.e. the Danish Straits and German waters.

The lack of studies involving direct detection of parasites in invertebrates that are predated by fish and that also may be a transmission route for parasites reflects the technical difficulty of the research and its time-consuming, laborious and expensive nature. Moreover, the abundance of invertebrates in the marine environment and their unequal distribution makes it impossible to examine a whole body of water for infected organisms. Such studies require experience, knowledge and patience.

The parasite fauna of cod in the Baltic Sea is well known. Less clear, however, are the specific organisms that act as intermediate hosts for particular parasite species. Invertebrates that represent an important component of the cod diet may be crucial for the life cycles of their parasites. This study is the first investigation of the presence of parasites *in situ* in the diet of cod from the Baltic Sea.

Aim of the study:

To determine possible sources of cod infection with parasites based on an analysis of the parasite fauna of invertebrates present in the diet of cod.

The following research **hypotheses** were proposed:

- invertebrates eaten by cod can also be a source of parasite infection;
- various invertebrate species act as intermediate hosts in the life cycle of different parasite species occurring in cod.

Invertebrates infection with parasites were described using the following parameters (Bush *et al*., 1997):

- prevalence - the number of individuals infected with parasites as a proportion of all individuals examined in a given area;
- intensity of infection - the number of individuals of a particular parasite species in a single host.

The biological material for research (digestive tracts of cod) was collected between 2012 and 2016 during commercial and research cruises in the Polish Exclusive Economic Zone of the Baltic Sea. In total, the food composition of 2,695 fish was examined. Parasitological analyses were performed on almost 25,000 invertebrates, of which 2,899 were *S. entomon*, 7,119 were *C. crangon*, and 1,977 were *Gammarus* sp., with approximately 13,000 other species or genera (Crustacea, Polychaeta, Bivalvia) also catalogued. Initially, each invertebrate food component was reviewed for the presence of parasites using a stereoscopic microscope. In case parasites were not visible during this initial analysis, the invertebrates were digested using artificial gastric juice (a solution of pepsin and hydrochloric acid) and each food component was checked again for parasites in the body cavity. This additional digestion was only necessarily for crustaceans. The parasites collected were subjected to taxonomic identification based on anatomical and morphological characteristics determined using a stereomicroscope. The initial taxonomic identification of the parasites was confirmed by DNA sequencing. Parasite DNA was purified and then amplified by polymerase chain reaction using specific primers. Amplicons were analyzed by DNA sequencing, which identified parasites to the species level.

The parasite-host system, *H. aduncum - S. entomon*, was described here for the first time (Fig. 1) (**publication 1**). L4 (n=1) and adult (n=1) stage *H. aduncum* were found in *S. entomon* for the first time. Molecular analyses of the parasites confirmed the nematode species, with the two sequences being deposited in GenBank. The presence of adult-stage *H. aduncum* in a crustacean suggests that invertebrates can act as final host for this parasite. On the other hand, the adult stage was found inside the undigested individual *S. entomon* in the cod stomach, suggesting that the transformation from larval L4 to adult stage took place in *S. entomon*, but after the crustacean's death in the cod stomach. The occurrence of a L4 larva in this Isopoda species might also indicate migration of the parasite to the crustacean in the fish stomach. Experimental studies have shown that pepsin, a component of both natural and artificial gastric juice, may drive the transformation of larvae to the next developmental stage (Iglesias *et al*., 2002; Adroher *et al*., 2004). In addition, in the body cavity of *S. entomon* four more *H. aduncum* individuals were observed. The presence of these parasites was only detected after additional digestion in artificial gastric juice. Unfortunately, the condition of the parasites did not allow for identification of the larval stage. Parasites were also found inside the cod stomach, where the nematode *H. aduncum* and the acanthocephalan *E. gadi* were predominant.

Fig. 1 S. *entomon* infected with *H. aduncum*

A completely new and at the same time very important discovery is the demonstration of the presence of *A. simplex* in *C. crangon* (**publication 2**). In the Baltic Sea, brown shrimp has never been indicated as an intermediate host for nematode parasites. Nevertheless, one individual was found to be infected a single L3 larva. Furthermore, three *Gammarus* sp. individuals were found to be infected with nematode *C. osculatum* L3 larvae (**publication 2**). Taxonomic identification was confirmed by molecular analyses and DNA sequences were deposited in GenBank. Individuals from the Anisakidae family (*A. simplex* and *C. osculatum*) have the ability to migrate in host tissues and may spread to various organs. *C. osculatum* is noticed most frequently in the liver, which may negatively influence the condition of fish. Cod stores energy reserves in the liver in the form of lipids. These reserves are used during the spawning period or when there is limited food in the environment. The parasite may damage liver tissue and feed on the nutrients, potentially leading to dysfunction of the liver. Consequently, the intensity of infection may negatively impact fish condition and could increase natural mortality (Horbowy *et al*., 2016). Generally, *A. simplex* migrate to muscle tissue and occasionally to the liver. In the Baltic Sea cod is important for fisheries and fish processing, therefore food safety is related with economic aspect. This represents a food safety issue, since the presence of parasitic nematodes in fish and fish products may pose a risk to the human health. Ingestion of fish products containing *A. simplex* and other anisakid larvae can cause a disease called anisakidosis. Human health may also be compromised by allergic reactions to parasite antigens (hypersensitivity) (Alonso-Gómez *et al*., 2004; Audicana and Kennedy, 2008; Valero *et al*., 2003; Mehrdana and Buchmann, 2017). Although adequate thermal processing kills the parasites (Wharton and Aalders, 2002), allergens present in Anisakidae are thermostable (Audicana *et al*., 2002; Moneo *et al*., 2005). It is also important to note that *A*. *simplex* larvae are tolerant to a wide range of temperatures and thus may survive freezing at -20°C (Podolska *et al*., 2019).

During the parasitological analyses it was found that *C*. *crangon* may also be an intermediate host for nematode *H*. *aduncum* (Fig. 2) (**publication 3**). This host-parasite system have never been observed before in the Baltic Sea. Based on anatomical features, nine larvae were identified as *Hysterothylacium* sp. (L3). Molecular identification was confirmed for seven larvae. Examples of sequences have been deposited in GenBank. *Hysterothylacium* sp. is one of the most numerous nematode species in fish and is common in the marine food chain. More than 70 different invertebrate species have been reported as intermediate hosts for this parasite (Lick, 1991).

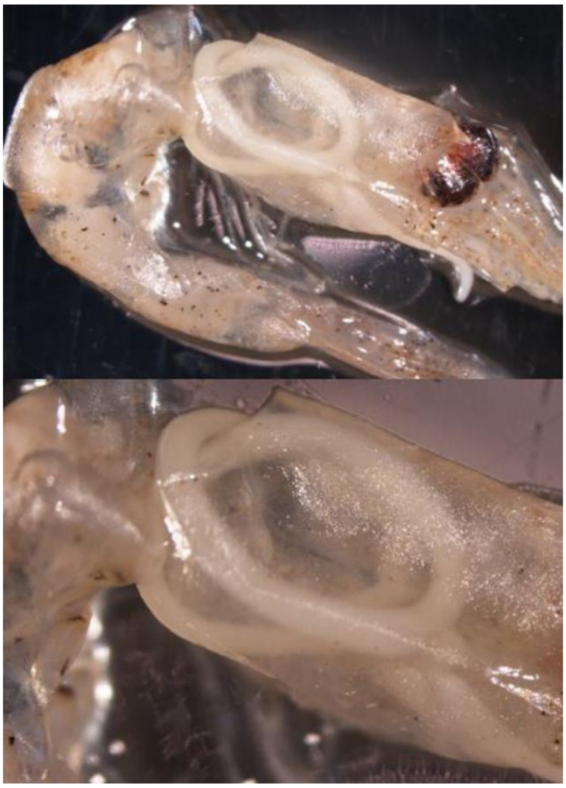

Fig.2 *C. crangon* infected with *H. aduncum*

The intended goal of this study was achieved: possible sources of cod infection with parasites were determined by analyzing the parasite fauna of invertebrates that form part of the diet of cod. The initial hypotheses were verified: invertebrates that are components of the cod diet may also be a source of infection with fish parasites; different species of invertebrate serve as intermediate hosts for different species of cod parasite.

Parasite-host systems that have not been recorded so far in the Baltic Sea were described for the first time. Thus, *S. entomon* and *C. crangon* may act as intermediate hosts in the *H. aduncum* life cycle, as shown in **publications 1** and **3**. A very important finding, in terms of food safety, is the demonstration of *C. crangon* infected with *A. simplex*, and of *Gammarus* sp. infected with *C. osculatum*. These relationships are described in **publication 2**.

The research results obtained during my studies have contributed to a broadening of basic knowledge about the sources of cod infection. Moreover, this work allows for a more detailed description of the life cycle of cod parasites in the Baltic Sea. Finally, it will also enable a better understanding of the role of particular food components in the transmission of certain parasite species.

The marine environment is currently experiencing progressive changes in climate, physicochemistry, the range of occurrence and condition of marine organisms, the occurrence of alien species, etc. Permanent environmental change is a challenge, but also creates new opportunities for parasites to modify their life cycle. Accordingly, further monitoring of this phenomenon is advisable and particular attention should be paid to intermediate hosts. The dominant crustaceans in the diet of cod are also part of the diet of other fish in the Baltic Sea. Therefore, it seems highly likely that such parasites will be transferred to new hosts. Climate change may also contribute to the migration of parasites, which then can occupy new hosts.

Bearing in mind the above facts, I would like to continue my research work in this topic using the rich biological data and new biological material collected so far. An important point that I would like to verify is whether there are any spatio-temporal changes in intensity and prevalence of infection in organisms constituting the diet of fish. I would ask whether the intensity and prevalence of infected food components vary depending on the biological parameters of the host (e.g. length or age of the fish). Since environmental conditions change over time, the diets of other fish should be considered and checked for the presence of parasites. In addition, it would be interesting to investigate areas located near seal colonies, e.g. the Vistula River estuary or near Bornholm island, for infected invertebrates.

REFERENCES

Adroher F.J., Malagon D., Valero A., Benitez R. 2004. In vitro development of the fish parasite *Hysterothylacium aduncum* from the third larval stage recovered from a host to the third larval stage hatched from the egg. Diseases of Aquatic Organisms, 58, 41–45.

Alonso-Gómez A., Moreno-Ancillo A., López-Serrano M.C., Suarez-de-Parga J.M., Daschner A., Caballero M.T., Barranco P., Cabañas R. 2004. *Anisakis simplex* only provokes allergic symptoms when the worm parasitises the gastrointestinal tract. Parasitology Research, 93, 378–384.

Aspholm P.E., Ugland K.I., Jødestøl K.A., Berland B. 1995. Sealworm (*Pseudoterranova decipiens*) infection in common seals (*Phoca vitulina*) and potential intermediate fish hosts from the outer Oslofjord. International Journal for Parasitology, 25, 367–373.

Audicana M.T., Ansotegui I.J., de Corres L.F., Kennedy M.W. 2002. *Anisakis simplex*: dangerous – dead and alive? Trends in Parasitology, 18, 20–25.

Audicana M.T., Kennedy, M.W. 2008. *Anisakis simplex*: from obscure infectious worm to inducer of immune hypersensitivity. Clinical Microbiology Review, 21, 360–379.

Bagge O., Thurow F., Steffensen E., Bay J. 1994. The Baltic cod. Dana 10, 1–28.

Buchmann K., Kania, P. 2012. Emerging *Pseudoterranova decipiens* (Krabbe, 1878) problems in Baltic cod, *Gadus morhua* L., associated with grey seal colonization of spawning grounds. Journal of Fish Diseases, 35, 861-866.

Bush A.O., Lafferty K.D., Lotz J.M., Shostak A.W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. The Journal of Parasitology, 83, 575–583.

Carstensen J., Andersen J.H., Gustafsson B.G., Conley D.J. 2014. Deoxygenation of the Baltic Sea during the last century. Proceedings of the National Academy of Sciences, 111, 5628–5633.

COM, 2019. ANNEX to the Proposal for a COUNCIL REGULATION fixing for 2020 the fishing opportunities for certain fish stocks and groups of fish stocks applicable in the Baltic Sea and amending Regulation (EU) 2019/124, as regards certain fishing opportunities in other waters, Brussels, 30 August 2019.

Conley D.J., Bjӧrck S., Bonsdorff E., Carstensen J., Destouni G., Gustafsson B.G., Hietanen S., Kortekaas M., Kuosa H., Meier H.E.M., Müller-Karulis B., Nordberg K., Norkko A., Nürnberg G., Pitkänen H., Rabalais N.N., Rosenberg R., Savchuk O.P., Slomp C.P., Voss M., Wulff F., Zillén L. 2009. Hypoxia-related processes in the Baltic Sea. Environmental Science & Technology, 43, 3412–3420.

EC, 2019. Commission approves emergency measures to protect eastern Baltic cod, Brussels, 23 July 2019

Eero M., Vinther M., Haslob H., Huwer B., Casini M., Storr-Paulsen M., Koster F.W. 2012. Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish. Conservation Letters, 5, 486–492.

Fagerholm H.P. 1987. *Gammarus oceanicus* (Crustacea: Amphipoda) as an intermediate host of *Hysterothylacium auctum* (Nematoda: Ascaridoidea); life-cycle and taxonomy of the parasite. Information 19. Proceedings of the XIII Symposium of the Scandinavian Society for Parasitology, 30.

Fagerholm H.P. 1990. Systematic Position and Delimitation of Ascaroid Nematode Parasites of the Genus *Contracaecum* with a Note on the Superfamily Ascaridoidea. Helsinki: National Veterinary Institute.

Gibson D.I. 1972. Flounder parasites as biological tags. Journal of Fish Biology, 4, 1–9.

Haarder S., Kania P.W., Galatius A., Buchmann K. 2014. Increased *Contracaecum osculatum* infection in Baltic cod (*Gadus morhua*) livers (1982–2012) associated with increasing grey seal (*Halichoerus gryphus*) populations. Journal of Wildlife Diseases, 50, 537–543.

Haase K., Orio A., **Pawlak J.**, Pachur M., Casini, M. 2020. Diet of dominant demersal fish species in the Baltic Sea: Is flounder stealing benthic food from cod? Marine Ecology Progress Series, 645, 159-170.

Hauksson E. 2011. The prevalence, abundance, and density of *Pseudoterranova* sp.(p) larvae in the flesh of cod (*Gadus morhua*) relative to proximity of grey seal (*Halichoerus grypus*) colonies on the coast off Drangar, Northwest Iceland. Journal of Marine Biology, 2011, ID 235832, 1-8.

Herreras M.V., Balbuena J.A., Aznar F.J., Kaarstad S.E. Fernandez M., Raga J.A. 2004. Population structure of *Anisakis simplex* (Nematoda) in harbor porpoises *Phocoena phocoena* off Denmark. Journal of Parasitology, 90, 933–938.

Horbowy J., Podolska M., Nadolna-Ałtyn K. 2016. Increasing occurrence of Anisakid nematodes in the liver of cod (*Gadus morhua*) from the Baltic Sea: does infection affect the condition and mortality of fish? Fisheries Research, 179, 98–103.

ICES, 2019. Cod (*Gadus morhua*) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). In Report of the ICES Advisory Committee, cod.27.24-32. https://doi.org/10.17895/ices.advice.4747.

ICES, 2020. Cod (*Gadus morhua*) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). In Report of the ICES Advisory Committee, 2020. ICES Advice 2020, cod.27.24-32. https://doi.org/10.17895/ices.advice.5943.

ICES, 2021a. Baltic Fisheries Assessment Working Group (WGBFAS). ICES Scientific Reports. 3:53. 717 pp. https://doi.org/10.17895/ices.pub.8187.

ICES, 2021b. Cod (*Gadus morhua*) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). In Report of the ICES Advisory Committee, 2021. ICES Advice 2021, cod.27.24-32.

Iglesias L., Valero A., Galvez L., Benitez R., Adroher F.J. 2002. *In vitro* cultivation of *Hysterothylacium aduncum* (Nematoda: Anisakidae) from 3rd-stage larvae to egg-laying adults. Parasitology, 125, 467–475.

Jackson C.J., Marcogliese D.J., Burt M.D.B. 1997. Role of hyperbenthic crustaceans in the transmission of marine helminth parasites. Canadian Journal of Fisheries and Aquatic Sciences, 54, 815–820.

Klimpel S., Palm, H.W. 2011. Anisakid nematode (Ascaridoidea) life cycles and distribution: increasing zoonotic potential in the time of climate change? In Mehlhorn H (ed.), Progress in Parasitology. Parasitology Research Monographs, vol. 2. Berlin, Heidelberg: Springer, pp. 201–222.

Klimpel S., Rückert S. 2005. Life cycle strategies of *Hysterothylacium aduncum* to become the most abundant Anisakid fish nematode in the North Sea. Parasitology Research, 97, 141–149.

Klimpel S., Palm H.W., Rückert S., Piatkowski U. 2004. The life cycle of *Anisakis simplex* in the Norwegian Deep (northern North Sea). Parasitology Research, 94, 1–9.

Køie M. 1993. Aspects of the life cycle and morphology of *Hysterothylacium aduncum* (Rudolphi, 1802) (Nematoda, Ascaridoidea, Anisakidae). Canadian Journal of Zoology, 71, 1289–1296.

Køie M. 2001. Experimental infections of copepods and sticklebacks *Gasterosteus aculeatus* with small ensheathed and large third-stage larvae of *Anisakis simplex* (Nematoda, Ascaridoidea, Anisakidae), Parasitology research, 87 (1), 32-36.

Køie M., Fagerholm H.P. 1995. The life cycle of *Contracaecum osculatum* (Rudolphi, 1802) *sensu stricto* (Nematoda, Ascaridoidea, Anisakidae) in view of experimental infection. Parasitology Research, 81, 481–489.

Lick R. 1991. Investigations concerning the life cycle (crustaceans – fish – marine mammals) and freezing tolerance of Anisakine nematodes in the North Sea and the Baltic Sea (in German). (PhD thesis). Christian-Albrechts-Universität, Kiel

Lindegren M., Möllmann C., Nielsen A., Stenseth N.C. 2009. Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. Proceedings of the National Academy of Sciences, 106, 14722–14727.

McClelland G., Misra R.K., Martell D.J. 1990. Larval anisakine nematodes in various fish species from Sable Island Bank and vicinity. Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its invertebrate and seal hosts. Canadian Bulletin of Fisheries and Aquatic Sciences, 222, 83–118.

Mehrdana F., Bahlool Q.Z.M., Skov J., Marana M.H., Sindberg D., Mundeling M., Overgaard B.C., Korbut R., Strøm S.B., Kania P.W., Buchmann K. 2014. Occurrence of zoonotic nematodes *Pseudoterranova decipiens*, *Contracaecum osculatum* and *Anisakis simplex* in cod (*Gadus morhua*) from the Baltic Sea. Veterinary Parasitology, 205, 581–587.

Mehrdana F., Buchmann, K. 2017. Excretory/secretory products of anisakid nematodes: biological and pathological roles. Acta Veterinaria Scandinavica, 59, 42.

Moneo I., Caballero M.L., Gonzalez-Munoz M., Rodriguez-Mahillo A.I., Rodriguez-Perez R., Silva A. 2005. Isolation of a heat-resistant allergen from the fish parasite *Anisakis simplex*. Parasitology Research, 96, 285–289.

Mouritsen K.N., Hederholm R., Schack H.B., Møller L.N., Storr-Paulsen M., Dzido J., Rokicki J. 2010. Occurrence of anisakid nematodes in Atlantic cod (*Gadus morhua*) and Greenland cod (*Gadus ogac*) West Greenland. Acta Parasitologica, 55, 81–89.

Nadolna K., Podolska M. 2014. Anisakid larvae in the liver of cod (*Gadus morhua*) L. from the southern Baltic Sea. Journal of Helminthology, 88, 237– 246.

Neuenfeldt S., Bartolino V., Orio A., Andersen K. H., Andersen N. G., Niiranen S., Bergström U., Ustups D., Kulatska N., Casini M. 2020. Feeding and growth of Atlantic cod (*Gadus morhua* L.) in the eastern Baltic Sea under environmental change. ICES Journal of Marine Science, 77(2), 624-632.

Orio A., Bergström U., Florin A. B., Lehmann A., Šics I., Casini M. 2019. Spatial contraction of demersal fish populations in a large marine ecosystem. Journal of Biogeography, 46(3), 633-645.

Pachur M.E., Horbowy J. 2013. Food composition and prey selection of cod, *Gadus morhua* (Actinopterygii: Gadiformes: Gadidae), in the southern Baltic Sea. Acta Ichthyologica et Piscatoria, 43, 109–118.

Pilecka-Rapacz M., Sobecka E. 2004. Parasites of young Baltic cod, *Gadus morhua callarias* L. in the Gulf of Puck, Poland. Acta Ichthyologica et Piscatoria, 34, 235–240.

Podolska M., Pawlikowski B., Nadolna-Ałtyn K., **Pawlak J.**, Komar-Szymczak K., Szostakowska B. 2019. How effective is freezing at killing *Anisakis simplex*, *Pseudoterranova krabbei*, and *P. decipiens* larvae? An experimental evaluation of time-temperature conditions. Parasitology Research, 118, 2139–2147.

Pojmańska T., Demiaszkiewicz A., Doligalska M., Głowska E., Kurnatowska A., Kurnatowski P., Lonc E., Majewska A.C., Matowicka-Karna J., Moskwa B., Okulewicz A., Wędrychowicz H. 2016. Leksykon parazytologiczny. Polskie Towarzystwo Parazytologiczne. ISBN 978-83-928239-2-6. 230 pp. (in Polish)

Sobecka E. 2007. Pasożyty dorsza atlantyckiego z podgatunków *Gaadus morhua morhua* L. i *Gadus morhua callarias* L. z wybranych rejonów Atlantyku i Bałtyku. Rozprawa habilitacyjna nr 245. Akademia Rolnicza w Szczecinie

Studnicka M. 1965. Internal parasites of the cod, *Gadus callarias* L., from the Gdańsk Bay of the Baltic Sea, Acta Parasitologica Polonica, 13, 283–290.

Szostakowska B., Myjak P., Wyszyński M., Pietkiewicz H., Rokicki J. 2005. Prevalence of anisakin nematodes in fish from Southern Baltic Sea. Polish Journal of Microbiology, 54, 41–45.

Valero A., Terrados S., Díaz V., Reguera V., Lozano J. 2003. Determination of IgE in the serum of patients with allergic reactions to four species of fish-parasite anisakids. Journal of Investigational Allergology & Clinical Immunology, 13(2), 94-98.

Wharton D.A., Aalders O. 2002. The response of Anisakis larvae to freezing. Journal of Helminthology, 76, 363–368.

Zander C. D., Groenewold S., Strohbach U. 1994. Parasite transfer from crustacean to fish hosts in the Lübeck Bight, SW Baltic Sea. Helgoländer Meeresuntersuchungen, 48(1), 89-105.

Zander D. C., Koçoglu Ö., Skroblies M., Strohbach U. 2002. Parasite populations and communities from the shallow littoral of the Orther Bight (Fehmarn, SW Baltic Sea). Parasitology Research, 88(8), 734-744.

Zander C.D., Reimer L.W., Barz K., Dietel G., Strohbach U. 2000. Parasite communities of the Salzhaff (Northwest Mecklenburg, Baltic Sea) II. Guild communities, with special regard to snails, benthic crustaceans, and small sized fish. Parasitology Research, 86, 359–372.

Załachowski W. 1977. Ilościowa i ekologiczna analiza pokarmu użytkowanego przez populację dorsza w południowym Bałtyku w latach 1972–1974. [Quantitative and ecological analysis of food consumed by southern Baltic cod population in the years 1972–1974]. Szczecin, Poland: Akademia Rolnicza w Szczecinie, 53, 1–109. (in Polish)

Załachowski W., Szypula J., Krzykawslu S., Krzykawski I. 1975. Feeding of some commercial fishes in the southern region of the Baltic Sea – in 1971 and 1972. Polskie Archiwum Hydrolobiologii, 22(3), 429-448.