A global checklist of the parasites of the harbor porpoise *Phocoena phocoena*, a critically-endangered species, including new findings from the Baltic Sea

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**ARTICLE INFO**

**Keywords:**
- Harbor porpoise
- Parasites
- Biodiversity
- Host-parasite interaction
- Odontoceti
- Marine mammals

**ABSTRACT**

The common harbor porpoise is a widely-distributed marine mammal with three known subspecies, including *P. phocoena phocoena*, with a clearly distinct and critically endangered (CR) subpopulation from the Baltic Sea (Baltic Proper). As part of an assessment of the condition and health threats of these mammals, it is important to conduct parasitological monitoring. The aim of the study was therefore to compare the data on harbor porpoise parasitofauna from this subpopulation with those on porpoises from other areas. The study included 37 individuals from 1995 to 2019; eight species of parasites were found (prevalence 83.8%, mean intensity 724.2, range 2–3940), with a predominance of lung nematodes (*Stenurus minor* (94.7%), *Torynurus convolutus* (69.4%), *Pseudalius inflexus* (63.8%), *Halocercus invaginatus* (22.2%); the highest intensity was recorded for *S. minor* (989, 53–2928). Two species of Anisakidae (*Anisakis simplex* – 33.3%, *Contracaecum sp.* – 20.0%) were found in the digestive tracts, which were a new record for this population. The fluke *Campula oblonga* was found in the livers of 31.3% of porpoises. The tapeworm *Diphylobothrium stemmacephalum* was also recorded in the intestine of one individual; this is typical for these hosts, but previously undetected in the Baltic subpopulation. Parasites coexisted in numerous hosts, constituting a heavy burden for them. The obtained data were compared with those from the *P. phocoena* parasitofauna from other regions, based on a compiled checklist (1809–2021) including all species of porpoise parasites (55 taxa). Compared to the worldwide porpoise parasitofauna checklist, the number of parasites found in the nominative subspecies (Baltic Proper subpopulation) is small: including only 10 taxa (eight in the current study). These species are typical of porpoises and usually the most common; however, the level of infection of Baltic porpoises (intensity and total parasite load) is very high, which can undoubtedly have a negative impact on their condition and overall health.

1. **Introduction**

Some of the smallest mammals found in oceanic waters are the porpoises (Cetacea; Odontoceti; Phocoenidae). This group comprises three genera and seven species, four of which occupy the widely-distributed genus *Phocoena* (Committee on Taxonomy, 2020). One of the best known taxa is the harbor porpoise *Phocoena phocoena* (Linnaeus, 1758). Its taxonomy seems to play a significant role in the diversity of its parasitofauna and its importance. The development of parasitofauna follows an evolutionary path associated with the formation of local populations and the scope and possibility of the exchange of host individuals, as well as local behavior patterns, including the quality and diversity of diet.

The harbor porpoise is viewed as a polytypic species, with geographically-varied populations forming three subspecies: *P. phocoena phocoena* (Linnaeus, 1758) the Atlantic harbor porpoise, *P. p. relicta* Abel, 1905 the Black Sea harbor porpoise and *P. p. vomerina* (Gill, 1865) the Pacific harbor porpoise. However, recently it was considered expedient to isolate a fourth subspecies, *P. p. meridionalis* Fontaine et al. (2014), from the southern waters of the Northeast Atlantic off the coasts of Iberia and Mauritania (Fontaine, 2016; Fontaine et al., 2014). All are included in the global The IUCN Red List as critically endangered species. As part of an assessment of the condition and health threats of these mammals, it is important to conduct parasitological monitoring. The aim of the study was therefore to compare the data on harbor porpoise parasitofauna from this subpopulation with those on porpoises from other areas. The study included 37 individuals from 1995 to 2019; eight species of parasites were found (prevalence 83.8%, mean intensity 724.2, range 2–3940), with a predominance of lung nematodes (*Stenurus minor* (94.7%), *Torynurus convolutus* (69.4%), *Pseudalius inflexus* (63.8%), *Halocercus invaginatus* (22.2%); the highest intensity was recorded for *S. minor* (989, 53–2928). Two species of Anisakidae (*Anisakis simplex* – 33.3%, *Contracaecum sp.* – 20.0%) were found in the digestive tracts, which were a new record for this population. The fluke *Campula oblonga* was found in the livers of 31.3% of porpoises. The tapeworm *Diphylobothrium stemmacephalum* was also recorded in the intestine of one individual; this is typical for these hosts, but previously undetected in the Baltic subpopulation. Parasites coexisted in numerous hosts, constituting a heavy burden for them. The obtained data were compared with those from the *P. phocoena* parasitofauna from other regions, based on a compiled checklist (1809–2021) including all species of porpoise parasites (55 taxa). Compared to the worldwide porpoise parasitofauna checklist, the number of parasites found in the nominative subspecies (Baltic Proper subpopulation) is small: including only 10 taxa (eight in the current study). These species are typical of porpoises and usually the most common; however, the level of infection of Baltic porpoises (intensity and total parasite load) is very high, which can undoubtedly have a negative impact on their condition and overall health.

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https://doi.org/10.1016/j.ijppaw.2021.07.002

Received 28 May 2021; Received in revised form 9 July 2021; Accepted 10 July 2021

Available online 13 July 2021

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being threatened to varying degrees, and the nominative subspecies has been assigned with LC (Least Concern), although there are regional differences here. Therefore the Western Baltic subpopulation has a status Vulnerable (VU), and the most threatened is the Baltic Sea subpopulation, which has been classified as Critically Endangered (CR) (HELCOM, 2013).

The harbor porpoise population of the Baltic Sea drastically decreased in the 20th century: according to data from 1995, there were only 599 individuals (Hiby and Lovel, 1996 as cited in Teilmann, 2011), and this number had fallen to 93 in 2002 (Berggren et al., 2004 as cited in Teilmann, 2011). However, these numbers were estimated based on a small amount of data. A more reliable determination of their numbers was made possible by the data collected as part of Static Acoustic Monitoring of the Baltic Sea Harbor Porpoise (SAMBAH), which in 2014 were estimated at 447 individuals (Pawliczka, 2011; Pawliczka personal comm.). Since the 1990s, regular observations of the harbor porpoise distribution have been conducted in the Polish zone of the Baltic Sea; although their constant presence has been noted, they remain rare animals, with no signs of improvement in their numbers (Pawliczka, 2011).

Genetic studies of P. p. phocoena show that a geographic stratification exists, resulting in the formation of two or three subpopulations depending on the source (Wiemann et al., 2010): apart from the mentioned Baltic Sea subpopulation (Baltic Proper), other subpopulations have been identified in the North Sea (including Skattegat) and the Belt Sea (Wiemann et al., 2011). These subpopulations demonstrate a minor dispersal level, amounting to about 1%, as the exchange of specimens between them is low in relation to the total population size (Wiemann et al., 2011). However, these subpopulations are characterized by substantial asymmetry in size, with only several hundred specimens recorded within the Baltic Proper against tens of thousands in the remaining regions (Hammond et al., 2002). Indeed, the harbor porpoises of the Baltic Proper subpopulation differ from other subpopulations of this subspecies in terms of morphology and genetics, and as such, they should be subject to a special level of conservation (Wiemann et al., 2010).

The formation of a local population is probably due to porpoises’ strong fidelity to their natal site. Although it was observed that they moved along the coasts, they are usually relatively sedentary and usually do not leave a certain area for a long time (Bjerge and Tolley, 2018). In turn, local conditions also determine the diet, as porpoises are considered not very picky and use the food base available in a given place and season, mainly small fish (Pawliczka, 2011; Winkler et al., 2011). However, their diet in the Baltic Sea differs from that in other regions. The food contains a relatively large proportion of gobies (especially in young porpoises), as well as herring Clupea harengus Linnaeus, 1758, Atlantic cod Gadus morhua Linnaeus, 1758, and eelpout Zoarces viviparus (Linnaeus, 1758). While in the transitional region between the Baltic Sea and the North Sea, the share of herring and gadids is significant, with a much smaller proportion of gobies (Winkler et al., 2011).

Undoubtedly, the existence of local populations may favor the formation of parasitofauna groupings with specific traits. On the other hand, their migration potential, as well as their certain flexibility in terms of food choice, i.e. small fish of various species, may result in the formation of universal parasitofauna patterns for the species throughout its distribution. The aim of the present analysis is to compare data on the parasitofauna of the critically-endangered Baltic Sea subpopulation with that obtained from other subspecies of harbor porpoise with different areas of distribution. The findings may prove valuable in the assessment of the parasitological threats to these rare mammals. Furthermore, an accurate determination of the prevalence may assist the assessment of the condition and health of the hosts.

2. Materials and methods

2.1. Detection of parasites in Phocoena phocoena from the polish coast of the Baltic Sea

The harbor porpoises used in the study were collected in the years 1995–2019; all were found dead on the shore or collected from fishing bycatches on the Polish coast of the Baltic Sea (Baltic Proper, South Baltic). The harbor porpoises were transported to the Hel Marine Station, University of Gdańsk (Hel, Poland). The specimens were stored at −20 °C until further analyses.

Thirty-seven harbor porpoises were examined (Table 1). However, it was not always possible to analyze whole mammals and all their organs. Only the digestive tracts, hearts, lungs and tracheae were available for porpoises no. 42–53, the heads, lungs, tracheae and hearts for porpoises no. 75–84, and only the stomach for porpoise no. 109. Furthermore, data concerning Stenurus minor nematodes from porpoises no. 54–60 were not included because they had already been published by Kijewska et al. (2003).

The animals were measured to an accuracy of 1 cm and weight to an accuracy of 1 kg, and the sex was determined, followed by a comprehensive parasitological (helminthological) examination. The ear canals, nasal cavity, throat, larynx, trachea, bronchi, lungs, oesophagus, stomach, small intestine, large intestine, pancreas, liver and bile ducts, heart, pulmonary arteries, spleen and kidneys were examined. The liver, kidneys, pancreas and spleen were dissected into smaller pieces and reviewed using a stereoscopic microscope. The trachea and bronchi were cut longitudinally; the lungs were cut along the bronchi, so as to avoid damaging the possible contents, followed by macroscopic examination, and the contents were rinsed with tap water. Similarly, the heart and blood vessels were cut, rinsed with water and the content was observed under a stereoscopic microscope. The contents of the digestive tracts were examined by decantation, in which heavier elements, including parasites, settle faster in water. After allowing the precipitate to settle (20–30 min), the supernatant was carefully poured off and more water was added to the remaining portion. This procedure was repeated one more time, and the parasites were collected from the sediment.

The collected parasites were fixed in 70%ethyl alcohol. The nematodes were cleared in lactophenol to allow identification; some nematodes were mounted in glycerol gelatin or in polyvinyl-lactophenol. Any trematodes or cestodes were stained with alcohol-borax carmine solution and lactic acid carmine, respectively, and then dehydrated in an alcohol series (80, 90, 2×99%), cleared in xylene/benzyl alcohol and mounted in Canada balsam (Rolfiecñi, 2002, 2007; Rolfiecñi et al., 2021).

The prevalence and intensity (range, mean) were calculated to determine the level of host infection (Margolis et al., 1982).

2.2. The checklist structure

The checklist was drawn up based on publications (112 items) from the period between 1809 and 2021. The bibliographic search was supplemented by information from Google Scholar, Marine Mammals Research and Conservation Discussion (MARMAM), PubMed, ResearchGate, Scopus, ScienceDirect, Web of Sciences, and World Register of Marine Species (WoRMS). It also contains own unpublished data, marked in the list as ‘this study’. The species have been arranged in systematic order, and then in alphabetical order. The list further includes information on the microhabitat and geographic distribution of the parasites. Data concerning individual subpopulations of the nominative subspecies are listed (Table 2).
Table 1
Sampling details for the harbor porpoises examined with numbers of recovered parasites.

| Host catalog no. | Collection date | Locality            | Sex (age) | Length [cm]/ weight [kg] | Parasite numbers |
|------------------|-----------------|---------------------|-----------|--------------------------|------------------|
|                  |                 |                     |           |                          | C. o.    | D. s.    | A. s.   | C. sp. | H. i. | P. l. | S. m. | T. c. |
| 42               | 10.1995         | Władysławowo       | F (4)     | 165/57                   | 98       | 7        |
| 43               | 12.1995         | Jantar               | F (6)     | 167/68                   | 47       |
| 44               | 03.1996         | Ustka               | F (2)     | 30/35                    | 5        |
| 45               | 03.1996         | Ustka               | M (0+)    | 127/38                   | 2        |
| 46               | 03.1996         | Jantar               | M (4)     | 153/44                   | 49       |
| 47               | 03.1996         | Rowy                | M (2)     | 135/36                   |          |
| 48               | 03.1996         | Krynica Morska      | F (1)     | 132/35                   |          |
| 49               | 04.1996         | Rewa-Jantar         | M (5)     | 146/45                   | 44       |
| 50               | 04.1996         | Jarosławiec         | M (3)     | 151/48                   | 3        |
| 51               | 04.1996         | Gąski               | M (1+)    | 143/37                   |          |
| 52               | 07.1996         | Jantar               | M        | 130/26                   | 15       |
| 54               | 07.1996         | Uściecie            | M        | 120/25                   | 9        |
| 55               | 09.1997         | Władysławowo        | M        | 110/25                   |          |
| 57               | 12.1997         | Jantar (Vistula Spit) | F    | 117/21                   | 53       |
| 58               | 01.1998         | Gulf of Gdańsk      | F        | 114/30                   | 1        |
| 59               | 01.1998         | Gulf of Gdańsk      | F        | 155/28                   | 32       |
| 60               | 11.1998         | Ustka               | M        | 134/33                   | 58       |
| 61               | 11.1999         | Niechorza           | M (1)     | 120/30                   | 89       |
| 62               | 12.1999         | Puck Bay            | M (2)     | 149/40                   | 17       |
| 63               | 03.2000         | Krynica Morska      | M (2)     | 144/46                   | 71       |
| 64               | 03.2000         | Goksi Wschodnie     | F (1)     | 115/29                   | 156      |
| 67               | 08.2008         | Ustka               | F (1)     | 131/44                   | 18       |
| 68               | 11.2000         | Ustka               | F (9)     | 171/80                   | 64       |
| 69               | 11.2000         | Kuznica             | M (1)     | 149/44                   | 12       |
| 70               | 01.2001         | Dziwno              | M (2)     | 142/43                   | 61       |
| 71               | 03.2000         | Jantar               | M (1)     | 139/36                   | 35       |
| 75               | 04.2003         | Darłówko            | F (2)     | 143/43                   | 34       |
| 76               | 01.2003         | Uściecie            | M (2)     | 134/47                   | 16       |
| 77               | 02.2003         | Darłówko            | F (1)     | 105/33                   | 53       |
| 78               | 03.2003         | Świebno             | M (1,5)   | 119/35                   | 26       |
| 79               | 04.2003         | Puck Bay            | M (2)     | 137/40                   | 14       |
| 80               | 04.2003         | Puck Bay            | M (2)     | 140/43                   | 56       |
| 84               | 11.2004         | Puck Bay            | F (2)     | 139/36                   | 21       |
| 109              | 08.2013         | Pogorzela            | M        | 141/32                   |          |
| 136              | 03.2018         | Rowy                | M (juv)   | 127/40                   | 52       |
| 149              | 07.2019         | Dubki               | M (juv)   | 122                     | 54       |
| 150              | 07.2019         | Ustka               | M        | 82/6                     |          |

A. s.: Anisakis simplex; C. o.: Campula oblonga; C. sp.: Contracaecum sp.; D. s.: Diphyllobothrium stemmacephalum; F: female; F+: pregnant female; H. i.: Halocercus invaginatus; juv: juvenile; M: male; P. i.: Pseudalius inflexus; S. m.: Stenurus minor; T. c.: Torynurus convolutus.

* The digestive tracts (stomachs, intestines, pancreas, livers and bile ducts), hearts and respiratory tracts (trachea and lungs) were examined.

* Data on parasites Stenurus minor in Kieżewska et al. (2003).

* The heads, hearts and respiratory tracts (trachea and lungs) were examined.

* The stomach was examined.

3. Results

3.1. Parasites in Phoinoa phocoena from the polish coast of the Baltic Sea

The studied harbor porpoises were found to contain eight parasite species, classified into digeneans, cestodes and nematodes (Table 1). The overall prevalence, i.e. including all parasites, among the hosts was 83.7%, mean intensity 724.2 and intensity 2–3940.

The predominant parasites were nematodes, particularly the species found in the respiratory system, and sometimes in the heart: Halocercus invaginatus, Pseudalius inflexus, Stenurus minor and Torynurus convolutus (Table 3). Of these, S. minor was predominant (94.7% of the infected harbor porpoises), followed by T. convolutus (69.4%) and P. inflexus (63.8%). In addition, the highest infection intensity was found for S. minor (range 53–2928; mean 989.0). Furthermore, the infection intensity of S. minor in individual specimens (data concerning only harbor porpoises no. 61–64, 67–71, 75–80, 84, 136 and 149) typically reached very high values of several hundred nematodes per host: maximum intensities were 1401 (left ear, porpoise no. 68) and 1527 (right ear, porpoise no. 68) (Table 4).

In addition, two Anisakidae species were recorded in the gastrointestinal tract of the examined harbor porpoises: the larvae and adults of Anisakis simplex in 33.3% of tested harbor porpoises and Contracaecum spp. in 20.0% of porpoises. The majority of gastrointestinal nematodes were found in the stomachs (A. simplex – 992 ind. Contracaecum spp. – 18 ind.), with only individual specimens being present in the intestines (A. simplex – 3 ind. Contracaecum spp. – 10 ind.). In two harbor porpoises (no. 68 and 69), the stomachs had ulcerative lesions of the gastric mucosa. In addition, the Campula oblonga trematode was found in the livers of 31.3% of the harbor porpoises, and two specimens of Diphyllobothrium stemmacephalum cestode were found in the intestine of a single individual. In addition, the presence of C. oblonga was noted in the bile ducts, resulting in their periductular fibrosis.

Parasite co-occurrence was also analyzed for 11 harbor porpoises which underwent full dissections, i.e. covering all organs/systems. All specimens contained S. minor nematodes, and they were always accompanied by other parasites of the respiratory system, heart or the digestive system (liver, intestines, stomach). Six parasite species were observed in three harbor porpoises, five specimens in three porpoises, four species in three porpoises and three species in two porpoises (Fig. 1). Regarding the co-occurrence of respiratory tract nematodes of the family Pseudaliidae, three porpoises were found to have four species (S. minor, H. invaginatus, P. inflexus and T. convolutus), five porpoises – three species (S. minor, P. inflexus and T. convolutus), one porpoise – three species (S. minor, H. invaginatus, P. inflexus), two porpoises – two species...
Table 2
Parasites species of the harbor porpoises in the Baltic Sea area, based on new records and the literature (for references see the section checklist in this paper).

| Parasite species Examined | Baltic Proper | Belt Sea | North Sea/ Skagerrak |
|--------------------------|---------------|----------|-----------------------|
| **APICOMPLEXA**          |               |          |                       |
| Toxoplasma gondii        | +             |          |                       |
| TREMATODA                |               |          |                       |
| Brauna cordiformis       | +             |          |                       |
| Campoda oblonga          | +             |          |                       |
| Pholeter gastrophilus    | +             |          |                       |
| GESTODA                  |               |          |                       |
| Diphyllobothrium        | +             |          |                       |
| stemmacephalum           | +             |          |                       |
| Diphyllobothrium sp.     | +             |          |                       |
| **NEMATODA**             |               |          |                       |
| Anisakis simplex         | +             |          |                       |
| Anisakis sp.             |               |          |                       |
| Contracaecum osculatum   | +             |          |                       |
| ACANTHOCEPHALA          |               |          |                       |
| Torynurus convolutus     | +             |          |                       |
| Stenurus minor           | +             |          |                       |
| Pseudalius inflexus      | +             |          |                       |
| Halocercus invaginatus   | +             |          |                       |
| Halocercus taurica       | +             |          |                       |
| Halocercus sp.           | +             |          |                       |
| Hypopterygion aduncum    | +             |          |                       |
| *Pseudolisa inflexus*    | +             |          |                       |
| Stemurus minor           | +             |          |                       |
| Torynurus convolutus     | +             |          |                       |
| ACANTHOCEPHALA          |               |          |                       |
| Bolbosoma sp.            | +             |          |                       |
| Corynosoma semmerme      | +             |          |                       |
| Corynosoma strumatum     | +             |          |                       |
| **AMPHIPODA**            |               |          |                       |
| Isocymaus delphinii      | +             |          |                       |

*This study.
1. Andersen (1974) only gives “Danish waters”.
2. Not detailed (Herreras et al., 1997).

Table 3
Prevalence, intensity and infection site of parasites species collected from the harbor porpoises in the Baltic Proper examined in present study (1995–2019).

| Parasite species Examined | Prevalence [%] | Intensity range | Mean intensity | Microhabitat                           |
|--------------------------|----------------|-----------------|----------------|----------------------------------------|
| TREMATODA                | 31.3           | 4-162           | 36.7           | liver, bile ducts                      |
| Campoda oblonga          | 3.4            | 2               | 2.0            | intestine                              |
| GESTODA                  | 33.3           | 1-777           | 90.5           | stomach, intestine                     |
| Diphyllobothrium        | 20.0           | 2-9             | 4.7            | stomach, intestine                     |
| stemmacephalum           |                |                 |                |                                        |
| **NEMATODA**             | 22.2           | 2-35            | 17.8           | lungs,                                |
| Anisakis simplex         | 36.8           | 4-156           | 49.3           | lungs, heart                           |
| Contracaecum sp.         | 94.7           | 53-2928         | 989.0          | middle ear, Eustachian tube, inner ear, nasal cavity, throat, larynx, lungs |
| Halocercus invaginatus   | 69.4           | 1-303           | 82.1           | lungs, heart, trachea                  |

* Selected organs were examined (see Materials and methods).
3.3.2. Apicomplexa

Cryptosporidium spp.
Microhabitat: large intestinal content
Locality: NE Atlantic (Spain)
References: Reboredo-Fernández et al., 2015

Sarcocystis neurona
Dubey, Davis, Speer, Bowman, De. Lahunta, Granstrom, Topper, Hamir and Suter 1991
Microhabitat: brain
Locality: NE Pacific (British Columbia/Washington)
References: Barbosa et al., 2015; Rejmanek et al., 2010; Gibson et al., 2011

Sarcocystis sp.
Microhabitat: skeletal musculature, tongue
Locality: Davis Strait (Greenland)
References: Lehnert et al., 2014; Wunschmann et al., 2001

Toxoplasma gondii (Nicolle et Manceaux, 1908)
Microhabitat: blood antibodies
Locality: NE Atlantic (England and Wales), North Sea (Netherlands)
References: Barbosa et al., 2015; Cabezón et al., 2004; Forman et al., 2009; Gibson et al., 2011; Herder et al., 2015; Van de Velde et al., 2016

Coccidia n. det.
Microhabitat: brain
Locality: NE Pacific (British Columbia/Washington)
References: Barbosa et al., 2015.

3.3.3. Digenea

Braunina cordiformis Wolf, 1903
Microhabitat: stomach, wall
Locality: North Sea (Netherlands), not mentioned
References: Gaskin et al., 1974; Kastelein and Lavaleije, 1992

Campula oblonga Cobbold, 1858
Microhabitat: bile/hepatic ducts, egg in feces, liver, mammary gland, pancreas, pancreatic ducts, stomach, not mentioned
Locality: NW Atlantic (Newfoundland and Labrador, New England, Newfoundland and Labrador, Quebec and Maritime Provinces Canada, Davies Strait, NE Atlantic (British waters, England, Wales, Faroe Islands, Firth of Forth, France, Iceland, English Channel/North Sea (Belgium and France), North Sea (Belgium, Denmark, Germany, Netherlands, Scotland), North Sea/Baltic Sea (Denmark, Germany), Norwegian waters, NE Pacific (British Columbia, Canada, Friday Harbor Washington, Oregon, Salish Sea), not mentioned
References: Andersen, 1974; Baker and Martin, 1992; Balbuena et al., 1987; Bratley and Stenson, 1995; Brosens et al., 1996; Ching and Robinson, 1959; Clausen and Andersen, 1988; Cobbold, 1858; Dailey and Stroud, 1978; Fenton et al., 2017; Fernandez et al., 1998; Fraija-Fernández et al., 2015; Geraci, 1978; Gibson and Harris, 1979; Gibson et al., 1996; Jauniaux et al., 2002; Kastelein et al., 1990; Kastelein and Lavaleije, 1992; Kinze, 1985; Larsen, 1995; Lehnert et al., 2005; 2014; Margolis and Araí, 1984; Norman et al., 2004; Rokicki et al., 1997; Siebert et al., 2001; 2006; 2010; 2020; Smith and Threlfall, 1979; Wunschmann et al., 2011; Zier and Gaydos, 2015

Synthesium mironovi (Krotov and Delyamure, 1952)
(= Orthosplanchus mironovi, = Hadwenius mironovi)
Microhabitat: duodenum, liver and pancreas, stomach, not mentioned
Locality: NE Pacific (Canada, Oregon, Salish Sea), Davis Strait (Greenland)
References: Aznar et al., 2006; Baker and Martin, 1992; Fraija-Fernández et al., 2017; Gibson and Harris, 1979; Gibson et al., 1998; Herreras et al., 1997; Jauniaux et al.; 2002; 2008; Kriukhizhin and Birkun, 1994; Lehnert et al., 2005; 2010; Odnhr, 1914; 1911; Price 1932; Siebert et al., 2001; 2006; 2014; 2020

Synthesium nipponicum (Yamaguti, 1951) (= Hadwenius nipponicus)
Microhabitat: duodenum, stomach, not mentioned
Locality: NE Pacific (Canada, Friday Harbor Washington, Oregon, Salish Sea)
References: Ching and Robinson, 1959; Dailey and Stroud, 1978; Margolis and Araí, 1989; Zier and Gaydos, 2015

3.3.4. Cestoda

Bothriocephalus sp.
Microhabitat: not mentioned  
Locality: Danish waters  
References: Andersen, 1974.

**Diphyllobothrium lanceolatum** (Krabbe, 1865)  
Microhabitat: not mentioned  
Locality: Baltic Sea  
References: Schmidt-Ries, 1939 as cited in Delyamure et al., 1985.

**Dibothriocephalus latus** (Linnaeus, 1758) (=Diphyllobothrium latum)  
Microhabitat: intestine  
Locality: Black Sea  
References: Borcea, 1935.

Remarks: doubtful record for *P. phocoena* (Delyamure et al., 1985)

**Diphyllobothrium stemmacephalum** Cobbold, 1858  
Microhabitat: intestine1-3,4,5, not mentioned6  
Locality: NW Atlantic (Newfoundland and Labrador), NE Atlantic (England and Wales), North Sea (Belgium, Denmark, Netherlands), North Sea/Baltic Sea (Denmark, Germany), Baltic Sea (Poland), Black Sea (Crimea), not mentioned7  
References: Andersen, 1974; Cobbold, 1858; Andersen, 1986; Brattey and Stenson, 1995; Andersen, 1986; Cobbold, 1858; Lehnert et al., 2014.

**Pyramicocephalus phocarum**  
Microhabitat: stomach  
Locality: NE Pacific (Washington, Oregon), PW Pacific (Japan)  
References: Mattiucci et al., 2014; Jauniaux et al., 2002.

Remarks: not mentioned8

**Anisakis simplex** (Diesing, 1860) (=Ascaris simplex)  
Microhabitat: stomach  
Locality: NE Atlantic (Scotland), not mentioned9  
References: Stiles and Hassall, 1899.

**Anisakis typica** (Diesing, 1860)  
Microhabitat: stomach  
Locality: NE Atlantic (Scotland), not mentioned10  
References: Stiles and Hassall, 1899; Smith, 1989.

**Ascarids n. det.**  
Microhabitat: feces2, stomach1,3  
Locality: North Sea (Netherlands), North Sea/Baltic Sea (Denmark), NE Pacific (Washington)  
References: Andersen, 1974; Kastelein and Lavaleije, 1992; Scott and Fisher, 1958; Siebert et al., 2006; Thompson et al., 1972.

**Contracaeum osculatum** (Rudolphi, 1802)  
Microhabitat: intestine  
Locality: NW Atlantic (Newfoundland and Labrador), NE Atlantic (Scotland), Baltic Sea (Denmark and Germany)  
References: Andersen, 1974; Siebert et al., 2006; Siebert et al., 2020.

**Crassicauda sp.**  
Microhabitat: blubber1-2,4,8, cranial sinuses4, frontal sinuses4, mammary1-2,10, muscle10, subcutaneous thoracic wall1, subcutis9,10,
perimyscular fascia and subcutaneous fat, not mentioned, not detailed
Locality: NW Atlantic (Quebec and Maritime provinces Canada), Gulf of St. Lawrence, Davies Strait (Greenland), NE Atlantic (British waters, England and Wales), Black Sea (Crimea), NE Pacific (British Columbia, Canada, Oregon, Salish Sea). References: Baker and Martin, 1992; Dailey and Stroud, 1978; Faulkner et al., 1998; Fenton et al., 2017; Gibson et al., 1998; Krivokhizhin and Birkun, 1994; Lehner et al., 2014; Margolis and Arau, 1989; Norman et al., 2004; Wunschmann et al., 2001; Zier and Gaydos, 2015.

**Halocercus inv agnatus** (Quckett, 1841) (=Filaria inflexocaudata, =H. inflexocaudata, =H. ponticus, =Pseudalium tumidus, =Strongylus invaginatus)

Microhabitat: branchioles, lungs, egg in feces, inner ear, lower airways, lungs, oesophagus, pulmonary blood vessels, respiratory tract, right ventricle of heart, trachea. References: Abollo et al., 1998; Anderssen, 1974; Arnold and Gaskin, 1975; Baker and Martin, 1992; Balbuena et al., 1994; Baylis and Daubney, 1925; Dailey and Stroud, 1978; Delyamure, 1955; Dougerty, 1943; Van Elk et al., 2019; Gibson and Harris, 1979; Gibson et al., 1998; Kastelein and Lavalee, 1992; Krivokhizhin and Birkun, 1994; Larsen, 1995; Lehner et al., 2005; 2007; 2014; Lukasiak, 1939; Moser and Rhinehart, 1990; 2002; Pekmezci et al., 2013; Quckett, 1844; 1845; Rogan and Berrow, 1996; 2003; Rokicki et al., 1997; Scheffer and Slipp, 1948; Schmidt-Ries, 1926; Schneider, 1866; Siebert et al., 2006; 2020; Slob et al., 1996; Smith and Threlfall, 1973; Stroud and Roife, 1979; Szefer et al., 1996; Verryi, 2012; Zier and Gaydos, 2015; this study.

**Halocercus taurica** Delyamure, 1942

Microhabitat: lungs, not mentioned
Locality: NW Atlantic (Bay of Fundy), NE Atlantic (England and Wales), Irish waters, North Sea (Netherlands), Marmara Sea (Turkey), Azov Sea/Black Sea (Crimea), NE Pacific (Vancouver Island). References: Arnold and Gaskin, 1975; Delyamure, 1955; Gibson et al., 1998; Krivokhizhin and Birkun, 1994; Pekmezci et al., 2013; Rogan and Berrow, 1996; Slob et al., 1997.

**Halocercus sp.**

Microhabitat: lungs, not mentioned
Locality: NW Atlantic (Newfoundland). References: Fenton et al., 2017; Jauniaux et al. 2002; Norman et al., 2004; Smith and Threlfall, 1973; Wunschmann et al., 2001; Zier and Gaydos, 2015.

**Hydrothylacium aduncum** (Rudolphi, 1802)

Microhabitat: stomach and intestine, not detailed
Locality: North Sea/Baltic Sea (Denmark), Baltic Sea (Denmark, Germany). References: Herreras et al., 1997; Siebert et al., 2020.

**Pharusus sp.** (=Pseudostenurus)

Microhabitat: not mentioned
Locality: NW Atlantic (Newfoundland).

References: Smith and Threlfall, 1973.

Remarks: doubtful record for *P. phocoena* (Arnold and Gaskin, 1975).
Canada¹³, Gulf of Saint Lawrence¹², Bay of Fundy², Newfoundland², Davis Strait (Greenland²⁰,²⁵,⁴¹), Marmara Sea (Turkey⁶), Azov Sea/Black Sea¹ (Crimea⁵), NE Pacific (Oregon³,³⁹, Salish Sea², San Francisco Bay¹⁵), not mentioned¹⁵,²⁹,³³,⁴² References: Andersen (1974)¹; Arnold and Gaskin (1975)²; Baker and Martin (1992)²; Balbuena et al. (1987)²; Baylis and Daubney (1925)⁵; Brosens et al. (1996)⁶; Clausen and Andersen (1988)⁷; Dailey and Stroud (1978)⁸; Delamare (1957)⁹; Dougherty (1943)¹⁰; Van Elk et al., 2013¹¹; Faulkner et al. (1998)¹²; Fenton et al. (2017)¹³; Gabel et al. (2020)¹⁴; Gibson and Harris (1979)¹⁵; Gibson et al. (1998)¹⁶; Jauniaux et al. (2002)¹⁷; 2008¹⁸; Kijewska et al. (2003)¹⁹; Kinze (1989)²⁰; Kirkwood et al. (1997)²¹; Krivokhizhin and Birkun (1994)²²; Larsen (1995)²³; Lehnter et al. (2005)²⁴; 2014²⁵; 2017²⁶; Morell et al. (2017)²⁷; Pekmezci et al. (2013)²⁸; Quekett (1844)²⁹; Ragan and Berrow (1996)³⁰; Rocki et al. (1997)³¹; Schmidt-Ries (1939)³²; Schneider (1866)³³; Siebert et al. (2001)³⁴; 2002³⁵; 2010³⁶; 2020³⁷; Slob et al. (1996)³⁸; Stroud and Roffe (1979)³⁹; Wohsein et al. (2019)⁴⁰; Wunschmann et al. (2001)⁴¹; Zier and Gaydos (2015)⁴², this study⁴³

Stenurus sp.
Microhabitat: lungs¹, not mentioned²
Locality: NW Atlantic (Quebec and Maritime Provinces Canda¹), NE Pacific (British Columbia¹, Salish Sea²)

References: Fenton et al. (2017)¹; Zier and Gaydos (2015)²

Torynorynus convolusus (Kühn, 1829) (≡Pharusus convolusus, =Prosthoeoacerus convolusus, =Pseudolus convolusus, =Strongylos convolusus, =Torynorynus bicostatus)
Microhabitat: air sacs¹⁰; airways⁵,¹¹,¹²; blood vessels¹⁶,²³,²⁸; bronchial¹¹,¹²,¹³,¹⁷; ear sinuses¹¹; bronchi¹¹,¹²,¹³,¹⁷; heart²⁹,³⁶; lungs²⁸,³⁹,¹₂,¹₆,¹₇,¹⁹,₂₁,₂₄,₂⁷,⁻; pulmonary blood vessels¹⁷,¹₉,₂₃, respiratory tract²²; trachea¹₃,¹₄,¹₈,¹₉,₂₅,⁻; not mentioned²,⁵,²⁹
Locality: NE Atlantic (British waters³, England and Wales¹³,¹₄,¹₇,²₀; Firth of Forth²; France⁴; Irish waters²⁴; Iceland²⁰; Davies Strait (Greenland¹⁵); Norwegian waters²⁵,³¹; English Channel (Luc-sur-Mer France¹); English Channel/North Sea (Belgium and France¹⁵,¹₆; North Sea (Belgium²⁰; England¹³; Germany¹₀,²₂,²₉,³₁,³₄; Netherlands²,¹₀,¹₆,¹₈,³₃; North Sea/Baltic Sea (German²,⁶;¹₀; Polish²,⁹,²₉,³₁; NW Atlantic (Bay of Fundy²; Gulf of Saint Lawrence¹⁵; Labrador¹⁵; New Brunswick¹⁵; Quebec a Maritime provinces Canada¹²), NE Pacific (British Columbia¹³; Oregon³; Salish Sea³⁹, Washington²⁹; San Francisco Bay¹⁵; Vancouver Island¹³); not mentioned²³
References: Abeloos (1932)¹; Arnold and Gaskin (1975)²; Baker and Martin (1992)²; Balbuena et al. (1987)¹⁸;¹⁹,⁴⁴; Brosens et al. (1996)⁶; Cobold (1858)²; Dailey and Stroud (1978)⁸; Dougherty (1943)⁵; Van Elk et al., 2013¹¹; Faulkner et al. (1998)¹²; Fenton et al. (2017)¹³; Gabel et al. (2020)¹⁴; Gibson and Harris (1979)¹⁵; Gibson et al. (1998)¹⁶; Jauniaux et al. (2002)¹⁷; 2008¹⁸; Kijewska et al. (2003)¹⁹; Kinze (1989)²⁰; Kirkwood et al. (1997)²¹; Krivokhizhin and Birkun (1994)²²; Larsen (1995)²³; Lehnter et al. (2005)²⁴; 2014²⁵; 2017²⁶; Morell et al. (2017)²⁷; Pekmezci et al. (2013)²⁸; Quekett (1844)²⁹; Ragan and Berrow (1996)³⁰; Rocki et al. (1997)³¹; Schmidt-Ries (1939)³²; Schneider (1866)³³; Siebert et al. (2001)³⁴; 2002³⁵; 2010³⁶; 2020³⁷; Slob et al. (1996)³⁸; Stroud and Roffe (1979)³⁹; Wohsein et al. (2019)⁴⁰; Wunschmann et al. (2001)⁴¹; Zier and Gaydos (2015)⁴², this study⁴³

References: Brattey and Stenson (1995)¹; Dailey and Stroud (1978)²; Herreras et al. (1997)³

Corynosoma alaksensis Golvan, 1959
Microhabitat: intestine
Locality: Bering Sea (Hooper Bay, Alaska)

Corynosoma somerme (Forssell, 1904) (=Echinorhynchus semerrmis)
Microhabitat: intestine¹⁻³

Locality: Baltic Sea (Finland¹⁻²), not mentioned ³

References: Forssell (1904)¹; 1905²; Lühe, 1911³

Corynosoma strumosum (Rudolphi, 1802) (=Echinorhynchus strumosus)
Microhabitat: intestine¹⁻²,³⁻⁵

Locality: NE Atlantic (Icelandic³), Baltic Sea (Finland¹⁻²), NW Pacific (Hokkaido Japan³), not mentioned³

References: Forssell (1904)¹; 1905²; Lühe (1911³; Sasaki et al. (2019)⁴; Siebert et al. (2006)⁵

Corynosoma spp.
Microhabitat: intestine
Locality: NE Pacific (Canada)

References: Margolis and Araï (1989)³.

3.3.7. Anhipoda

Isocyamus delphini (Guérin-Méneville, 1836)
Microhabitat: skin¹⁻³

Locality: English Channel/North Sea (Belgium and France¹), North Sea (Germany², Netherlands³)

References: Jauniaux et al. (2002)¹; Lehnter et al. (2007)²; Stock, 1973a,b,³

Isocyamus deltobranchium Sedlak-Weinstein, 1992
Microhabitat: skin

Locality: North Sea (Germany, Netherlands)

References: Lehnter et al. (2021).

3.3.8. Copepoda

Pennella balaenopterae Koen et Danielissen, 1877
Microhabitat: skin

Locality: Aegean Sea (Bodrum Peninsula Turkey)

References: Danyer et al. (2014).

4. Discussion

The present study examined the parasitofauna of the harbor porpoise P. p. phocoena from the harbor Proper (south) subpopulation based on examinations of 37 specimens collected over a period of 24 years. The findings indicate the regular occurrence of eight helminth species, which have also been recorded in other studies from different regions of the world (see checklist). The results of the survey in the present study included the first finding of D. stemmacephalum cestodes and Anisakidae nematodes in the area. However, it should be noted that individual parasites exhibit different relationship ranges with different porpoises, reflected in the incidence rate and infection intensity. Typical parasites include the C. oblonga trematode, D. stemmacephalum cestode, H. invaginatus, P. inflexus, S. minor and T. convolutes nematodes; some of which are specific parasite species for this host (Delyamure, 1955; Arnold and Gaskin, 1975; Delamare et al., 1985).

Undoubtedly, the most commonly observed parasites are the nematodes; their infection prevalence typically reaches very high values, e.g. for P. inflexus it ranges from 99.0% (Belgian and German coasts), 88.0% (west of England and Wales) to 34.4% (Norwegian waters) (Balbuena et al., 1994; Brosens et al., 1996; Gibson et al., 1998). A high prevalence was also noted in the present study (63.8%), and an earlier study of southern Baltic Sea recorded a level of 88.2% (Rocki et al., 1997). Similarly, the prevalence of S. minor was found to be high as 94.7% in...
the presently-studied southern Baltic Sea population; this value is significantly higher than in previous studies from this region (47.0%). Very high prevalence values were also observed in other regions: 86.0% and 95% (consistency) in Greenland, and 88.0% off the coast of England and Wales (Rokicki et al., 1997; Gibson et al., 1998; Lehner et al., 2014).

_Torynurus convolutus_ has also demonstrated a very high prevalence in the southern Baltic Sea, i.e. 82.3% in previous studies and 69.4% in the present study, with lower levels observed in other regions: 49.0% off the coast of England and Wales, 44.0% off the Belgian and German coasts and 42.2% in Norwegian waters (Balbuena et al., 1994; Brosens et al., 1996; Rokicki et al., 1997; Gibson et al., 1998). Interestingly, regarding _H. invaginatus_, very high prevalence values were observed in Norwegian waters (98.4%), but considerably lower ones in other regions: prevalence was found to be 22.2% (present study) and only 11.8% (previously) in the southern Baltic Sea, and as low as 1.2% off the coast of England and Wales (Balbuena et al., 1994; Brosens et al., 1996; Rokicki et al., 1997; Gibson et al., 1998).

In contrast, the prevalence of _C. oblonga_ trematode infection ranged from 42.2% off the coast of England and Wales, to 28.0%, off the Belgian and German coasts, to 7.5%, around Newfoundland and Labrador (Brattey and Stenson, 1995; Brosens et al., 1996; Gibson et al., 1998). Currently, for the southern Baltic Sea, this value was 31.3%; this value is considerably lower than in the preceding study period, where only 5.9% was recorded (Rokicki et al., 1997).

The _D. stemmacephalum_ cestode, although it was described from _P. phocoena_ and has regularly been found in harbor porpoises, typically exhibits a low prevalence, ranging from 11.0% (Belgian and German coasts), 6.9% (Newfoundland and Labrador), 4.0% (coast of England and Wales), 3.4% (present, southern Baltic Sea), to 2.9% (Danish waters) (Brattey and Stenson, 1995; Brosens et al., 1996; Herreras et al., 1997; Gibson et al., 1998). In the present study on the southern Baltic Sea, it was only found in a single host. This cestode is a typical parasite of different toothed whales, and perhaps the prevalence is linked to the size of the host species reservoir, i.e. only one whale species is constantly present in the Baltic Sea, or the different availability of intermediate hosts.

A high prevalence was also observed for _A. simplex_ and _Contracecum_ spp. nematodes; however, regarding the latter, most data concerns _C. osculatum_ or specimens without any identification to a species-level, but that are supposed to be of this genus. The particularly high infection parameters of _C. osculatum_ in harbor porpoises are related to the widespread occurrence of these nematodes in the Phocidae as other final hosts. For example, _C. osculatum_ exhibited 83.8/75.9% (stomach/intestine) prevalence at Newfoundland and Labrador (Brattey and Stenson, 1995).

In turn, the level of harbor porpoise infection with _A. simplex_ varied from 60.0% (Greenland; Lehner et al., 2014), 59.5% (coast of England and Wales; Gibson et al., 1998), 47.5% (Newfoundland and Labrador; Brattey and Stenson, 1995), 38.6% (Danish waters; Herreras et al., 1997), 33.3% (southern Baltic Sea; present), 33.0% (Belgian and German coasts; Brosens et al., 1996).

One important issue concerns the predominance of nematodes inhabiting the respiratory system. Lungworms of the family Pseudaliidae were here represented by _S. minor_, a species typical for harbor porpoise and found in all _P. phocoena_ subspecies; however, it exhibited very high infection parameters in the present study (prevalence 94.7%, mean intensity 989.0, intensity 53–2928). The particularly significant value in this case is the infection intensity, which reflects the host parasite load, i.e. its pressure on the host. This high mean intensity in the population stemmed from the very high prevalence observed in certain host specimens: e.g. 2928 specimens of these parasites were found in one porpoise (no. 68), including 1401 in the left ear and 1527 in the right ear. Although opinions differ on the significance of these nematodes for the health and overall condition of harbor porpoises (Delyamure, 1955; Geraci, 1978), such a high prevalence must surely have an influence on the functioning of this system/organ, which is important for this marine mammal. Examinations of harbor porpoise from the Polish Baltic zone have already reported the presence of pathological lesions associated with a similar prevalence of these parasites (83.3%, 779.6 ind. per ear) (Kijewska et al., 2003), suggesting a possible disruption of their echolocation capabilities.

Three other Pseudaliidae species were found to have a lower prevalence in the present study (total prevalence 77.8%, mean intensity 61.0): _Torynurus convolutus_ (69.4%, 82.1), _Pseudalius inflatus_ (63.8%, 49.3) and _Halocercus invaginitus_ (22.2%, 17.8). The same three species were determined i.a. in the study on harbor porpoises from the German Wadden Sea (the southeastern part of the North Sea) in the period 2006–2018 (Reckendorf et al., 2021). It was noted that infection with pulmonary nematodes and associated secondary bronchopneumonia may have a profound impact on the health status of harbor porpoises in this region, and may even constitute the main cause for harbor porpoise mortality in the North Sea (Siebert et al., 2001, 2006; Jauniaux et al., 2002; Lehner et al., 2005; Van Els et al., 2019). However, the total prevalence of infection with these nematodes was lower than in the present study, amounting to 45.6%, and the majority of infected harbor porpoises were found to have moderate or acute infection of 38.1% and 39.0%, respectively, of harbor porpoises with a positive test result for the presence of pulmonary nematodes. In contrast, 22.9% of other specimens were found to demonstrate non-severe infection symptoms (Reckendorf et al., 2021). Based on an analysis of data from different areas of the range of _P. p. phocoena_, the authors suggest that despite the higher prevalence of infection in the northern regions (Norway, Iceland), the parasitism, is typically characterized by mild symptoms, whereas cases of severe symptoms are more numerous in research from the North Sea and Baltic Sea.

An analysis of parasite checklists of harbor porpoises according to subspecies and distribution indicates the existence of other potential threats to this cetacean. Representatives of the Apicomplexa, including _Toxoplasma gondii_, or the genera _Cryptosporidium_ and _Sarcocystis_ are sporadically mentioned. However, the absence of more comprehensive data probably stems from the fact that these unicellular parasites are rarely included in parasitological analyses of whales, which is usually include directed towards helminths. _Toxoplasma gondii_, whose life cycle is linked to terrestrial environment (final host — cat, intermediate — rodents), is often analyzed in the context of importance for accidental hosts, particularly humans, where it may have a negative impact on fetal development in the form of congenital toxoplasmosis, which can contribute to abortions or malformations. Fortunately, the knowledge base concerning the neurological importance of _Toxoplasma_ for different hosts is also increasing, including its contribution to so-called _risky_ behavior (Webster, 2001; Conrad et al., 2005).

Other records of this parasite in aquatic species, including marine mammals, suggest that its transmission and dispersal have considerably wider potential than that resulting from the simple realization of its life cycle. Although atypical hosts do not enable its sexual reproduction, they may also suffer health consequences associated with contact with the parasite. Both _T. gondii_ infection and toxoplasmosis have been described around the world in marine mammals, including whales. Congenital toxoplasmosis related to fetus infection has been reported in the Risso’s dolphin _Grampus griseus_ (Resendes et al., 2002), and in the Indo-Pacific bottlenose dolphin _Tursiops aduncus_ (Jardine and Dubey, 2002). Cases of toxoplasmosis have also been recorded in the beluga whale _Delphinapterus leucas_ (Mikaelian et al., 2003), Indo-Pacific humpback dolphin _Sousa chinensis_ (Bowier et al., 2003), spinner dolphin _Stenella longirostris_ (Migaki et al., 1990), as well as in numerous pinnipeds (Migaki et al., 1977; Holshuh et al., 1985; Conrad et al., 2005; Honmold et al., 2005) and manatees (Dubey et al., 2003; Buergel and Bonde, 1983). Cerebral toxoplasmosis and sarcocystosis have been identified as significant causes of mortality in a southern sea otter, _Enhydra lutris nereis_ (Cole et al., 2000; Kreuder et al., 2003). Therefore, it seems to be of paramount importance to determine the distribution and effect of this incidental, but pathogenic parasite of...
harbor porpoises from the threatened Baltic Sea population. So far such research has not been conducted here; this would require a change in the methodological approach and an expansion of the spectrum of the methods used.

Undoubtedly, the main research elements were analyzes of species diversity of parasitofauna and the functioning of individual parasite-host systems, including the relationship with the host (specificity, topological and topographic preferences), as well as that of the level of infection for a given species and the impact on the host. Another important issue addressed by the present study is the total load placed on the host by the parasites. Many of the examined harbor porpoises were characterized by the co-occurrence of several species of parasites, some of which were found to inhabit the same, or similar habitats, e.g. the respiratory nematodes. In such cases, it is important to obtain physical observations or case studies, as these enable the analysis of parasites of a specific host individual. In the present study, the largest (probably the oldest) specimen no. 68, a female porpoise, had the largest parasite load: 3940 specimens from five species, located in various organs, with a tropism to the ears and gastrointestinal tract. Such infection intensity not only undoubtedly results in reduced fitness and adaptability to environmental conditions, but may have an impact on the overall health of the animal and its survival. Although the parasite communities should be analyzed not only in terms of quantity, but also in qualitative terms. Some parasites, as a result of the long-term evolution of the parasite-host system, are well adapted to function in a given host, well tolerated and usually non-pathogenic. However, in this context, parasites that are less specific or new to the host, obtained as a result of favorable conditions, e.g. environmental changes, can more dangerous (Izdebska et al., 2020).

Against the global checklist of the parasites of the harbor porpoise, including 55 taxa (46 helminths), the list of parasites for the nominative subspecies from the Baltic Sea subpopulation is rather limited, being only 10 taxa. However, it should be taken into account that many records from other subspecies or populations in other regions are only singular or incidental. The parasitofauna may be influenced by various environmental factors, including the presence and availability of intermedate and parentic hosts or other final hosts; these can serve as a reservoir of parasites typical of the harbor porpoise or as a potential source of infection with sporadic or incidental parasites. The species diversity of parasites in the harbor porpoises from the Baltic subpopulation appears small, even compared to neighboring subpopulations of this subspecies. However, it is important to note that only a relatively small number of hosts were examined in this study. The small size of this critically-endangered population is undoubtedly a limitation when conducting this type of survey, and the small number of specimens examined allows the detection of only the most common parasite species; even so, it should be emphasized that the prevalence is undoubtedly very high, reaching 87%, with a mean infection intensity of approx. 724 specimens.

It is difficult to compare this data to other research, as the body of evidence on harbor porpoises from this subpopulation is derived from just five publications. Of these, three examine only a single species in various contexts (Łukasiak, 1939; Szerer et al., 1998; Kijewska et al., 2003), one is based on data from different subpopulations in the context of the harbor porpoise health (Siebert et al., 2020), while the other, directly preceding the present study, recorded five helminth species in 17 harbor porpoises from the Polish zone of the Baltic Sea, with a comparable or lower prevalence of infection (5.9–88.2%, 9.0–163 ind.) (Schmidt et al., 1989).

Although the research carried out so far cannot unequivocally indicate that the level of Baltic harbor porpoise parasitic infection is increasing, it nevertheless demonstrates the constant presence of a parasite population with high importance for these mammals, especially respiratory nematodes. The parasites are widely dispersed with this porpoise population and although their presence in the host is not tantamount to the development of parasitoses, infected individuals are undoubtedly a significant reservoir of parasites. In turn, the increasing pace of change in environmental conditions, especially those related to human pressure, local and global climate change, may adversely affect the fitness or the level of immunity of marine mammals, reflected in increasing susceptibility to the development of diseases. It is worth noting that the current level of intensity of infection, and thus the parameter directly illustrating the influence of parasites on the hosts, is very high. This doubtlessly impairs the fitness, adaptation capacity or even health status of the host, affecting survival and reproduction. It should be remembered that the functioning of the Baltic Sea ecosystem, all its elements including porpoises, is influenced by various factors directly or indirectly related to human activity (global climate changes, pollution, fisheries management, etc.). While some factors (various types of pollution and contamination) are limited by protective measures, others are intensified (Rheineheimer, 1998; Elmgren, 2001; Garnag, 2012). Thus, the ecosystem of the Baltic Sea is a dynamic system, to which organisms living here must adapt. Perhaps the factors resulting in the decline in the number of fish populations (eutrophication, oxygen deficiency, overfishing) (Jonzen et al., 2002), with the simultaneous appearance of invasive species (e.g. gobies) here (Sapota and Skorn, 2005; Schranda et al., 2016), are important for the formation of the porpoise diet. Which, in turn, is important in the context of the pathways of infection and spread of parasites, or the condition and well-being of these mammals.

Certainly, the individual and random studies did not reflect all aspects of the occurrence and impact of parasitofauna on the fitness and the health status of harbor porpoises from the Baltic Proper subpopulation. In spite of the fact that this subpopulation is the most endangered of all the porpoise populations, the body of research is scarce and requires further supplementation. The presence and level of infection of these harbor porpoises requires ongoing monitoring can provide an important insight into not only the current status of the population, but also the changes to which it is subject.

Declaration of competing interest

Authors have no conflict of interest to declare.

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