Polar Biology (2022) 45:45–57
https://doi.org/10.1007/s00300-021-02970-w

ORIGINAL PAPER

Pathological findings in bycaught harbour porpoises (*Phocoena phocoena*) from the coast of Northern Norway

Kathrine A. Ryeng[1] · Jan Lakemeyer[2] · Marco Roller[2] · Peter Wohlsein[3] · Ursula Siebert[2]

Received: 12 February 2021 / Revised: 26 October 2021 / Accepted: 2 November 2021 / Published online: 19 November 2021

Abstract

Due to little prior knowledge, the present study aims to investigate the health status of bycaught harbour porpoises from the northernmost Arctic Norwegian coastline. Gross, histopathological and parasitological investigations were conducted on 61 harbour porpoises (*Phocoena phocoena phocoena*) accidentally captured in fishing gear from February to April 2017 along the coast of Northern Norway. Most animals displayed a good nutritional status, none were emaciated. Pulmonary nematodiasis (*Pseudalius inflexus*, *Halocercus invaginatus* and *Torynurus convolutus*) was found in 77% and associated with severe bronchopneumonia in 33% of the animals. The majority (92%) had parasites in the stomach and intestine (*Anisakis simplex* sensu stricto (s. s.), *Pholeter gastrophilus*, *Diphyllobothrium stemmacephalum*, *Hysterothylacium aduncum* and *Pseudoterranova decipiens* s. s.). The prevalence of gastric nematodiasis was 69%. In the 1st stomach compartment *A. simplex* s. s. was found in 30% of the animals, causing severe chronic ulcerative gastritis in 23%. *Campula oblonga* infected the liver and pancreas of 90% and 10% of the animals, respectively, causing severe cholangitis/pericholangitis/hepatitis in 67% and moderate pancreatitis in 10% of the animals. Mesenteric and pulmonary lymphadenitis was detected in 82% and 7% of the animals, respectively. In conclusion, the major pathological findings in the investigated Arctic porpoises were parasitoses in multiple organs with associated severe lesions, particularly in the lung, liver and stomach. The animals were generally well nourished and most showed freshly ingested prey in their stomachs. The present study indicates that the harbour porpoises were able to tolerate the detected parasitic burden and associated lesions without significant health problems.

Keywords Harbour porpoise · *Phocoena phocoena* · Pathology · Parasitic infection · Arctic

Introduction

Marine mammals may be used as sentinel organisms to evaluate the health of marine ecosystems. The harbour porpoise (*Phocoena phocoena*) is one of the smallest cetacean species and common in shallow coastal waters of the Northern hemisphere (Benke et al. 1998). The subspecies *P. p. phocoena* is continuously distributed in the European continental shelf waters from the Northern Bay of Biscay up to the Arctic waters of Norway and Iceland (Fontaine et al. 2014; NAMMCO and IMR 2019). In Norwegian waters, it is widely distributed from the shallow North Sea and consistently along the entire Norwegian coast including the fjords and into the shallow Barents Sea north to the polar front (Andersen 2003).

The population size of harbour porpoises in Norwegian waters is estimated to be > 180,000 animals (Moan et al. 2020). The single greatest threat to harbour porpoises is bottom-set large-mesh gillnets operated by the Norwegian small-vessel fleet. Most porpoises are taken in gillnets intended to catch Atlantic cod (*Gadus morhua*), monkfish (*Lophius piscatorius*), and to some extent, saithe (*Pollachius virens*) (Moan et al. 2020).

Several studies on the health status of harbour porpoises in European waters have been reported (Clausen and Andersen 1988; Baker and Martin 1992; Siebert et al. 2001, 2006, 2009, 2020; Wünschmann et al. 2001;

✉ Ursula Siebert
Ursula.Siebert@tiho-hannover.de

1 Institute of Marine Research, Fram Centre, P.O. Box 6606 Stakkevollan, NO-9296 Tromsø, Norway

2 Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover, Foundation, Werftstrasse 6, 25761 Büsum, Germany

3 Department of Pathology, University of Veterinary Medicine Hannover, Foundation, Bünteweg 17, 30559 Hannover, Germany

Jauniaux et al. 2002; Jepson et al. 2005; Lehnert et al. 2014), including harbour porpoises from Norwegian waters with a special focus on infectious agents such as parasites, bacteria and viruses as well as anthropogenic impacts like bycatch (Lehnert et al. 2005; Siebert et al. 2006, 2009). Harbour porpoises from Norwegian waters showed a thicker blubber layer and a lower prevalence of lesions, especially in the respiratory tract, compared to bycaught Baltic harbour porpoises (Siebert et al. 2009). Moreover, Arctic harbour porpoises displayed significantly lower concentrations of polychlorinated biphenyls (PCB) (Kleivane et al. 1995; Bruhn et al. 1999) and polybrominated diphenyl ethers (PBDE) (Thron et al. 2004) than North Sea and Baltic harbour porpoises. In contrast to North Sea and Baltic animals, Norwegian harbour porpoises showed a higher prevalence of gastrointestinal parasitic infections, potentially caused by life cycle or diet differences (Lehnert et al. 2005; Siebert et al. 2006). However, no studies exist on the health status of the northernmost harbour porpoise population along the Norwegian coastline.

The aim of the present study was to investigate the health status of harbour porpoises accidentally captured in fishing gear along the coast of Northern Norway.

Materials and methods

Animals

A total of 61 harbour porpoises (HP) were included in the study. The animals had been accidentally captured in commercial gill net fisheries along the coast of Northern Norway from Senja Island in the south to the Varanger Fjord in the northeast (69.52–71.05°N/17.18–29.03°E), from February 2nd to April 4th, 2017. Along this coastline, the following bycatch hotspot areas were identified: Senja–Tromsø (S–T) (69.52–69.98°N/17.18–19.65°E) ($n=23$), Kvænangen (KV) (69.97–70.10°N/21.58–22.07°E) ($n=7$), Kjøllefjord (KF) (70.97–71.05°N/27.16–27.38°E) ($n=6$) and the Varanger Fjord (VF) (70.10–70.11°N/28.90–29.03°E) ($n=25$) (Fig. 1).

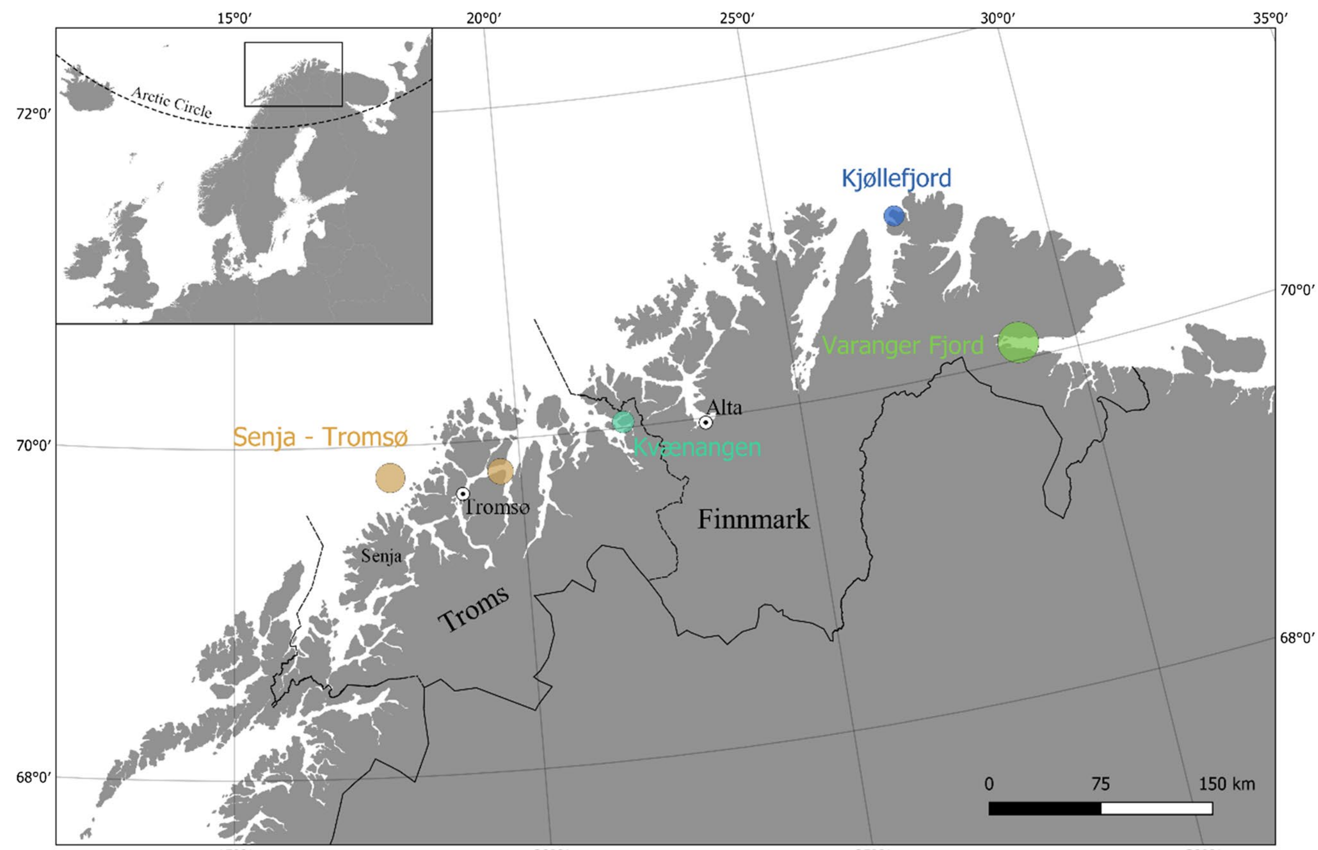

Fig. 1 Sampling location of 61 harbour porpoises bycaught in February–April 2017 along the coast of Northern Norway from Senja island in the south to the Varanger Fjord in the northeast. The size of the circles is proportional to the number of animals collected in the four bycatch hotspot areas: Senja–Tromsø ($n=23$), Kvænangen ($n=7$), Kjøllefjord ($n=6$) and Varanger Fjord ($n=25$). A small-scale map of Northern Europe is inserted (top left) to indicate the regional setting of the study in the Arctic

Brought in by fishermen, all animals were stored at − 20 °C until necropsy at the Institute of Marine Research, Tromsø, and the Norwegian Veterinary Institute, Tromsø, during March to June 2017. Necropsies were performed following the cetacean protocol developed by Siebert et al. (2001).

The nutritional status was assessed based on blubber thickness and state of longissimus dorsi muscle, as well as taking into consideration age and reproductive status of the individual. It was divided into good, moderate or poor (equal emaciated) nutritional status (Siebert et al. 2001, 2006; IJsseldijk et al. 2019).

Teeth were extracted from the lower jaw for age determination by counting the annual growth layers (Lockyer 1995). Animals were assigned to the following age groups: (1) $X \le 1 = 1$ year or younger, (2) $1 < X \le 3 =$ between one up to and including 3 years, (3) $3 < X \le 5 =$ between three up to and including 5 years (maturation), (4) $5 < X \le 10 =$ between five up to and including 10 years and (5) $X > 10 =$ older than 10 years. Assigned age was rounded up to the nearest full year, based on an assumed time of birth of North Atlantic HPs in June (Lockyer et al. 2003; Ólafsdóttir et al. 2003).

Post-mortem diagnostic procedures

The carcasses were examined for external lesions, including net marks. Organ systems were examined macroscopically, and samples of lesions and tissues from the following organ systems were collected and fixed in 10% neutral buffered formalin: lung, stomach (1st, 2nd and 4th compartments) (Horstmann 2018), intestine, liver, pancreas, thyroid glands, adrenal glands, kidneys, spleen, thymus, tonsils, lymph nodes (pulmonary, mesenteric and retropharyngeal), heart, skeletal muscles and brain (brain; $n = 31$). These samples were embedded in paraffin wax for histological examination and sections (3 µm) were stained with haematoxylin and eosin. Ear bones were extracted and the aural peribullar cavities examined in 47 of the 61 animals. The level of parasitic infection in the different organ systems was determined semi-quantitatively during necropsy as mild, moderate or severe (Lehnert et al. 2007). Parasites were collected from infected organs, fixed in 70% ethanol and identified macroscopically and microscopically according to scientific literature (Delyamure 1955) using a stereomicroscope (Olympus SZ61). In the case of the gastric nematodes the PCR-based method restriction fragment length polymorphism (RFLP) was applied for species identification (Lakemeyer et al. 2020).

Statistical analysis

The results are expressed in counted numbers with percent. Hepatic trematode infection related to age classification was performed using Cross Tabulation analysis and Binomial sequences (Agresti 2013).

Results

Sex and age distribution

The five age groups were evenly distributed between sexes (Table 1). Most of the bycaught HPs were from age group 2 (36%). Nine of the females were pregnant. Milk was present in the mammary glands in two of them. The foetuses were not included in the study.

Nutritional status

The nutritional status was assessed as good in 59 animals and as moderate in two. None of the animals were emaciated.

Pathological findings

Gross pathology

Net marks were noted in 53 of the 61 animals (Table 2). The net marks were found on the pectoral fins, the dorsal fin, the tail flukes and the head. These lesions were about 2–5 mm wide and 3–10 mm deep. Additionally, net marks were often seen as weak linear impressions encircling the head or neck.

Table 1 Sex and age distribution of 61 bycaught harbour porpoises from Northern Norwegian waters

Sex	Age group					Total
	1	2	3	4	5	
	Calves	Juveniles	Adults			
Female	4	11	5	4	3	27
Male	2	11	4	9	8	34
Total	6 (10%)	22 (36%)	9 (15%)	13 (21%)	11 (18%)	61
			33 (54%)			

Age groups: 1 = 1 year or younger, 2 = between one up to and including 3 years, 3 = between three up to and including 5 years, 4 = between five up to and including 10 years and 5 = older than 10 years

Table 2 Selected pathological findings in 61 bycaught harbour porpoises from Northern Norwegian waters

Observation	Classification				Total (%)
	None	Mild	Moderate	Severe	
	Number (%)				
Skin					
Net marks					53 (87)
Respiratory system					
Pulmonary oedema					61 (100)
Pulmonary congestion					61 (100)
Pulmonary emphysema	13 (21)	48 (79)			48 (79)
Pulmonary nematodiasis[a]	14 (23)	31 (51)	1 (2)	2 (3)	47 (77)
Bronchopneumonia[b]	9 (15)	5 (8)	27 (44)	20 (33)	52 (85)
Alimentary system					
Gastric nematodiasis[c]	19 (31)				42 (69)
1st stomach compartment	23 (38)	24 (39)	8 (13)	6 (10)	38 (62)
2nd stomach compartment	46 (75)	15 (25)	0 (0)	0 (0)	15 (25)
4th stomach compartment	52 (85)	9 (15)	0 (0)	0 (0)	9 (15)
Gastric trematodiasis[d]	55 (90)				6 (10)
2nd stomach compartment	57 (93)	4 (7)	0 (0)	0 (0)	4 (7)
4th stomach compartment	59 (97)	0 (0)	1 (2)	1 (2)	2 (3)
Gastritis	37 (61)				24 (39)
1st stomach compartment[e]	43 (70)	0 (0)	4 (7)	14 (23)	18 (30)
2nd stomach compartment[f]	57 (93)	2 (3)	1 (2)	1 (2)	4 (7)
4th stomach compartment[f]	59 (97)	0 (0)	1 (2)	1 (2)	2 (3)
Intestinal parasites[g]	53 (87)	8 (13)	0 (0)	0 (0)	8 (13)
Enteritis[h]	52 (85)	9 (15)	0 (0)	0 (0)	9 (15)
Hepatic trematodiasis	6 (10)	47 (77)	6 (10)	2 (3)	55 (90)
Cholangitis/pericholangitis/hepatitis/fibrosis[i]	9 (15)	3 (5)	6 (10)	41 (67)	52 (85)
Pancreatic trematodiasis	55 (90)	0 (0)	6 (10)	0 (0)	6 (10)
Pancreatitis	55 (90)	0 (0)	6 (10)	0 (0)	6 (10)
Urinary system					
Degenerated kidney (unilateral)	60 (98)			1 (2)	1 (2)
Ear and central nervous system					
Peribullar cavity nematodiasis	7 (15)				40 (85)
Left	8 (17)	17 (36)	18 (38)	4 (9)	39 (83)
Right	7 (15)	18 (38)	16 (34)	6 (13)	40 (85)
Encephalitis	30 (97)				1 (3)
Lymphatic system					
Lymphadenitis					
Mesenteric	11 (18)				50 (82)
Pulmonary	57 (93)				4 (7)
Follicular hyperplasia					
Tonsil	57 (93)				4 (7)
Retropharyngeal lymph node	58 (95)				3 (5)
Pulmonary lymph node	46 (75)				15 (25)
Spleen	60 (98)				1 (2)

Brain examinations ($n=31$), aural peribullar cavity examinations ($n=47$). The results are expressed as counted numbers with percent in ()

[a]13 animals with histologically detected nematodiasis were not included in the severity classification

[b]Bronchopneumonia was diagnosed histologically

[c]Caused exclusively by *A. simplex* s. s.

[d]Caused exclusively by *P. gastrophilus*

[e]Gastritis caused exclusively by *A. simplex* s. s. was diagnosed histologically

[f]Gastritis caused exclusively by *P. gastrophilus* was diagnosed histologically

Table 2 (continued)

[g]*D. stemmacephalum* ($n=2$), *A. simplex* s.s. ($n=6$)

[h]Animals with no parasites found in the intestine

[i]Cholangitis/pericholangitis/hepatitis/fibrosis was diagnosed histologically

Recent skin lacerations, subcutaneous haemorrhages as well as haemorrhages and oedema in the musculature of the thoracic back and in the peri-cranial and mandibular regions were frequently observed. Bleeding in the melon fat was detected in three animals. Acute mandibular fractures were found in four animals, of which surrounding tissue haemorrhages were noted in three. Congestion of parenchymatous organs was seen in all animals. None of the HPs showed gross evidence of severe disease. The most common findings were parasitoses in multiple organs.

Respiratory system

Pulmonary congestion was in all cases accompanied by pulmonary oedema with abundant white, often blood-tinged froth in the airways (Table 2). Pulmonary emphysema was also present in most animals.

Pulmonary nematodiasis caused by *Pseudalius inflexus*, *Halocercus invaginatus* and *Torynurus convolutus* was detected macroscopically in 34 of the HPs (Table 2; Fig. 2a, b). Due to the complexity of finding all small nematodes like *H. invaginatus*, the level of infection was difficult to classify grossly. However, it

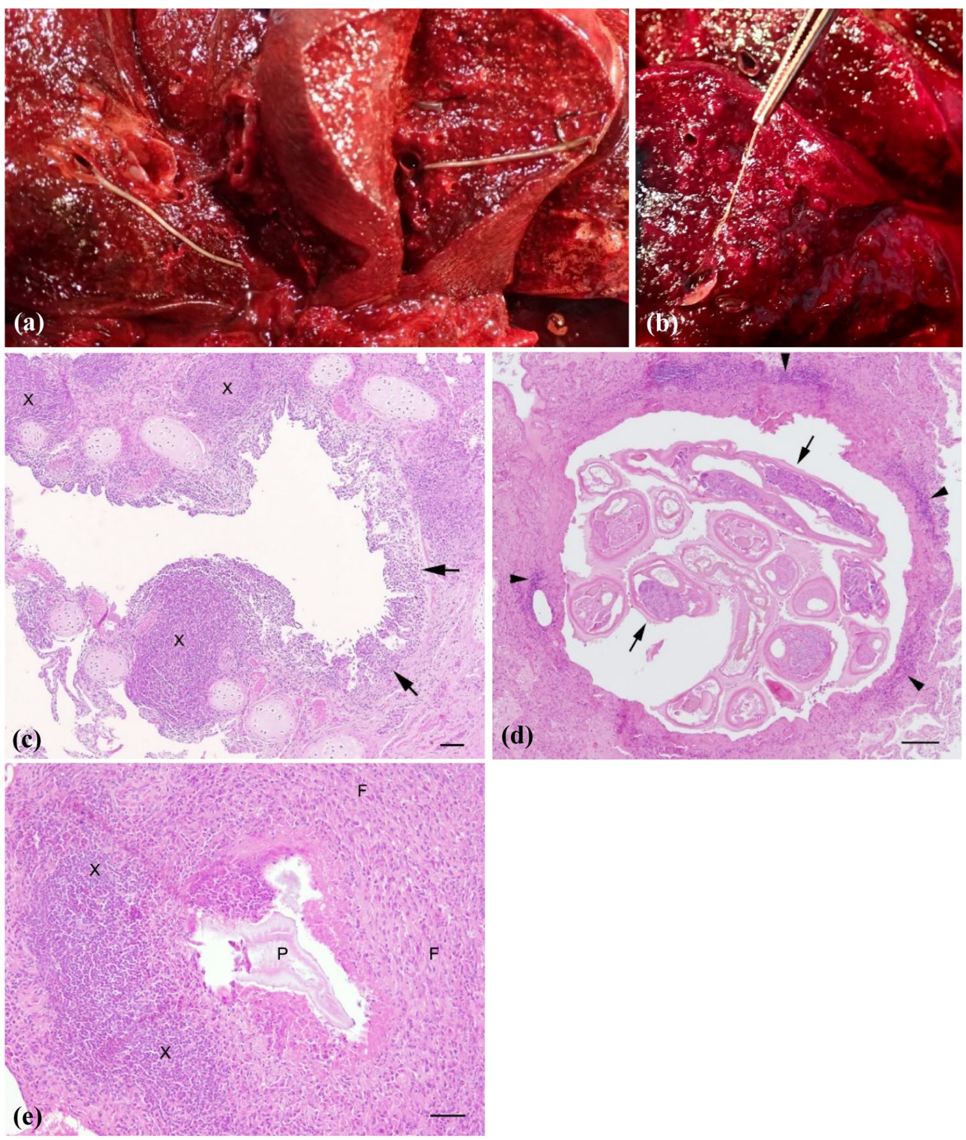

Fig. 2 Lung of a harbour porpoise with **a** intrabronchial nematodes (species: *Pseudalius inflexus*), **b** intraparenchymal nematodes (species: *Halocercus invaginatus*), **c** severe, chronic non-suppurative bronchitis with marked subepithelial infiltration (arrows) and hyperplasia of the bronchus-associated lymphoid tissue (X) (bar = 100 µm), **d** vasculitis, showing numerous nematodes within the vascular lumen (arrows) associated with mural and perivascular inflammatory cell infiltration (arrowheads) (bar = 200 µm) and **e** focal severe chronic granulomatous pneumonia with intralesional parasitic structure (P), segmentally severe inflammatory cell infiltration (X) and semi-circular fibrosis (F) (bar = 100 µm). Haematoxylin and eosin staining

Table 3 Infections with *Pseudalius inflexus*, *Torynurus convolutus* and *Halocercus invaginatus* in the lung, *Anisakis simplex* sensu stricto in the stomach compartments and *Campula oblonga* in the liver and pancreas of 61 harbour porpoises bycaught along the coast of Northern Norway, separated into the bycatch hotspot areas Senja–Tromsø, Kvænangen, Kjøllefjord and the Varanger Fjord

Bycatch area		Senja–Tromsø	Kvænangen	Kjøllefjord	Varanger Fjord	Total
Bycatch (*n*)		23	7	6	25	61
Parasite species	Organ	Infected *n* (%)				
P. inflexus	Lung	12 (52%)	0 (0%)	1 (17%)	3 (12%)	16 (26%)
T. convolutus	Lung	3 (13%)	0 (0%)	0 (0%)	0 (0%)	3 (5%)
H. invaginatus	Lung	8 (35%)*10 (43%)	6 (86%)*7 (100%)	4 (67%)*5 (83%)	5 (20%)*14 (56%)	23 (38%)*36 (59%)
A. simplex s. s.	1st stomach comp	16 (70%)	5 (71%)	5 (83%)	12 (48%)	38 (62%)
	1st, 2nd and 4th comp	17 (74%)	5 (71%)	5 (83%)	15 (60%)	42 (69%)
C. oblonga	Liver	20 (87%)	6 (86)	4 (67%)	25 (100%)	55 (90%)
C. oblonga	Pancreas	0 (0%)	1 (14%)	1 (17%)	4 (16%)	6 (10%)

The results are expressed as counted numbers with percent in ()

*Assuming *H. invaginatus* being present in the 13 animals with histologically detected nematodiasis

was classified as mild in 31 animals, as moderate in one and as severe in two (Table 2). Histologically, pulmonary nematodes were found in another 13 animals, but the nematode species could not be identified. However, it is reasonable to assume that the microscopically detected nematodes were *H. invaginatus*. Grossly, *H. invaginatus* was found in 23 HPs (38%), *P. inflexus* in 16 (26%) and *T. convolutus* in three (5%) (Table 3). Assuming that the 13 histologically detected nematode cases were *H. invaginatus*, the real prevalence of this nematode species was 59%. *Pseudalius inflexus* was mostly detected, and *T. convolutus* only found in animals from the S–T area. In contrast, *H. invaginatus* dominated in all areas, except for the southernmost S–T area, where *P. inflexus* dominated (Table 3).

Lungworm burdens did not cause pulmonary airway obstruction. Small solitary nodules, about 5 mm in diameter, containing nematodes, indicating an infection with *H. invaginatus*, were regularly found in the lung parenchyma.

Bronchopneumonia was diagnosed in 52 (85%) of the animals, and classified as mild in five, moderate in 27 and severe in 20 animals (Table 2). These included 34 animals in which lungworms were detected grossly and 18 animals without macroscopically detected nematode infection. Lungworm infection was detected histologically in 13 of these 18 animals. Pulmonary nematode infections were commonly associated with a broncho-interstitial pneumonia, with a combination of lympho-plasmacytic, granulomatous and eosinophilic inflammation. In addition, granulomatous and eosinophilic as well as lympho-plasmacytic thrombotic vasculitis and perivasculitis were the most frequent pathological findings associated with pulmonary nematodiasis (Fig. 2c–e).

Alimentary system

The gastric compartments were infected by nematodes causing ulcers in the 1st compartment and trematodes inducing granulomas in the 2nd and 4th compartments. Gastric nematodiasis caused by *A. simplex* s. s. was detected in 42 of the animals (Table 2). The 1st stomach compartment was mainly affected, and the level of infection was predominantly mild. The prevalence of *A. simplex* s. s. was lowest in the northernmost VF area, as compared to the other bycatch hotspot areas (Table 3). Grossly, infection with *A. simplex* s. s. was associated with gastric ulcers in the 1st compartment as detected in 18 animals. 12 HPs had one single ulcer, three had two and another three animals had three or more ulcers. The ulcers varied from 1 to 4 cm in diameter and had a punched-out appearance with a thickened mucosa and nematodes attached to the centre (Fig. 3a). Histologically, a chronic ulcerative granulomatous gastritis, confined to the areas of ulceration, was diagnosed and classified as severe

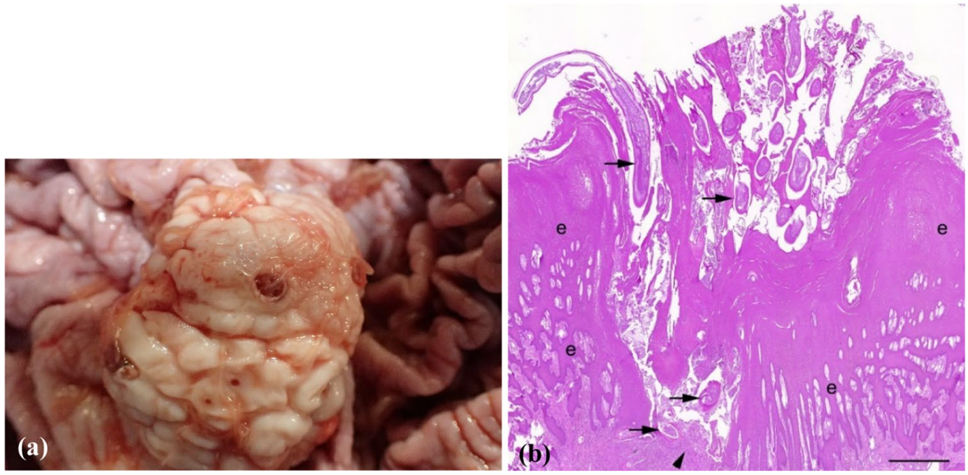

Fig. 3 First stomach compartment of a harbour porpoise showing **a** chronic ulcerative gastritis caused by *Anisakis simplex* sensu stricto, and **b** focal gastritis with intralesional nematodes (arrows), focal ulceration (arrowhead) and severe hyperplasia of the adjacent squamous epithelium (e), (bar = 1 mm). Haematoxylin and eosin staining

in most cases (Table 2; Fig. 3b). Additionally, *Hysterothylacium aduncum* and *Pseudoterranova decipiens* s. s. were identified by RFLP in one HP each.

Gastric trematodiasis caused by *Pholeter gastrophilus* (Digenea, Heterophyidae) was detected in six of the animals with associated parasitic granulomas in the 2nd and 4th stomach compartments (Table 2). Histologically, a multifocal chronic granulomatous and lympho-histiocytic mural gastritis was found.

Mild helminthic infections in the intestine were detected in eight animals (Table 2). In six HPs, *A. simplex* s. s. was present in the intestine, whilst intestinal cestodiasis caused by *Diphyllobothrium stemmacephalum* was detected in two animals. Histologically, only one of the animals with *A. simplex* s. s. in the intestine displayed a mild diffuse eosinophilic infiltration of the intestinal mucosa. Intestinal inflammation was found in nine non-infected animals, classified as mural granulomatous eosinophilic lympho-histiocytic or lympho-plasmacytic enteritis.

Trematode (*Campula oblonga*) infection in the liver was found in 55 animals (90%) (Table 2). The level of infection was classified as mild in most cases. Within the bycatch areas, the prevalence of hepatic trematodiasis was 87%, 86%, 67% and 100% in the S–T, KV, KF and VF areas, respectively (Table 3). In the total material, 93.9% (95% CI: 79.8–99.3) of animals older than 3 years were infected as compared to 85.7% (95% CI: 67.3–96.0) of those younger than 3 years. The prevalence seemed to increase with age and with increasing latitude. In the northernmost VF area, where all animals were infected, 20% (95% CI: 6.8–40.7) were younger than 3 years compared to the southernmost S–T area where 65.2% (95% CI: 42.7–83.6) were younger than 3 years.

Grossly, varying degrees of bile duct proliferation was seen in all animals. However, in four HPs no intraluminal trematodes were present. In 11 of the 55 animals, one to several spherical parasitic nodules were found, mostly in animals older than 5 years with mild infection. The nodules were 0.5–2.5 cm in diameter, with a thick, fibrous, partly calcified wall and dark green to black caseous contents with no parasites inside. This lesion was described histologically as tissue cavity with fibrous demarcation, containing intraluminal as well as intracapsular trematode eggs in some cases. Chronic proliferative lympho-plasmacytic, eosinophilic and granulomatous cholangitis and pericholangitis with perifocal fibrosis as well as granulomatous eosinophilic interstitial hepatitis were found in 52 of the animals, whereas three did not show specific lesions in the liver. The inflammation was classified as severe in most cases (Table 2).

Pancreatic trematodiasis caused by *C. oblonga* was detected in six HPs. The level of infection was assessed as

Table 4 Cross tabulation between "Age classification" and "Infected/Non-infected" animals regarding *Campula oblonga* infection in the liver and pancreas of 61 harbour porpoises bycaught along the coast of Northern Norway within the bycatch hotspot areas Senja–Tromsø, Kvænangen, Kjøllefjord and the Varanger Fjord

Bycatch area	Age classification (years)	Liver		Total	Pancreas
		Non-infected	Infected		Infected
Senja–Tromsø	≤ 3	2	13	15	0
	> 3	1	7	8	0
Kvænangen	≤ 3	1	2	3	0
	> 3	0	4	4	1
Kjøllefjord	≤ 3	1	4	5	1
	> 3	1	0	1	0
Varanger Fjord	≤ 3	0	5	5	1
	> 3	0	20	20	3
Total	≤ 3	4	24	28	2
	> 3	2	31	33	4
Sum		6	55	61	6

moderate in all cases (Table 2). Within the bycatch areas, none of the animals in the S–T area were infected. The prevalence of pancreatic trematodiasis was 14%, 17% and 16% in the KV, KF and VF areas, respectively (Table 3). As for the hepatic trematodiasis, the largest proportion of infected animals older than 3 years was found in the VF area (Table 4). The infections in the pancreas were concomitant with mild ($n=4$) and severe ($n=2$) infections in the liver. Two of the animals had a caseous nodule in the pancreas similar to those found in the liver. The presence of the parasite in the pancreatic ducts was associated with perifocal fibrosis and moderate chronic lympho-plasmacytic eosinophilic pancreatitis.

Urinary system

In one animal, cystic degeneration of the right kidney was observed (Table 2). Histologically, it showed a complete loss of functional parenchyma and multifocal epithelium-lined cysts in association with severe perifocal fibrosis.

Lymphatic system

Eosinophilic and granulomatous lymphadenitis were detected in the mesenteric and pulmonary lymph nodes of 50 and four animals, respectively (Table 2). The lymphadenitis was suggestive of a parasitic origin. Immunological reactions in terms of follicular hyperplasia were detected in tonsils, retropharyngeal and pulmonary lymph nodes and spleen (Table 2).

Aural peribullar cavity and central nervous system

Infection with the nematode *Stenurus minor* in one or both peribullar cavities was detected in 40 of the 47 investigated HPs (Table 2). The number of *S. minor* was distributed equally between the left and right peribullar cavities of infected animals. The level of parasitic infection in both ears was assessed as mild and moderate in most animals. No gross lesions due to *S. minor* were observed. Of the 31 investigated brains, one HP histologically displayed a mild focal lympho-histiocytic encephalitis in the brain stem of unknown origin.

Discussion

The present study reports for the second time the pathological findings in HPs bycaught in gill net fisheries along the Norwegian coast, and focuses on the northernmost part of the coastline, between Senja in the south and the Varanger Fjord in the northeast. In the first study (Siebert et al. 2006), the animals were bycaught in the year 2000 and originated from the Norwegian southern North Sea coastline in the south to the Alta Fjord in the north (58–70°N/5–23°E). Hence, the origin of the animals included in the two studies overlaps in the S–T and the KV areas. In both the previous and the present study, the animals were bycaught in February–April (winter/spring period).

The higher number of bycaught animals between 1 and 3 years of age is consistent with previous studies of bycaught HPs from the North and Baltic Seas and Norwegian waters (Siebert et al. 2001, 2006, 2020; Wünschmann et al. 2001), indicating that young animals are more prone to being caught accidentally in fishing gear. The cause of this phenomenon still remains unclear.

All animals had a good nutritional status, except for two that appeared to be moderately nourished. One of these animals, a juvenile female, was diagnosed with the cestode *D. stemmacephalum* in the intestine. The other animal, a non-pregnant adult female, had no particular increase in parasite burden or other pathologies.

Future studies are needed to establish normal ranges of relevant markers of energy status such as blubber thickness in HPs from Norwegian waters. None of the animals were emaciated. This is comparable to previous studies of bycaught HPs from Norwegian and Icelandic waters, where no emaciated animals were reported (Siebert et al. 2006). In contrast, 10% of investigated bycaught HPs from the German North and Baltic Seas were emaciated (Siebert et al. 2001; Wünschmann et al. 2001). In the present study, the animals were bycaught during wintertime fisheries. In this cold Arctic water, the likelihood of finding animals with a near complete functional depletion of energy stores as bycatch is potentially low due to reduced survival from hypothermia (Rojano-Doñate et al. 2018; Kastelein et al. 2019).

The detected prevalence and location of net marks as well as subcutaneous and muscular haemorrhages are similar to those previously reported by Siebert et al. (2006). These lesions together with bruises consistent with entanglement in the peri-cranial and mandibular regions, fractures and associated haemorrhages in the mandible are all evidence of contact with fishing gear and suggest some degree of struggle prior to death (Moore et al. 2013; Epple et al. 2020).

Respiratory system

Although not diagnostic to peracute underwater entrapment, the general presence of pulmonary congestion, oedema and froth in the airways are indicative of hypoxia and asphyxiation as the cause of death in these animals since they had a known history of bycatch (Moore et al. 2013; Epple et al. 2020).

The prevalence of pulmonary nematodiasis (77%) caused by *P. inflexus*, *H. invaginatus* and *T. convolutus* is comparable to those earlier reported for bycaught HPs from Icelandic waters (84%), but lower than those reported from Norwegian waters (91%) (Siebert et al. 2006). In the previous study, the levels of infection in the Norwegian HPs were classified as mild in 59% and as moderate in 32% of the animals. Severe nematodiasis was not reported from any of the animals. In the present study, the grossly detected nematode infections were classified as mild in 51%, as moderate in 2% and as severe in 3% of the animals. It should be noted that the smallest nematodes, presumably *H. invaginatus,* were often difficult to find and that the 13 animals with histologically detected nematodes were not included in the classification. *Halocercus invaginatus* appeared most frequently in the lungs, followed by *P. inflexus* and *T. convolutus.* However, the real prevalence of *H. invaginatus* may have been higher than that grossly observed due to its different habitat in the lungs in comparison to the two larger lung nematode species.

The severity of bronchopneumonia associated with lung nematode infection was clearly different between the previously and currently studied Norwegian HPs. Whilst bronchopneumonia was classified as mild in 36%, as moderate in 50% and as severe in 9% of the animals in the former study, it was mild in 8%, moderate in 44% and severe in 33% of the animals in the present study. Pulmonary nematode infections were commonly associated with eosinophilic bronchitis, a chronic granulomatous eosinophilic interstitial pneumonia as well as granulomatous eosinophilic vasculitis and perivasculitis. In the previous study (Siebert et al. 2006), the inflammatory changes were in most cases granulomatous or suppurative, and in a few cases characterised by necrosis or abscess formation. In contrast to the present study, suppurative pneumonia seems to be common in bycaught and stranded HPs from the North and Baltic Seas (Siebert et al. 2001, 2020). These differences may be attributed to the level of infection and indications of immune and endocrine disturbance of animals in those areas (Beineke et al. 2005; Das et al. 2006). The granulomatous changes in the lungs, as detected in both studies, could mainly be attributed to the presence of *H. invaginatus,* which occurs in small cysts within the parenchyma. *Pseudalius inflexus* infects bronchi, trachea and pulmonary vessels, and *T. convolutus* infects bronchi and bronchioles (Gibson et al. 1998). These nematodes may have been mainly responsible for the detected eosinophilic bronchitis. The lesions in the pulmonary vasculature may have been caused by *P. inflexus* (van Elk et al. 2019). Although the relative numbers of the three nematode species were not reported in Siebert et al. (2006), it could be speculated that the difference in severity of parasitic bronchopneumonia between the studies is related to the relative occurrence of the three nematode species, with *H. invaginatus* dominating in the present study and not in the previous. Diet composition will influence porpoise parasite fauna as fish species occurring in temperate and Arctic waters play different roles as intermediate hosts (Lehnert et al. 2014). The bycatch areas of the former study were mostly located along the Norwegian coastline below the Arctic Circle, whilst all animals in the present study were bycaught in Arctic waters. In fact, *H. invaginatus* dominated in all areas, except for the S–T area, the southernmost area overlapping with the former study. In this area, *P. inflexus* dominated and *T. convolutus* was only detected here in mixed infections with *P. inflexus*. *Pseudalius inflexus* and *T. convolutus* are common findings in the lungs of HPs from German, Dutch and Baltic waters (Siebert et al. 2001, 2020; van Elk et al. 2019). However, *H. invaginatus* was first reported in HPs from the German North and Baltic Seas by Lehnert et al. (2005) and is rarely found in HPs in British waters (Gibson et al. 1998; Jepson et al. 2000). In Greenlandic HPs, however, *P. inflexus* and *T. convolutus* have not been found, but *H. invaginatus* has been detected in high prevalence and the infections were in most cases associated with a moderate to severe granulomatous pneumonia (Wünschmann et al. 2001; Lehnert et al. 2014). It has been suggested that flatfish, like turbot (*Scophthalmus maximus*), are potential intermediate hosts for *P. inflexus* and *T. convolutus* in marine mammals (Lehnert et al. 2010), and that *H. invaginatus* and congeners may also use other mechanisms, such as transplacental or transmammary infection (Dailey et al. 1991; Balbuena et al. 1994; Reckendorf et al. 2018), albeit horizontal transmission may be more important (Measures 2018). In the present study *H. invaginatus* was only found in one of the six calves. If an intermediate host is involved, it may be pelagic fish or cephalopods (Lehnert et al. 2014). Preliminary results from a parallel feeding ecology investigation of the HPs included in the present study suggest that saithe dominated the diet in the S–T and KV areas, whilst capelin (*Mallotus villosus*) dominated in the KF and VF areas. This study also revealed that a large proportion, 93.4%, of the animals had food in their stomachs, indicating recent foraging (Ulf Lindstrøm, unpublished data). Regarding the two northernmost areas where capelin dominated, it should be noted that the sampling time coincided with spawning of the Barents Sea capelin (Olsen et al. 2010).

Similar to the former study by Siebert et al. (2006), infections with *P. inflexus* and *T. convolutus* did not occur in sufficient numbers to cause obstruction of the pulmonary airways, as reported in HPs from the North Sea, the Skagerak and the Danish domestic waters (Clausen and Andersen 1988), and in up to 18% of the bycaught and stranded HPs from the North and Baltic Seas (Siebert et al. 2001).

Alimentary system

56 animals (92%) displayed helminth infection in the stomach and intestine (*A. simplex* s. s., *P. gastrophilus, D. stemmacephalum, H. aduncum, P. decipiens* s. s.), which is comparable to the previously studied HPs from Icelandic and Norwegian waters. Unlike the previous study by Siebert et al. (2006), *Contracaecum osculatum* and *S. minor* were not found in the gastrointestinal tract, but *P. decipiens* s. s. was. *Hysterothylacium aduncum* was probably ingested by the respective HP via a prey item as this nematode species matures in fish (Herreras et al. 1997). *Pseudoterranova decipiens* s. s. rarely matures in cetaceans, because pinnipeds are its final hosts (Aspholm et al. 1995; McClelland 2002). Larval gastric nematodes of seals were detected in HPs in sympatric areas like Newfoundland and the eastern North Sea, but HPs are regarded as accidental hosts (Brattey and Stenson 1995; Herreras et al. 1997).

As in the previous study of Norwegian bycaught HPs, gastric nematodiasis was mainly caused by *A. simplex* s. s. It was detected in 69% of the animals as compared to 86% in the earlier study. Although a few *A. simplex* s. s. could be found in the 2nd and 4th stomach compartments of some animals, numerous specimens were predominantly located in the 1st stomach compartment where it was present in 62% of the animals. This is lower than the infection rate of 80% in this compartment as previously reported for Norwegian HPs (Lehnert et al. 2005), but much higher than those found in bycaught and stranded HPs from the North and Baltic Seas (Clausen and Andersen 1988; Siebert et al. 2001, 2020; Wünschmann et al. 2001; Lehnert et al. 2005). Chronic ulcerative gastritis in the 1st stomach compartment associated with *A. simplex* s. s. infection was detected in 30% of the animals. This is lower than the prevalence of gastritis caused by *A. simplex* s. s. previously reported for Norwegian and Icelandic HPs, being 82% and 58%, respectively, and closer to the prevalence of gastritis in bycaught and stranded HPs from the German North and Baltic Seas (Siebert et al. 2001, 2020; Wünschmann et al. 2001). The lower prevalence of gastritis detected in the present study may be reflected in the lower infection rate of *A. simplex* s. s. in the stomach. As pointed out by Lehnert et al. (2005), the difference in infection rate probably reflects a certain species composition in the diet of HPs in different areas. In the present study, the infection rate of *A. simplex* s. s. and the severity of gastritis were much lower in the large proportion of animals bycaught in the VF area, where capelin dominated the diet, as compared to the other areas, particularly the S–T area, where saithe, a member of the cod family (*Gadinae*), dominated. *Anisakis simplex* s. s. appears to be the only *Anisakis* species present in the Arctic and sub-Arctic areas of the Northeast Atlantic including the Barents Sea (Levsen et al. 2016). Capelin acts as a paratenic host to *A. simplex* s. s., either transferring the larvae to a fish host in a higher trophic level such as Atlantic cod or is being eaten by a final host for this nematode species such as the HP. In contrast to Atlantic cod, however, no particular accumulation of *A. simplex* s. s. larvae seems to take place in capelin (Levsen et al. 2016). This might explain the lower *A. simplex* s. s. infection rate and gastritis found in the present study. However, the gastritis was severe in 14 of the 18 cases (78%), of which 10 and 3 were found in animals from the S–T and KV areas, respectively. The ulcers appeared to be at least the size and even larger than those previously found in Norwegian bycaught HPs and HPs from the North and Baltic Seas as well as Belgian waters (Siebert et al. 2001, 2006; Jauniaux et al. 2002).

The low occurrence of granulomatous gastritis caused by *P. gastrophilus* in the 4th stomach compartment is in line with previous findings in Norwegian HPs (Lehnert et al. 2005; Siebert et al. 2006). Unlike the cited studies, however, the gastritis was more severe, and this parasite also caused mild gastritis in the 2nd compartment.

The mild intestinal infections with *A. simplex* s. s. and the cestode *D. stemmacephalum*, as detected in six and two animals, respectively, did not appear to cause serious reactions in the mucosa. Preceding parasitic infection or larval migration were regarded as potential causes of the intestinal inflammation detected in nine non-infected animals. *Diphyllobothrium* sp. was found in the previously studied Icelandic HPs, but not in those from Norwegian waters (Siebert et al. 2006).

The observed prevalence of hepatic trematodiasis (90%) caused by *C. oblonga* is comparable to those previously reported for both Norwegian (86%) and Icelandic HPs (92%). Unlike the formerly studied Norwegian HPs (Lehnert et al. 2005; Siebert et al. 2006) where no animal exhibited severe infection, the present study revealed severe infection in 3% (2/61) of the animals. However, we found a lower prevalence of chronic cholangitis, pericholangitis and hepatitis (85%), as compared to the previously studied Norwegian (95%) and Icelandic HPs (100%). In both studies, lesions caused by the parasite could be present without detection of the parasite. Despite the lower prevalence of lesions, the degree of the lesions was predominantly severe, as opposed to the generally mild lesions found in the formerly studied Norwegian HPs. The detected differences in the prevalence of hepatic lesions between the two studies may have been related to age. In our study, 54% (33/61) of the animals were older than 3 years, compared to 45% in the Norwegian HPs in the previous study. We found that the overall prevalence of hepatic trematodiasis increased with age, which is in line with other studies (Lehnert et al. 2014; van Elk et al. 2019). It even increased with increasing latitude. All animals in the northernmost VF area were infected, of which 80% (20/25) were older than 3 years. However, in the southernmost S–T area the largest proportion of the infected animals, 65.2% (15/23), were younger than 3 years. Hence, there may be other age-related mechanisms that resulted in a lower prevalence of hepatic lesions in the present study compared to the previous. Nine of the 11 animals with parasitic caseous nodules were older than 5 years, and five were older than 10 years. Most (7/11) came from the VF area, and one from the S–T area. In these animals the level of infection was predominantly mild, and no parasite or lesions in the bile ducts were found in two (although they were classified as infected due to trematode eggs in the nodules). These findings may indicate that although the prevalence of *C. oblonga* increases with age, the lesions in the bile ducts decrease with older age probably due to repairing and immunity mechanisms.

Pancreatic trematodiasis was detected in 6 (10%) of the animals. All infections in the pancreas were concomitant with both mild and severe infections in the liver. Hence, infections in the pancreas were related to infections in the liver. The overall prevalence is lower than that previously reported from Norwegian (18%) and Icelandic (25%) HPs. Separating into the bycatch areas, none of the animals from the S–T area had infections in the pancreas. In this area, most of the animals with hepatic trematodiasis were younger than 3 years. Four of the total of six animals with pancreatic infections were older than 3 years. The associated moderate chronic eosinophilic pancreatitis as diagnosed histologically in six animals (10%) differed from the generally mild lesions in both the Norwegian (18%) and the Icelandic HPs (42%) in the former study (Siebert et al. 2006).

Urinary system

Whilst a single case of interstitial fibrosis of the kidneys was formerly detected in Icelandic HPs (Siebert et al. 2006), a single case of unilateral cystic kidney degeneration was found in the present study. Hence, kidney diseases or lesions do not seem to play an important role in Arctic HP health.

Lymphatic system

The observed prevalence of eosinophilic lymphadenitis is comparable to that previously found in Norwegian HPs. Mesenteric lymphadenitis as detected in 82% of the animals reflects the relative importance of parasitosis in the alimentary system, as opposed to pulmonary lymphadenitis, which was detected in only 7% of the animals. However, immunological reactions in terms of hyperplasia were noted in the tonsils as well as pulmonary and retropharyngeal lymph nodes in 36% of the animals.

Ear and central nervous system

The high prevalence of peribullar cavity nematodiasis caused by *S. minor* without associated gross lesions is similar to those previously reported in bycaught animals from Norway, Iceland, North and Baltic Seas and Canada (Clausen and Andersen 1988; Faulkner et al. 1998; Wünschmann et al. 2001; Siebert et al. 2006). However, unlike the previously studied Norwegian HPs (Lehnert et al. 2005), and similar to the Canadian HPs (Faulkner et al. 1998), the number of *S. minor* was distributed evenly between the left and right ear.

Conclusion

The most common pathological findings in these Arctic bycaught HPs were parasitoses in multiple organs with associated lesions, often severe, particularly in the lungs and liver, but also in the stomachs. The animals were generally well nourished and nearly all of them had food in their stomachs, indicating recent foraging. Obviously, the HPs living in this cold Arctic marine environment were able to tolerate the detected parasitic burden and associated lesions without significant health problems.

Acknowledgements We thank Dr Ulf Lindstrøm at the Institute of Marine Research (IMR), Tromsø, Norway for his cooperation to make this health assessment project a spin-off to the main project entitled “The role of harbour porpoise in Norwegian coastal marine communities”. We also thank Michael Poltermann, Nils Erik Skavberg, Kristin Windsland and Lotta Lindblom at the IMR for technical assistance during necropsies. In particular, we would like to thank the Norwegian Veterinary Institute, Tromsø and Dr Torill Mørk for help and assistance, as well as Dr Christina H. Lockyer at Age Dynamics, Tromsø, and Dr Anne Kirstine Frie at the IMR for their effort regarding age determination. Finally, we thank Prof Dr Pierre-Yves Daoust and Prof Dr Tomasz Ciesielski for reviewing the manuscript.

Author contributions KAR conceptualised the study and conducted the harbour porpoise necropsies with assistance of MR. Furthermore, KAR prepared the samples for histological investigations assisted by JL. The histopathological analysis was performed by PW. The parasitological identification was carried out by JL, supervised by US. KAR, JL, PW and MR prepared the manuscript. All authors provided comments on the manuscript and approved the final version.

Funding This study was funded by the FRAM Centre flagship project “The role of harbor porpoise in Norwegian coastal marine communities” (Project No. 14808-03) and by the Norwegian Institute of Marine Research through Project Nos. 14254 and 15590-03.

Data availability Aggregated data can be available upon request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare lack of any potential competing interests.

Ethical approval Not applicable.

Consent to participate All authors have agreed to participate in the study.

Consent for publication All authors have approved the manuscript for submission to "Polar Biology".

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