IJP: Parasites and Wildlife 9 (2019) 112–118

Contents lists available at ScienceDirect

IJP: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

There and back again – The return of the nasal mite *Halarachne halichoeri* to seals in German waters

Anja Reckendorf[a], Peter Wohlsein[b], Jan Lakemeyer[a], Iben Stokholm[a], Vivica von Vietinghoff[c], Kristina Lehnert[a,*]

[a] Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover, Foundation, Werftstr. 6, D-25761, Buesum, Germany
[b] Department of Pathology, University of Veterinary Medicine Hannover, Foundation, Buenteweg 17, D-30559, Hannover, Germany
[c] Deutsches Meeresmuseum, Katharinenberg 14-20, D-18439, Stralsund, Germany

ARTICLE INFO

Keywords:
Acari
Pinnipeds
Endoparasitic mite
Coevolution
Recolonisation
Halichoerus grypus

ABSTRACT

The nasal mite *Halarachne halichoeri* (Acari; Halarachnidae) is adapted to live in the marine environment with pinnipeds as its primary host and can cause different levels of upper respiratory disease in both harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*). Historical reports of *H. halichoeri* occurring in seals from German waters date back to the end of the 19th century. However, with the disappearance of the grey seal from German waters as a consequence of human over-exploitation, the mite vanished from the records and the fauna found in Germany for more than a century. Although a stranding network has been monitoring marine mammal health along the German coasts since the mid 1980s with extensive post-mortem investigations, this study reports the first and subsequent findings of *H. halichoeri* in grey and harbour seals from the North and Baltic Sea from 2014 onwards. The re-emergence of this endoparasitic mite in North and Baltic Sea habitats seems to have occurred simultaneously with the recolonisation of its primary host, the grey seal. During the course of its recolonisation, it was probably transmitted to harbour seals sharing the same haul-out sites. Molecular analyses showed a high similarity of rDNA sequences with *H. halichoeri* collected from sea otters (*Enhydra lutris*) in the USA. However, more thorough analyses of additional gene loci are required to fully assess the exchange and diversity of this parasite between geographically isolated regions and species.

1. Introduction

Marine mammals are upper trophic level predators and important bioindicators for ecosystem health. Their distribution, health status and pollutant burdens can indicate changes in the ecosystem (Hilty and Merenlender, 2000). Marine mammal parasites are increasingly used as biomarkers for habitat use, health monitoring, understanding migrations of marine mammal hosts in various geographical areas as well as species interactions and their ecology (Balbuena et al., 1995; MacKenzie, 2002; Vidal-Martínez et al., 2010; Lehnert et al., 2014).

Mites (Arachnida; Acari) are usually free-living or ectoparasites of land vertebrates. However, the family Halarachnidae (Acari, Gamasida) mainly consists of obligatory endoparasitic mites of the respiratory tract. They coevolved with the carnivorous ancestors of pinnipeds in the marine environment and during their long evolutionary history they established a relatively benign relationship with their phocid hosts. Their morphological adaptations to life in a semi-aquatic host make them uniquely different from other Gamasidae and specific to their host and its habitat (Furman, 1979; Fain, 1994). Two genera are parasites of the respiratory tract in pinniped species: *Halarachne* spp. Allman (1847) have been observed affecting the nasal tract of phocids, while *Orthohalarachne* spp. Newell (1947) is commonly found in otariids and odobenids (Newell, 1947; Furman and Dailey, 1980).

The first specimen of *Halarachne* (*H.*) *halichoeri* (Allman, 1847) was found in July 1837 by Dr O'Brien Bellingham in the posterior nares of a grey seal (*Halichoerus grypus*) shot on the Dublin coast of Ireland (Allman, 1844). Nonetheless, the first detailed and official description of fresh specimens was published in 1847 by George James Allman. This peculiar naso-pharyngeal mite instigated broad research interest during the late 19th century (Oudemans, 1925). German zoologist and palaeontologist Alfred Nehring described the first finding of *H. halichoeri* in German waters from a dead Baltic grey seal from the Bay of

* Corresponding author.
E-mail addresses: Anja.Reckendorf@tiho-hannover.de (A. Reckendorf), peter.wohlsein@tiho-hannover.de (P. Wohlsein), Jan.Lakemeyer@tiho-hannover.de (J. Lakemeyer), Iben.Stokholm@tiho-hannover.de (I. Stokholm), vivicavv@web.de (V. von Vietinghoff), Kristina.Lehnert@tiho-hannover.de (K. Lehnert).

https://doi.org/10.1016/j.ijppaw.2019.04.003
Received 8 January 2019; Received in revised form 26 March 2019; Accepted 6 April 2019

Table 1
Background information of harbour and grey seals infected with *Halarachne halichoeri* from the North and Baltic Sea, including general pathological findings (n. a. = not assessed due to advanced decomposition).

Species ID	Date of death/ discovery	Age	Sex	Origin	Observations	Number of nasal mites	Pathology
H.g. 1	11.02.2014	adult	♀	Baltic Sea. Binz, Island of Ruegen	found dead	> 60 adults, few larvae	Severe alveolar and interstitial oedema; multifocal moderate interstitial emphysema; multifocal ulcerative enterocolitis with acanthocephalans
H.g. 2	26.07.2015	adult	♀	North Sea. Hoernum, Island of Sylt	emaciated, apathetic, mild diarrhoea, respiratory distress, coughing, unilateral bleeding from one nostril	~30 larvae, ~6 adults	Severe suppurative bronchopneumonia; moderate alveolar/interstitial oedema, moderate alveolar emphysema; severe granulomatous gastritis
H.g. 3	13.02.2016	adult	♂	Baltic Sea. Sierksdorf, Bay of Luebeck	apathetic, poor nutritional status, respiratory distress	Multiple adults & larvae	Mild alveolar oedema; severe interstitial emphysema; amyloidosis in kidney, stomach, pancreas, adrenal glands
H.g. 4	31.07.2018	adult	♀	North Sea. Brunsbuettel	apathetic, respiratory distress, coughing	Multiple adults & larvae	Severe suppurative bronchopneumonia; moderate granulomatous and eosinophilic mural gastritis with intralesional nematodes
P.v. 1	17.08.2015	juvenile	♂	Baltic Sea. Gelting Bay	found dead	One decaying adult	n. a.
P.v. 2	13.10.2015	yearling	♀	North Sea. Helgoland island	found dead	Five adults	Severe pulmonary endoparasitosis (nematodes); multifocal suppurative pneumonia; severe alveolar/interstitial oedema and emphysema; moderate granulomatous and eosinophilic lymphadenitis (mesenterial)

Greifswald in 1884 (Nehring, 1884). Further detailed descriptions by Nehring in 1895 were from two Baltic individuals shot close to Gdansk in Poland (Nehring, 1895). Since only one genus and one species of these mites were known from pinnipeds at that time, there is no certainty that Nehring correctly identified the species. Unfortunately, Nehring's specimens have not been preserved or were lost during the Second World War, so a verification is no longer possible.

Motile *H. halichoeri* larvae are concentrated in the anterior nares and are mainly transmitted through convulsive coughing and close nasal or body contact (Furman and Smith, 1973). The non-motile adults are true endoparasites, which are anchored to mucosal surfaces deeper inside the nares and cannot survive for long outside their host environment (Geraci and St. Aubin, 1987). Nasal mite infections of phocids in Europe have been observed in British waters since the 1970s (Baker, 1987) and have recently been reported at the Northern Spanish Atlantic coast and in Poland (Alonso-Farré et al., 2012; Rolbiecki et al., 2018). *Halarachne halichoeri* is mainly associated with minor morphological changes in harbour seals (*Phoca vitulina*) and grey seals, but can cause different levels of respiratory disease by damaging mucous membranes and impairing respiration (Baker, 1987; Geraci and St. Aubin, 1987; Alonso-Farré et al., 2012; Measures, 2018).

Grey seals are Germany's largest predators, residing along the German North and Baltic Sea coasts. Up to the Middle Ages, the grey seal was the most common seal species in the German Wadden Sea region (Requate, 1957; Lotze, 2005). However, due to an increase in the human population, colonisation, human-induced habitat alterations and extensive, unsustainable hunting, grey seals had almost completely disappeared from the Wadden Sea (The Netherlands, Germany and Denmark) coasts in the 16th century (Reijnders et al., 1995). Around 1960, the Wadden Sea harbour seal numbers dropped in a similarly dramatic way (Reijnders, 1983). Responding to the dwindling numbers, seal hunting was gradually prohibited throughout the Wadden Sea in the mid-1970s. Since seal protection in the United Kingdom preceded the Wadden Sea countries by decades (Kiely et al., 2000), British grey seal stocks were already subject to exponential increase prior to the 1970s (Bonner, 1972).

Based on old hunting statistics, the number of Baltic grey seals was estimated to be between 88,000–100,000 in the early 1900s. As a consequence of excessive hunting and following severe exposure to reproduction impairing organochlorines, the population was gradually reduced to less than 4000 individuals by the late 1970s. In 1988, the hunting of seals was prohibited in the Baltic Sea, supporting an increase in populations since 1980 (Harding and Haerkoenen, 1999). Following the protection of seals in the Baltic and all North Sea bordering countries, a slow return of grey seals was observed throughout both Seas, in the Wadden Sea especially supported by an influx of animals from the United Kingdom (Reijnders et al., 1995; Brasseur et al., 2015, 2017).

This study is the first report and record on the (re)occurrence of an endoparasitic mite specific to seal species, including pathological lesions and molecular data, in relation to historical records and the ecological context of host abundance in German waters.

2. Material and methods

2.1. Animals and post-mortem examination

Post-mortem investigations on all marine mammals found on the coasts of the German Federal State of Schleswig-Holstein (S-H) are performed at the Institute for Terrestrial and Aquatic Wildlife Research (ITAW) in regard to their decomposition status (Lehnert et al., 2005; Siebert et al., 2007). Within a coordinated stranding network that was established in 1990, carcasses are screened for ecto- and endoparasites and histopathological and microbiological investigations are conducted (Siebert et al., 2007, 2017). In the federal state of Mecklenburg-West Pomerania, a similar network collects marine mammal carcasses for inspection at the Deutsches Meeresmuseum. In the context of this

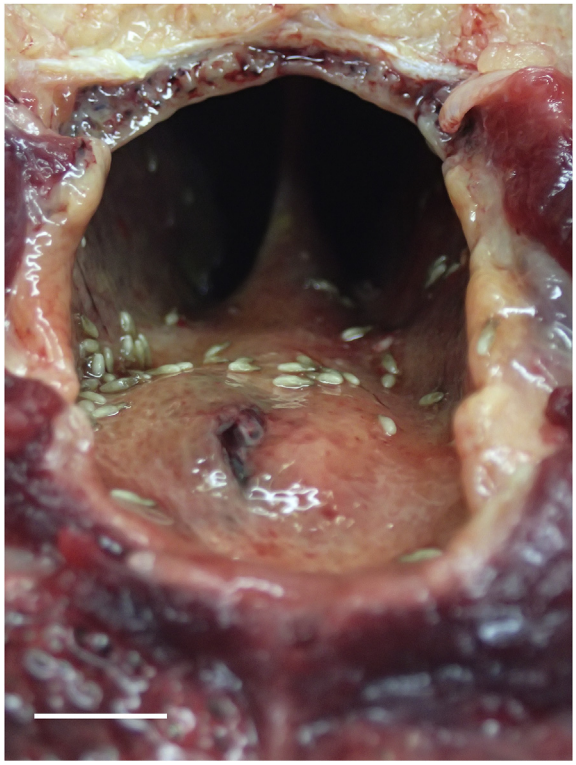

Fig. 1. Macroscopic image of in situ nasal mites within the caudal nares of H.g. 3, ventrodorsal view, animal lying on its back. Scale bar approximately 1 cm.

continuous marine mammal health monitoring project, six seals, four grey seals (H.g. 1–4) and two harbour seals (P.v. 1, 2) were found to harbour nasal mites (Table 1). Of these six individuals, one seal (P.v. 1) was only examined macroscopically as it was too decomposed for further investigations.

Mite individuals were collected with soft forceps, cleaned in tap water and preserved in 70% ethanol. For histopathology, samples of nasopharyngeal tissue and other organs were collected, fixed in 10% neutral buffered formalin and routinely embedded in paraffin wax. Tissue sections of 3–4 µm were cut and subsequently stained with haematoxylin and eosin (HE). Representative mite specimens (adults n = 45 and larvae n = 45) from four grey seals and one harbour seal were measured. The total idiosoma length was measured to the base of the gnathosoma, while the width was taken caudally to the last leg pairs. Dorsal shield measurements were only taken where shield margins could be clearly determined. Selected *H. halichoeri* examples were photographed using CellSens Entry software with a Stereomicroscope (Olympus CX 41) with 100x magnification and attached camera (Olympus SC30). For documenting and comparing historical specimens at the Centre of Natural History of the Zoological Museum Hamburg, Germany (CeNak), two adults and two larvae were photographed using the BK Plus Lab System (Dun, Inc.) with 5x and 10x LD Mitutoyo objectives and integrated Canon camera. The images were captured and stacked with the Zerene Stacker software version 1.04.

2.2. Morphological and molecular identification

Larval and adult mites were identified on the basis of their morphological characteristics and in accordance with the descriptions by Oudemans (1925), Newell (1947) and Furman and Dailey (1980). To also achieve parasite identification using gene sequence data, genomic DNA was isolated from seven mite specimens (five adults and two larvae) from two hosts using a QIAamp Tissue Kit (Qiagen, Hilden, Germany). The ribosomal DNA (rDNA) ITS-2 was amplified from six individuals. DNA concentrations and purity were determined using a Nanodrop 2000c (Thermo Scientific) spectrophotometer. Approximately 300 bp of the 545/683 large subunit ribosomal ribonucleic acid (LSU rRNA) gene was amplified using oligonucleotide primers 5′- TCC AACGGTGGCGCAG -3′ (forward) and 5′- CAGCTGAATCGACAACCA ACG -3′ (reverse) designed from the *H. halichoeri* sequence available at GenBank (Sequence ID: MH426848.1). Reactions were performed in a total volume of 50 mL, comprising MyTaq Red DNA polymerase (Bioline) and MyTaqTM Red reaction buffer (Bioline (Aust) Pty Ltd., Alexandria, New South Wales, Australia), primers at 20 µM each and 2–4 µl of DNA template in a TGradient cycler (Biometra). Cycling conditions were initial denaturation at 95 °C for 1 min, followed by 35 cycles of denaturation at 95 °C for 15 s, annealing at 60 °C for 15 s and extension at 72 °C for 10 s. PCR products were visualised in a 1.5% agarose gel using SYBRSafe DNA Gel stain on a gel documentation system (Vilber Lourmat, France). PCR products were sent premixed with primers to Microsynth (Göttingen, Germany) for Sanger Sequencing. The closest match to the sequence was determined using BLASTn on GenBank. Voucher specimens were deposited at the CeNak Department of Arachnology, Zoological Museum - University Hamburg, Germany (accession nos. ZMH-A0002181, ZMH-A0002182).

2.3. Comparative material from museum collections

An extensive literature review and comparison of old *H. halichoeri* descriptions was conducted to find historical records of *H. halichoeri* from Germany. Specimens from 1890 (11 larvae, two teneral females, two specimen slides; ex H.g. Zoological Garden Hamburg, List No. 635; specified by A. C. Oudemans in 1910, reviewed by D. P. Furman in 1979) and 1901 (one larva, three females, two specimen slides; ex H.g. Bay of Greifswald; specified by A. C. Oudemans in 1910, reviewed by D. P. Furman in 1979) were found archived in the collection of the CeNak's Arachnology Department, University of Hamburg, Germany. The mites collected within this study were compared with this historical material.

3. Results

3.1. Parasitological findings

The first new discovery of *H. halichoeri* occurred in an adult female grey seal from the Baltic island of Ruegen, Germany, in 2014. Subsequently, three grey seals and two harbour seals from the Baltic and North Sea were found to harbour nasal mites between 2015 and 2018 (Table 1). The level of infection varied among cases without a clear pattern (Table 1). All nasal mites were found within the nasopharynx, anchored to the choanae and palate (Fig. 1). *Halarachne halichoeri* individuals from H.g. 2 stayed alive for at least three days after their host's death.

The adults of *H. halichoeri* presented a whitish elongated opisthosoma with a prominent dorsal shield on the prosoma and smooth body cuticle, typical setae on the legs and four pairs of long maxillary ventral setae (Fig. 2). The mean idiosoma length of 45 randomly chosen adult individuals was 2783.11 µm (± 148.37 µm SD) and the mean width was 927.95 µm (± 93.74 µm SD, n = 45). Measured adult specimens had a mean dorsal shield length of 1012.13 µm (± 31.10 µm SD, n = 26) and width of 470.22 µm (± 103.96 µm SD, n = 26). The larvae were smaller with a spider-like habitus, a blunt ovoid idiosoma, setae on the legs, two large claws on tarsi II and III and post-anal setae longer than the adanal setae (Fig. 3). The mean idiosoma length of 45 randomly chosen larvae was 1174.18 µm (± 57.13 µm SD, n = 45).

The 300 bp sequence obtained confirmed this identification, the closest match when blasted in GenBank being *H. halichoeri* (Sequence ID: MH426848.1) with 99% identity.

3.2. Pathomorphological findings

In most cases, *H. halichoeri* infection was associated with

Fig. 2. Dark field binocular image of *Halarachne halichoeri* adult ventral and dorsal view (A) from H.g. 2 in comparison with (B) CeNak museum specimen from 1890.

hyperaemia and a mild sinus inflammation. Specific case details including general pathological results are listed in Table 1. Histology of the nasopharynx was performed in three animals with macroscopic alterations to the nasal mucosa. H.g. 2 revealed severe, diffuse lympho-plasmacytic infiltration of the nasal mucosa (Figs. 4 and 5). During necropsy of H.g. 3, the nasal mucosa appeared reddish and revealed moderate to severe multifocal to confluent lympho-plasmacytic infiltration with intraluminal parasite structures (Fig. 5). Necropsy of H.g. 4 revealed a slightly hyperaemic mucosa of the frontal nares and presence of yellowish mucus. Two polyp-like growths of the nasal mucosa of approximately 10 × 5 mm were present on the nasal side of the hard palate, on which adult mites resided (Fig. 6). These polypous proliferations were associated with a severe diffuse lympho-plasmacytic infiltration. In addition, there were focal ulcerations and partly re-epithelialised granulation tissues with marked diffuse, predominantly plasmacytic infiltration.

4. Discussion

This study reports the first findings of a re-emerging arthropod endoparasite in seal species of the German North and Baltic Sea. *Halarachne halichoeri*'s disappearance and subsequent re-occurrence after more than a century is most likely correlated to the recovery and recolonisation of grey seals throughout the last decades. Coextinctions of associates with extinction events of their hosts are a known phenomenon in other species (Dunn, 2005). The absence of further *H. halichoeri* records for over 100 years could be related to minimal sampling efforts in the past. However, an ever improving network has been monitoring marine mammal strandings along the German coasts since the mid 1980s, including extensive post-mortem investigations on hundreds of seals (Siebert et al., 2007, Lehnert et al. 2007). Thus, the absence of *H. halichoeri* over the past decades is unlikely to be related to an insufficient sampling and examination effort, rather than to an actual absence of the parasite from the German fauna.

Halarachne halichoeri's prevalence in harbour seals and grey seals underlines that both species live in close proximity in German waters and often use the same haul-out sites, e.g. on Helgoland, where interspecies contacts occur and mites can be transmitted. *Halarachne halichoeri* seems to have evolved as a generalist arachnid endoparasite in the marine environment, which can occur in a broad geographical range from the Alaskan waters (Fay and Furman, 1982) to the Galician coast (Alonso-Farré et al., 2012). It can form parasite-host-complexes with carnivorous marine mammals, including several seal species, e.g. spotted seals (*Phoca largha*) (Fay and Furman, 1982) and also sea otters (Kenyon et al., 1965).

General pathological findings reported in Table 1 were not directly related to *H. halichoeri* infections, but influenced the hosts' health and contributed to the cause of death. Pathomorphological nasal mucosa alterations of the presented cases were mild, including hyperaemia and inflammation. For the two polyp-like proliferations of H.g. 4, it could not be established whether the mites were just incidental or causative agents.

The morphology and measurements of the present specimens corresponded to the historic specimens previously described by Oudemans (1925) and by Furman and Dailey (1980). The larva from the Hamburg Museum depicted in Oudemans' 1925 publication measured 1320 µm in idiosoma length and 725 µm in width and an adult female from the same host measured 2818 µm in idiosoma length and 891 µm in width. It can thus be assumed that Oudemans used the still existing CeNak specimen for his studies, just like Deane P. Furman had done in 1979 for his subsequent publication. Furman described mature females as being up to 2820 µm in idiosomal length, while measured dorsal shields were 1000 to 1180 µm long and 403–540 µm wide. A slight variability among the current and historic measurements may be due to physiological individual differences, the preservation and fixation as well as the age of the historical samples.

The rDNA sequences derived from *H. halichoeri* specimens from seals in German waters showed a close similarity between *H. halichoeri* specimens from the US coast where the samples originated from sea otters (Pesapane et al., 2018). Further research also investigating other gene loci is needed to investigate whether geographical isolation between areas has contributed to genetic variation.

Many museums house century-old and unique collections of skeletal parts, frozen and fixed tissues, as well as mounted parasites of various marine mammal species. These materials and data sets are highly valuable for current research since they facilitate investigations into global and local species fluctuations, human impacts, changes in ecosystem and animal health and the results of conservation and management efforts. The CeNak specimens archived from grey seals from 1901 (and 1890) enabled comparison of recent specimens from this

Fig. 3. Dark field binocular image of *Halarachne halichoeri* larvae ventral and dorsal view (A) from H.g. 2 in comparison with (B) CeNak museum specimen from 1890.

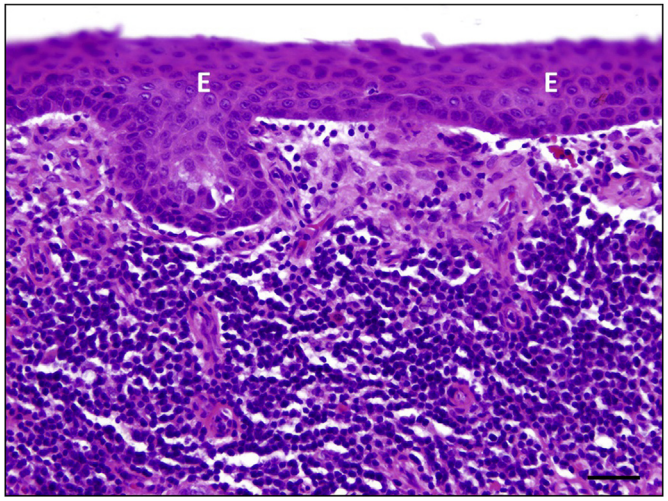

Fig. 4. Grey seal, nasal mucosa with severe, diffuse lympho-plasmacytic infiltration; HE; E = epithelium; bar = 100 µm.

study with historical findings. Furthermore, they allowed new findings to be put in a historical context and a better understanding of the development of marine mammal ecology over longer periods of time. Unfortunately, much of the former Hamburg Natural History museum, its collection and catalogue were destroyed during the Second World War. Therefore, it is not possible to obtain further details such as host origin for the 1890 specimens. Further investigations at other collections revealed no additional archived samples. These historical findings in conjunction with the contemporary stranding and necropsy records dating back to the mid-1980s show no cases of *H. halichoeri* in German waters for over 100 years, while the mite was found in areas where the grey seal was still present (Anderson et al., 1974; Baker, 1980; Munro et al., 1992).

The prevalence of *Halarachne* in German waters might be underreported, due to post-mortem emigration from dead host individuals or due to losses during carcass transport. The here presented cases are in agreement with previous findings that grey seals act as a major host species (Cooreman, 1958; Furman and Dailey, 1980), playing the most important role in the life cycle of *H. halichoeri*. However, since grey seals share their habitat with other marine mammals, interspecies transmission of the nasal mite occurs. Three live observed animals showed typical clinical symptomatology associated with respiratory tract infections. These symptoms were most likely due to bronchopneumonia and pulmonary emphysema diagnosed in these animals. These can, however, be adversely affected by nasal passage obstruction due to swollen mucosae or larger amounts of parasites. The extent of current pathological findings in seals from German waters supports preceding conclusions that this naso-pharyngeal mite commonly causes minor changes when not present in extensive numbers (Furman, 1979; Fay and Furman, 1982; Baker, 1987). Furthermore, it did not contribute to the cause of illness or death in the presented cases. Compared to a recent study from Spain, which identified the nasal mite as the primary cause of the upper respiratory tract infections of juvenile seals (Alonso-

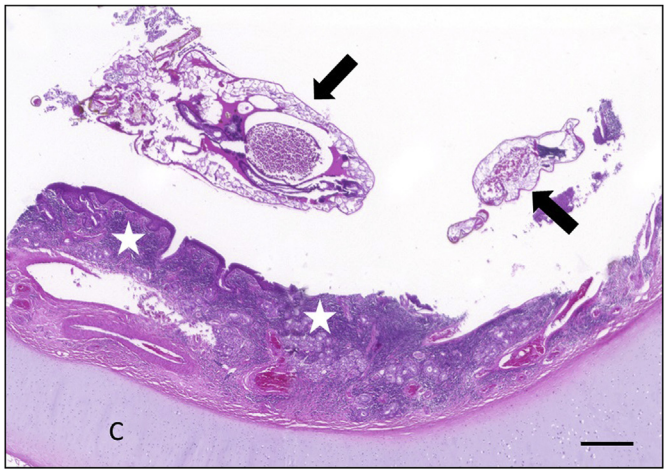

Fig. 5. Grey seal, nasal cavity with intraluminal mites (arrows) and severe, diffuse inflammatory infiltration of the mucosa (asterisks); HE; C = cartilage; bar = 250 µm.

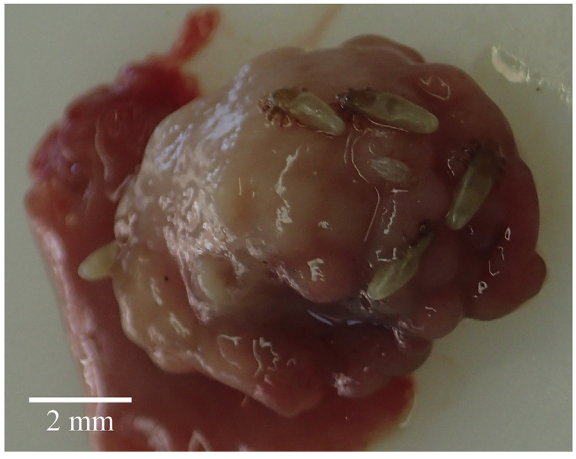

Fig. 6. Polyp-like growths with adult mites present. Tissue extracted from H.g. 4's inferior nasal meatus adjacent to the hard palate.

Farré et al., 2012), *H. halichoeri* findings in Germany are much rarer and seem to be associated with only minor macroscopical lesions.

5. Conclusion

This study reports on the occurrence of a re-emerging parasitic nasal mite in grey and harbour seals in German waters. *Halarachne halichoeri* had vanished from the German Baltic and North Sea fauna during the course of the last century with the disappearance of its main host. However, due to successful reestablishment of grey seal populations in both Seas, the seal nasal mite has likewise returned to German waters. Further examinations, including genetic studies comparing specimens from different hosts and different localities are desirable to gain more knowledge about this neglected parasite.

Conflicts of interest

The authors declare no conflict of interest.

Ethical standards

Not applicable.

Funding

Kristina Lehnert was funded by the Volkswagen Foundation under the “Research in Museums” (AZ 89911) programme. The post-mortem investigations were partly funded by the Ministry of Energy, Agriculture Environment and Rural Affairs, and the S-H National Park Service. This publication was supported by Deutsche Forschungsgemeinschaft and the University of Veterinary Medicine Hannover, Foundation within the funding programme Open Access Publishing.

Acknowledgements

The authors wish to thank Danilo Harms and Nadine Dupérré at CeNak, Hamburg for allowing us access to the arachnology collection samples and to the photo equipment. Furthermore, we would like to thank Jason Dunlop from the Museum of Natural History Naturkunde Berlin; Gert Troester from the Zoological Museum Goettingen; Hans-Joachim Krammer from the Zoological Research Museum Alexander Koenig, Bonn; Lina Rosotta from the Zoological Museum at the University of Kiel and Thomas Kaiser and Frederik Jessen from the CeNak Mammalogy Department for providing information on samples in their collections. The authors wish to thank all individuals who report and collect marine mammals in Germany, in particular the S-H national park rangers and seal hunters, as well as all ITAW colleagues and assistants for their support during necropsies.

References

Allman, G.J., 1844. In: Thompson, W. (Ed.), Report on the Fauna of Ireland, Div. Invertebrata. Report of the Thirteenth Meeting of the British Association for the Advancement of Science; Cork, August 1843, pp. 291.

Allman, G.J., 1847. Description of a new genus and species of tracheary arachnidans. Ann. Mag. Nat. Hist. 20, 47–52.

Alonso-Farré, J.M., D'Silva, J.I.D., Gestal, C., 2012. Naso-pharyngeal mites *Halarachne halichoeri* (Allman, 1847) in grey seals stranded on the NW Spanish Atlantic Coast. Vet. Parasitol. 183, 317–322.

Anderson, S.S., Bonner, W.N., Baker, J.R., Richards, R., 1974. Grey seals, *Halichoerus grypus*, of the Dee Estuary and observations on a characteristic skin lesion in British seals. J. Zool., Lond. 174, 429–440.

Baker, J.R., 1980. The pathology of the grey seal (*Halichoerus grypus*). II. Juveniles and Adults. Br. Vet. J. 136, 443–447.

Baker, J.R., 1987. Causes of mortality and morbidity in wild juvenile and adult grey seals (*Halichoerus grypus*). Br. Vet. J. 143, 203–220.

Balbuena, J.A., Aznar, F.J., Fernandez, M., Raga, J.A., 1995. The use of parasites as indicators of social structure and stock identity of marine mammals. In: Blix, A.S., Walloe, L., Ulltang, O. (Eds.), Developments in Marine Biology. 4. Whales, Seals, Fish and Man: Proceedings of the International Symposium on the Biology of Marine Mammals in the Northeast Atlantic. Tromso, Norway, 29 Nov.-1 Dec., 1994. Elsevier Science, Amsterdam, pp. 133–139.

Bonner, W.N., 1972. The grey seal and common seal in European waters. Oceanogr. Mar. Biol. Annu. Rev. 10, 461–507.

Brasseur, S.M.J.M., Van Polanen Petel, T.D., Gerrodette, T., Meesters, E.H.W.G., Reijnders, P.J.H., Aarts, G., 2015. Rapid recovery of Dutch gray seal colonies fueled by immigration. Mar. Mamm. Sci. 31, 405–426.

Brasseur, S.M.J.M., Aarts, G., Reijnders, P.J.H., Kirkwood, R., 2017. Gray seal tracking reveals different behaviours of resident and transient population components. (Chapter 6) (PhD Thesis) In: Brasseur, S.M.J.M. (Ed.), Seals in Motion – How Movements Drive Population Development of Harbour Seals and Grey Seals in the North Sea. Wageningen University, The Netherlands, pp. 98–109.

Cooreman, J., 1958. *Halarachne halichoeri* Allman, acarien parasite du phoque *Halichoerus grypus* (Fabricius). Bull. ann. Soc. r. belge entomolog. 94, 159–168.

Dunn, R.R., 2005. Modern insect extinctions, the neglected majority. Conserv. Biol. 19, 1030–1036.

Fay, F.H., Furman, D.P., 1982. Nasal mites (Acari: Halarachnidae) in the spotted seal, *Phoca largha* Pallas, and other pinnipeds of Alaskan waters. J. Wildl. Dis. 18, 63–68.

Fain, A., 1994. Adaptation, specificity and host-parasite coevolution in mites (Acari). Int. J. Parasitol. 24, 1273–1283.

Furman, D.P., Dailey, M.D., 1980. The genus *Halarachne* (Acari: Halarachnidae), with the description of a new species from the Hawaiian Monk Seal. J. Med. Entomol. 17, 352–359.

Furman, D.P., Smith, A.W., 1973. In vitro development of two species of *Orthohalarachne* (Acarina: Halarachnidae) and adaptations of the life cycle for endoparasitism in mammals. J. Med. Entomol. 10, 415–416.

Furman, D.P., 1979. Specificity adaptation and parallel evolution in the endoparasitic Mesostigmata of mammals. In: In: Rodriguez, J.G. (Ed.), Recent Advances in Acarology, vol. II. Acad Press, New York, pp. 329–337.

Geraci, J.R., St Aubin, D.J., 1987. Effects of parasites on marine mammals. Int. J. Parasitol. 17, 407–414.
Hilty, J., Merenlender, A., 2000. Faunal indicator taxa selection for monitoring ecosystem health. Biol. Conserv. 92, 185–197.
Harding, K.C., Haerkoenen, T.J., 1999. Development in the Baltic grey seal (*Halichoerus grypus*) and ringed seal (*Phoca hispida*) populations during the 20th Century. Ambio 28, 619–627.
Kenyon, A.S., Salyer, I.O., Kurz, J.E., Brown, D.R., 1965. Large-scale elution fractionation of polymers. J. Polym. Sci. C. 8, 205.
Kiely, O., Lidgard, D., McKibben, M., Connolly, N., Baines, M., 2000. Grey Seals: Status and Monitoring in the Irish and Celtic Seas. Maritime Ireland/Wales INTERREG Report No, vol. 3. Marine Institute, Dublin, pp. 77 ISSN: 1393-9025.
Lehnert, K., Raga, J.A., Siebert, U., 2005. Macroparasites in stranded and by caught harbour porpoises from German and Norwegian waters. Dis. Aquat. Org. 64, 265–269.
Lehnert, K., Raga, J.A., Siebert, U., 2007. Parasites in harbour seals (*Phoca vitulina*) from the German Wadden Sea between two phocine distember virus epidemics. Helgol. Mar. Res. 61, 239–245.
Lehnert, K., Seibel, H., Hasselmeier, I., Wohlsein, P., Iversen, M., Nielsen, N.H., Siebert, U., 2014. Increase in parasite burden and associated pathology in harbour porpoises (*Phocoena phocoena*) in West Greenland. Polar Biol. 37 (3), 321–331.
Lotze, H.K., 2005. Radical changes in the Wadden Sea fauna and flora over the last 2000 years. Helgol. Mar. Res. 59, 71–83.
MacKenzie, K., 2002. Parasites as biological tags in population studies of marine organisms: an update. Parasitology 124, 153–163.
Measures, L.N., 2018. Helminths and parasitic arthropods. In: Gulland, F.M.D., Dierauf, L.A., Whitman, K.L. (Eds.), CRC Handbook of Marine Mammal Medicine, third ed. CRC Press, Boca Raton, FL, pp. 471–497.
Munro, R., Ross, H., Cornwell, C., Gilmour, J., 1992. Disease conditions affecting common seals (*Phoca vitulina*) around the Scottish mainland, September-November 1988. Sci. Total Environ. 115, 67–82.
Nehring, A., 1884. Ueber *Halarachne halichoeri* allmann, sowie ueber einige *halichoerus* schaedel. Sitzb. Ges. Naturfr. Berlin 4, 57–64.
Nehring, A., 1895. Die nasenmilbe der Kegelrobbe. Naturw. Wochenschrift. 10, 225–226.
Newell, I.M., 1947. Studies on the morphology and systematics of the family Halarachnidae, Oudemans 1906 (Acari, parasitoidea). Bingham Oceanogr. Coll. Bull. 10, 235–266.
Oudemans, A.C., 1925. Halarachne-studien. Arch. Naturgesch., Abt. A. 91, 48–108.
Pesapane, R., Dodd, E., Javeed, N., Miller, M., Foley, J., 2018. Molecular characterization and prevalence of *Halarachne halichoeri* in threatened southern sea otters (*Enhydra lutris nereis*). Int J Parasitol Parasites Wildl 7, 386–390.
Reijnders, P.J.H., 1983. The effect of seal hunting in Germany on the further existence of a harbour seal population in the Dutch Wadden Sea. Z. Saugetierkd. (Mamm. Biol.) 48, 50–54.
Reijnders, P.J.H., van Dijk, J., Kuiper, D., 1995. Recolonization of the Dutch Wadden Sea by the grey seal *Halichoerus grypus*. Biol. Conserv. 71, 231–235.
Requate, H., 1957. Zur nacheiszeitlichen geschichte der Säugetiere schleswig-holsteins. Bonn. Zool. Beitr. 8, 207–229.
Rolbiecki, L., Izdebska, J.N., Bidziński, K., Jankowska-Jarek, M., 2018. Nasopharyngeal mites *Halarachne halichoeri* (Allman, 1847) parasitizing the gray seal *Halichoerus grypus* (Fabricius, 1791) in the Baltic Sea with notes on other parasitic Halarachnidae associated with marine mammals. Oceanol. Hydrobiol. Stud. 47, 398–404.
Siebert, U., Wohlsein, P., Lehnert, K., Baumgärtner, W., 2007. Pathological findings in harbour seals (*Phoca vitulina*): 1996-2005. J. Comp. Pathol. 137, 47–58.
Siebert, U., Rademaker, M., Ulrich, S.A., Wohlsein, P., Ronnenberg, K., Prenger-Berninghoff, E., 2017. Bacterial microbiota in harbour seals (*Phoca vitulina*) from the North Sea of Schleswig-Holstein, Germany, around the time of morbillivirus and influenza epidemics. J. Wildl. Dis. 53, 201–214.
Vidal-Martínez, V.M., Pech, D., Sures, B., Purucker, S.T., Poulin, R., 2010. Can parasites really reveal environmental impact? Trends Parasitol. 26, 44–51.