Polar Biology (2025) 48:60
https://doi.org/10.1007/s00300-025-03379-5

RESEARCH

The Scaly Notothen *Trematomus loennbergii* a new host, and the Ross Sea, Antarctica, a new locality for dermal X-cell parasites *Notoxcellia* spp.

Thomas Desvignes[1,2] · Clara Péron[3] · Jennifer Devine[4] · John H. Postlethwait[1]

Received: 13 December 2024 / Revised: 14 March 2025 / Accepted: 19 March 2025

Abstract
Pathogens affecting Antarctic fishes remain mostly unknown and are largely limited to the description of macroparasites such as leeches and endoparasitic worms. Fish, however, occupy a crucial role in the functioning of the Antarctic ecosystem and deterioration of their health can alter the entire Antarctic food chain. In recent years, several studies have identified novel viruses and unicellular parasites affecting the health of notothenioid fishes. Among those, the unicellular parasitic family Xcellidae has received attention following the discovery of an unprecedented disease outbreak in a fjord on the Western Antarctic Peninsula. This pathological situation was caused by a novel X-cell genus *Notoxcellia*. Soon thereafter, an additional X-cell genus, *Cryoxcellia*, was described infecting the Bald Notothen *Trematomus borchgrevinki* in the Ross Sea. These studies raised awareness and drew observers' and researchers' attention to pathologies in Antarctic fishes. Here, we report that during a 2023 Ross Sea shelf survey, a specimen of the Scaly Notothen *Trematomus loennbergii* displaying skin lesions reminiscent of *Notoxcellia* infection had been ingested by an Antarctic Toothfish *Dissostichus mawsoni* and was recovered from its stomach. Molecular analyses confirmed the presence of *Notoxcellia* sp. X-cell parasites in the fish's lesions. This new case of X-cell disease suggests that *Notoxcellia* spp. may have a circumpolar distribution and stresses the need for monitoring Antarctic fish health similar to surveillance protocols for Antarctic birds and marine mammals.

Keywords Cryonotothenioid · Nototheniidae · Trematominae · Xcellidae · Ross Sea · Toothfish

Introduction

X-cells (Order Perkinsida, Family Xcellidae) are unicellular parasitic alveolates known from several marine fish species throughout the world (Freeman et al. 2011, 2017). Recent genetic analyses of diverse fish pathologies led to the description of novel X-cell genera and species (Karlsbakk et al. 2021; Desvignes et al. 2022; Evans et al. 2023). In Antarctica, until recently, only *Xcellia lamelliphila* was known to infect the gills of several fish species of the genus *Trematomus* in the Ross Sea (Evans and Tupmongkol 2014). But an unprecedented fish disease outbreak in Andvord Bay, a fjord of the Western Antarctic Peninsula, led to the description of the new genus *Notoxcellia* that proliferated in the dermis of two notothenioid species, the Crowned Notothen *Trematomus scotti* and the Painted Notothen *Nototheniops larseni* (see Desvignes et al. 2022). Infected fish displayed skin xenomas of various degrees of severity that could be located anywhere on the body, although most frequently around the head and close to the anus (Desvignes et al. 2022). Soon after, *Cryoxcellia*, another new genus of Antarctic X-cell parasites was described from the Bald Notothen *Trematomus borchgrevinki* in the Ross Sea (Evans et al. 2023). In contrast to *Notoxcellia*, the *Cryoxcellia* and *Xcellia lamelliphila* parasites infected the gills of the host fish (Evans and Tupmongkol 2014). Whether in the skin or in the gills, X-cells are large unicellular parasites that proliferate

✉ Thomas Desvignes
tdesvignes@uab.edu

1 Institute of Neuroscience, University of Oregon, Eugene, OR 97403, USA

2 Department of Biology, University of Alabama at Birmingham, Birmingham, AL 35233, USA

3 Laboratoire de Biologie des Organismes et des Écosystèmes Aquatiques-BOREA, Muséum national d'Histoire naturelle (MNHN), SU, CNRS, IRD, UA, F-75005 Paris, France

4 National Institute of Water and Atmospheric Research (NIWA) Ltd, Nelson, New Zealand

Published online: 01 April 2025

extracellularly within the host tissues, usually forming aggregates surrounded by thin layers of fish cells (Freeman et al. 2017; Desvignes et al. 2022; Evans et al. 2023). Furthermore, analyses showed that X-cell infections negatively affect fish physiology and health (Davison 1998; Freeman et al. 2017; Karlsbakk et al. 2021; Desvignes et al. 2022).

The recent description of two new genera of X-cell parasites in Antarctica revealed how little is known about pathogens in Antarctic fishes (Smeele et al. 2018; Caccavo et al. 2021), in stark contrast to our knowledge of Antarctic bird and marine mammal pathogens (e.g., Smeele et al. 2018; Vanstreels et al. 2020; Barbosa et al. 2021; Banyard et al. 2024). Although macroparasites, such as leeches and endoparasitic worms, have been fairly well documented in the most common Antarctic fish host-species (e.g., Oguz et al. 2015; Klimpel et al. 2017; Parker et al. 2020; Faltýnková et al. 2022; Utevsky et al. 2023; Rubtsova et al. 2024), to date, only few viruses and unicellular parasites have been described in Antarctic fishes (Evans and Tupmongkol 2014; Buck et al. 2016; Van Doorslaer et al. 2018; Kraberger et al. 2022; Desvignes et al. 2022; Evans et al. 2023). As fish pathologies are brought to attention, however, novel emerging or previously overlooked pathological observations are now being recorded. In this context, a specimen of Scaly Notothen *Trematomus loennbergii* that had been ingested by an Antarctic toothfish *Dissostichus mawsoni* in the Ross Sea was recovered from the predator's stomach and displayed skin lesions reminiscent of X-cell infections. Genetic analyses confirmed the presence of *Notoxcellia* sp. parasites in the skin sores.

Methods

Specimen collection and analysis

The specimen of Scaly Notothen *Trematomus loennbergii* was recovered on February 5th, 2023 from the stomach of an Antarctic Toothfish *Dissostichus mawsoni* captured in the polynya of Terra Nova Bay, Ross Sea, Antarctica (CCAMLR Subarea 88.1 M, 75°17′10.5″S 165°43′04.8″E) during the 2023 Ross Sea shelf survey (Fig. 1a, b) (Devine and Péron 2023). The *T. loennbergii* specimen was immediately frozen and kept at – 20 °C until preserved in 85% Ethanol and subsequently imaged, weighed, and measured. After thawing and ethanol fixation, a fragment of skin xenoma and the fish's gonads were fixed in Bouin's fixative for 2 weeks, thoroughly washed in 70% ethanol, embedded in paraffin wax, sectioned at 3–5 mm, deparaffinized, and stained with Hematoxylin and Eosin. To maximize the use of Antarctic specimens for research, education, conservation, and management following FAIR standards (Findable, Accessible, Interoperable, and Reusable) (O'Brien et al. 2022), the infected *T. loennbergii* specimen was deposited in the Smithsonian Institution National Museum of Natural History (NMNH) Division of Fishes along with a histological slide of the specimen's gonads (USNM 477322).

Genetic analysis

DNA was extracted from a fragment of visually healthy muscle sampled from the fish tail and from a fragment of xenoma from the right pectoral girdle of the fish using the Qiagen DNeasy Blood and tissue kit (Hilden, Germany). PCR amplifications of the X-cell rDNA region were done as previously described (Desvignes et al. 2022) using 1 µl of DNA extract as input for each PCR reaction and using primers provided in Table 1. The final 5122 nucleotide-long sequence of X-cell rDNA region contained part of the External Transcribed Spacer (ETS), the full *18S* rDNA, the Internal Transcribed Spacer 1 (ITS1), the full *5.8S* rDNA, the ITS2, and part of the *28S* rDNA. Amplification of the notothenioid fish marker *cytochrome c oxidase I, mitochondrial* (*mt-co1*) was performed using primers as previously described (Desvignes et al. 2019). PCR products were Sanger sequenced in both directions at GENEWIZ (Cambridge, MA, USA) followed by BLAST searches in the NCBI nucleotide database. A DNA extract from the xenoma was deposited in the Smithsonian Institution National Museum of Natural History (NMNH) Department of Invertebrate Zoology (USNM 1752238) and all newly produced and extended rDNA region sequences were deposited in NCBI GenBank (Accession Numbers PQ722883-PQ722889).

To first place the *T. loennbergii* parasite within the Xcellidae family, all X-cell *18S* rDNA sequences available in GenBank were retrieved along with three representative sequences from the sister genus *Perkinsus*.

To gain further resolution within the *Notoxcellia* genus, each existing *Notoxcellia* sequence (Desvignes et al. 2022) was verified by Sanger sequencing and extended if necessary using primers in Table 1. The *18S* rDNA sequence from *Cryoxcellia borchgrevinki* was used to root the tree.

Sequences in each sequence set were aligned with MAFFT v.7.407 using the E-INS-i algorithm and otherwise default parameters (Katoh et al. 2019). The resulting alignments were visually inspected for mis-alignment errors. The *18S* sequence set was then trimmed to the size of the full length *18S* rDNA gene. The longer rDNA sequence set was annotated for partitions using the homologous *Perkinsus atlanticus* sequence (AF509333.1) as reference.

The optimal substitution models were searched using ModelFinder and selected based on the Bayesian Information Criterion (BIC) (Kalyaanamoorthy et al. 2017). The phylogenetic trees were then reconstructed using IQ-TREE and optimal models (TIM3 + F + G4 for the *18S* sequence set; and K2P: ETS; TIM3 + F: *18S*; JC: ITS1, *5.8S*, and

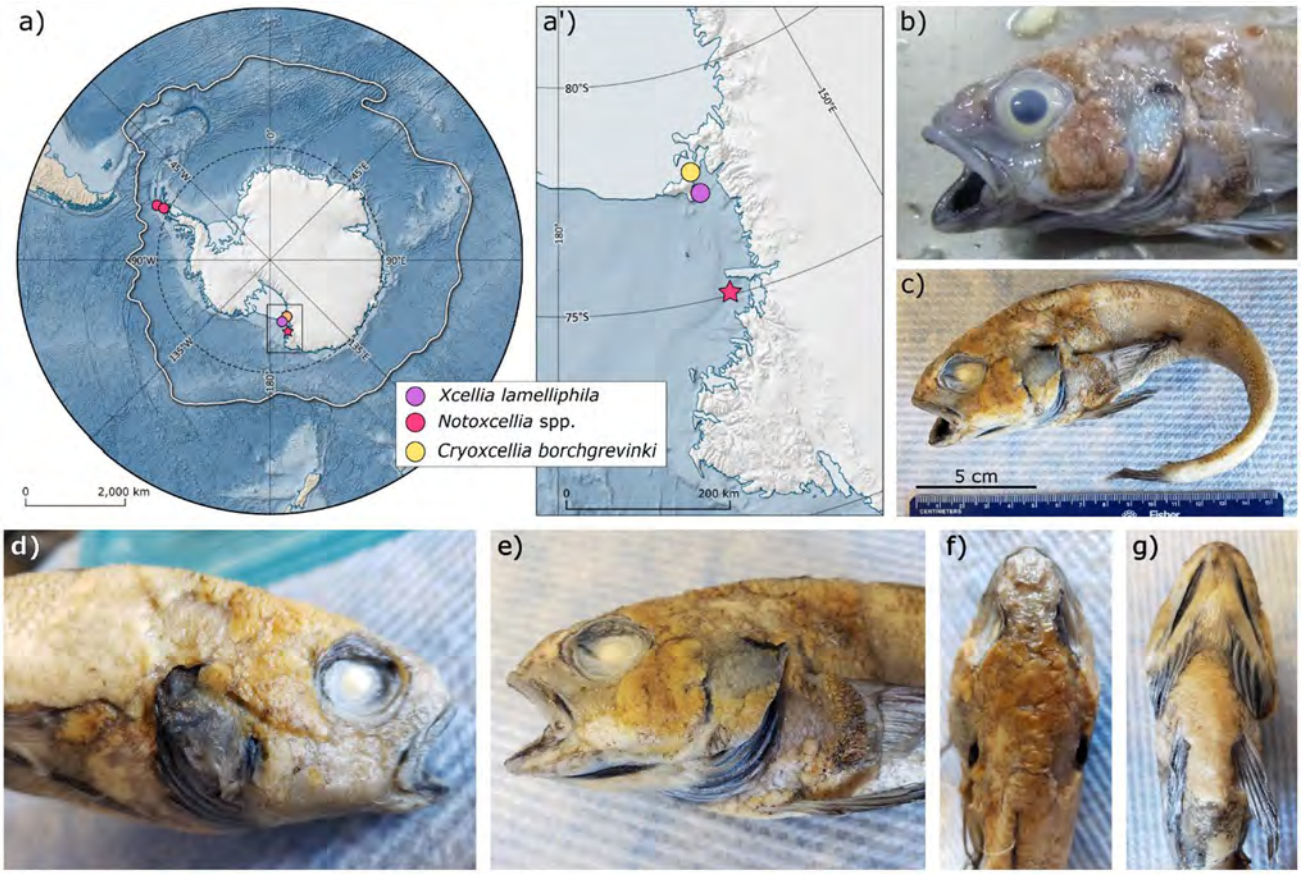

Fig. 1 A *Trematomus loennbergii* with skin lesions. **a** Map of Antarctica showing the location of capture of X-cell-infected fish. The dashed black line represents the Antarctic Circle and the thick white line represents the Polar Front. **a'** Detailed map of the portion of the Ross Sea where X-cell infected fish were captured. The collection location for the specimen reported in the present work is labeled with a red star on the maps. The maps were made using the GIS Quantarctica package (Matsuoka et al. 2021). **b** Image of the *T. loennbergii* specimen freshly recovered from the stomach of an Antarctic Toothfish. **c** Image of the *T. loennbergii* specimen after preservation in 85% ethanol. Close-up views of the specimen: right view (**d**), left view (**e**), dorsal view (**f**), and ventral view (**g**)

ITS2; F81 + F: *28S* for the rDNA sequence set) followed by 10,000 ultrafast bootstraps, SH-aLRT branch test with 10,000 replicates, and approximate Bayes test (Minh et al. 2020).

Phylogenetic tree displays were generated using FigTree v1.4.4. All alignments, ModelFinder, and IQ-TREE results are available in the United States Antarctic Program Data Center (USAP-DC Project p0010221, https://doi.org/10.15784/601915).

Results

The Scaly Notothen *Trematomus loennbergii* displaying skin lesions measured 19.5 cm standard length and 22.5 cm total length for a weight of 74.76 g after being frozen, thawed, and preserved in 85% ethanol (Fig. 1c). Amplification of the fish *mt-co1* mitochondrial marker and the absence of scales on the anterior part of the snout (Fig. 1b) confirmed the fish species field identification. The low degree of digestion of the *T. loennbergii* specimen suggested it had been recently ingested (Fig. 1b). Histological analyses of the gonads revealed it was a male (data not shown but images available in the dedicated USAP-DC Project p0010221, https://doi.org/10.15784/601916).

Skin lesions reminiscent of *Notoxcellia* xenomas were observed on the anterior part of the body, from the snout to just posterior to the pectoral fins. Lesions were present on both sides of the head, the top of the head, and between the pelvic fins (Fig. 1b–g). Approximatively, 75% of the anterior portion of the specimen displayed signs of skin lesions, while the posterior part of the body behind the pectoral fins appeared visually unaffected. The gills and pseudobranch also did not appear affected.

PCR amplification targeting the *18S* rDNA of X-cells (Desvignes et al. 2022) confirmed the presence of *Notoxcellia* DNA within the skin lesions (Fig. 2a).

Table 1 PCR primers for the amplification of *Notoxcellia* rDNA region

Primer pair	Region amplified	Forward primer	Reverse primer	Amplicon length (bp)	Annealing temp. (°C)	Primer reference(s)
NotoX_ETS-5p F/R	ETS-18S	GACGACTATGTT GCATGCGA	AACGTCTGAAGC TGATGGGT	970	65	This study
18e_AllX/NLR-1300r_AllX	18S	CTGGTTGATYCT GCCAGT	YCSTCCRAT CCTCA	1020	55	(Hillis and Dixon 1991; Freeman 2009; Desvignes et al. 2022)
18_Int_F1/R1	18S	CAGGCGCGTAAA TTACCCAA	CAGACAAATCGC TCCACCAA	870	55	(Desvignes et al. 2022)
18_Int_F2/R2	18S	TCAGATACCGTC GTAGTCCT	AAAGGGCAGGGA CGTAATCA	670	55	(Desvignes et al. 2022)
X-F1M_AllX /18gMd	18S	GYTCTTTCTTGA TTYTATRRG	ATCCTTCYGCWG GTTCACCTAC	580	55	(Freeman et al. 2017; Desvignes et al. 2022)
NotoX_ITS-5S F/R	18S-ITS1-5.8S-ITS2-28S	GATTGAATGACC CGGTGAGC	ACAGCCCTAACT TCCACGAA	1250	65	This study
NotoX_28S-1 F/R	28S	GYGAGGGAAAGG TGAAAAGWACT	GCGGCTCTACTG TTGACTTG	900	56	This study
NotoX_28S-2 F/R	28S	TGTAACAACTCA CCTGCCGA	CCCGCGCTTGTT YGAATTTC	930	56	This study
NotoX_28S-3 F/R	28S	CTGGAACGAACA MRGRGAAC	GACGTCGCTATG AACGCTTG	760	56	This study

Using a combination of new primers designed based on *Notoxcellia coronata* and *N. picta* sequences, the rDNA region was successfully extended to a 5122 nucleotide-long sequence containing part of the External Transcribed Spacer (ETS), the complete *18S* rDNA, Internal Transcribed Spacer 1 (ITS1), *5.8S* rDNA, ITS2, and part of the *28S* rDNA. The same primers were used to elongate previously published shorter *Notoxcellia coronata* sequences (Desvignes et al. 2022). Phylogenetic reconstruction using this partitioned, extended rDNA region resolved the *Notoxcellia* parasite infecting *T. loennbergii* as a genetically separate branch from the two previously identified *Notoxcellia* species, *N. coronata,* and *N. picta* (Fig. 2b) (Desvignes et al. 2022). Over the 5122 nucleotide-long sequence, the *Notoxcellia* sp. infecting *T. loennbergii* was 99.2% identical to *N. coronata* and 98.9% identical to *N. picta*, and *N. coronata* and *N. picta* were 98.7% identical (Sequence identity matrix available in the dedicated USAP-DC Project p0010221). Nucleotide substitutions between sequences were found in each partition; however, substitutions were more frequent in the ETS and the two ITS (sequence identity ranging from 90.9% to 95.5%) compared to the *18S*, *5.8S*, and *28S* (sequence identity ranging from 98.1% to 99.8%) (Individual sequence identity matrices available in the dedicated USAP-DC Project p0010221, https://doi.org/10.15784/601917).

The preservation of the *T. loennbergii* specimens by freezing, thawing, and ethanol fixation did not permit observing the morphology of the *Notoxcellia* sp. parasites, thus precluding evidence to evaluate whether the infecting parasite merits the description of a novel *Notoxcellia* species or sub-species. Nevertheless, histological analysis of affected skin from the right pectoral fin girdle confirmed that the *Notoxcellia* sp. parasite proliferated within the fish's dermis (data not shown but images available in the dedicated USAP-DC Project p0010221, https://doi.org/10.15784/601916), similar to what was observed for *N. coronata* and *N. picta* (Desvignes et al. 2022).

Discussion

We report here the identification of a X-cell parasitic alveolate *Notoxcellia* sp. infecting the skin of the Antarctic Scaly Notothen *Trematomus loennbergii*, a newly identified host for this parasitic genus. To date, three of the five described X-cell genera are known to infect Antarctic fishes: *Xcellia* (see Evans and Tupmongkol 2014), *Notoxcellia* (see Desvignes et al. 2022), and *Cryoxcellia* (see Evans et al. 2023), with *Notoxcellia* and *Cryoxcellia* so far known only from the Southern Ocean. With *Notoxcellia* originally described from the Western Antarctic Peninsula, the identification of *Notoxcellia* sp. in the Ross Sea reported here suggests that the genus may have an extensive or even circumpolar distribution.

During the 2023 Ross Sea shelf survey, 334 Scaly Notothens were captured as by-catch on longlines and 97 identifiable ingested Scaly Notothens were recovered from toothfish stomachs (Devine and Péron 2023); however, only

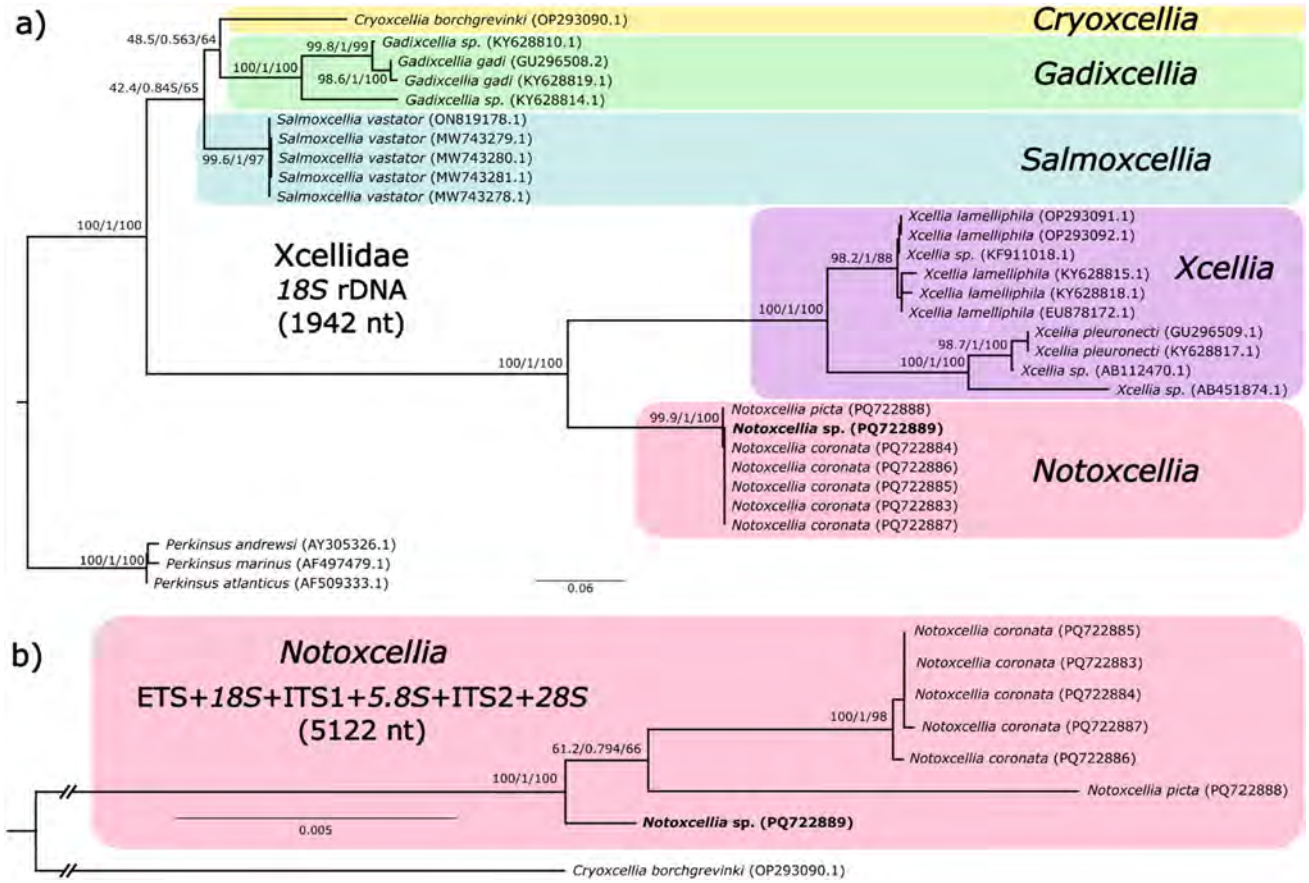

Fig. 2 Phylogenetic analyses identified *Notoxcellia* sp. parasites in *Trematomus loennbergii*. **a** Phylogenetic analysis of X-cell parasite *18S* rDNA sequences. Three *Perkinsus* sequences were used to root the tree. **b** Phylogenetic analysis of *Notoxcellia* parasites using partial ETS, complete *18S* rDNA, ITS1, *5.8S* rDNA, ITS2, and partial *28S* rDNA sequences. *Cryoxcellia borchgrevinki 18S* rDNA sequence was used to root the tree. Values at nodes represent the SH-aLRT support (%)/aBayes support / ultrafast bootstrap support (%). Scale bar indicates the number of substitutions per site

one of these 431 Scaly Notothen specimens was identified as displaying obvious skin infections, suggesting that the prevalence of the parasites is low compared to what has been reported for *Xcellia* and *Notoxcellia coronata* (Evans and Tupmongkol 2014; Desvignes et al. 2022).

It is likely, however, that additional *Notoxcellia* species or sub-species infect other notothenioid species, such as the Grey Notothen *Lepidonotothen squamifrons* in which tumor-like skin lesions have been reported that resemble *Notoxcellia* infections (Bucke and Everson 1992). Biological material from these infected Grey Notothens is, however, unavailable to test this hypothesis.

Notoxcellia is the only X-cell genus known to affect the skin of Antarctic fishes as *Xcellia lamelliphila* and *Cryoxcellia borchgrevinki* proliferate in the gills of their hosts (Evans and Tupmongkol 2014; Evans et al. 2023). While the X-cell life cycle is unknown, both Xcellidae rRNA and rDNA sequences were found in numerous open-ocean meta-genomic analyses of water eDNA samples in oceans around the world, especially in the mesopelagic zone (i.e., 200–1000 m deep), suggesting the presence of living X-cells in the marine water column (Metz et al. 2023). Further, it is unknown how X-cells infect fish. Previous experiments have failed to infect fish by gavage or by intracoelomic injection of xenoma homogenates (Freeman et al. 2011). The frequent location of X-cell skin lesions around the head and the anus of the Crowned Notothen *T. scotti*, however, suggested that infection could be linked to feeding (Desvignes et al. 2022) and that sediments might be an X-cell reservoir (Freeman et al. 2011; Desvignes et al. 2022). Recovering the current infected *T. loennbergii* specimen from the stomach of an Antarctic Toothfish *Dissostichus mawsoni* raises concerns about whether toothfishes might become infected by X-cells while preying on *T. loennbergii*, one of its common prey items in the Ross Sea (Lee et al. 2022; Devine and Péron 2023). So far, however, no cases of X-cell-related pathologies have been reported in toothfishes, but as awareness of fish

pathologies increases, or as environmental shifts occur in Antarctic waters, it is not excluded that more Antarctic and non-Antarctic fish species will be found to be infected by X-cells.

Because Antarctic fishes are keystones of the Antarctic ecosystem, contributing to carbon cycling and constituting major food sources to higher trophic animals, the recent discovery of novel fish viruses and parasites underscores the pressing need for Antarctic fish health to be actively monitored on a regular and continuing basis as now occurs for Antarctic birds and marine mammals.

Acknowledgements This work was funded by NSF grants OPP-1947040 and OPP-2232891 to JHP and TD. We thank Captain Kesomi Paasi, first officer Peter Lynch, the crew of *San Aotea II*, and Sanford Limited for their co-operation and assistance throughout Ross Sea Shelf Survey. Funding for the survey was provided by New Zealand MPI project ANT2019-01D.

Author contributions Conceptualization: TD; Methodology: TD; Validation: TD; Formal analysis: TD; Investigation: TD; Resources: TD, CP, JD, JHP; Data Curation: TD; Visualization: TD; Writing—Original Draft: TD; Writing—Review & Editing: TD, CP, JD, JHP; Supervision: TD; Project administration: TD; Funding acquisition: TD, CP, JD, JHP.

Data availability Data is provided within the manuscript or have been deposited in NCBI GenBank (Accession Numbers PQ722883-PQ722889) or in a dedicated United States Antarctic Program Data Center repository (USAP-DC Project p0010221). Further, biological material have been deposited in the Smithsonian Institution National Museum of Natural History (NMNH).

Declarations

Conflict of interest The authors declare no competing interests.

References

Banyard AC, Bennison A, Byrne AMP et al (2024) Detection and spread of high pathogenicity avian influenza virus H5N1 in the Antarctic region. Nat Commun 15:7433. https://doi.org/10.1038/s41467-024-51490-8

Barbosa A, Varsani A, Morandini V et al (2021) Risk assessment of SARS-CoV-2 in Antarctic wildlife. Sci Total Environ 755:143352. https://doi.org/10.1016/j.scitotenv.2020.143352

Buck CB, Doorslaer KV, Peretti A et al (2016) The ancient evolutionary history of polyomaviruses. Plos Pathog 12:e1005574. https://doi.org/10.1371/journal.ppat.1005574

Bucke D, Everson I (1992) "X-cell" lesions in Notothenia (Lepidonotothen) squamifrons Gunther. Bull Eur Assoc Fish Pathol 12:83–86

Caccavo JA, Christiansen H, Constable AJ et al (2021) Productivity and change in fish and squid in the southern ocean. Front Ecol Evol. https://doi.org/10.3389/fevo.2021.624918

Davison W (1998) X-cell gill disease in pagothenia borchgrevinki from McMurdo sound, Antarctica. Polar Biol 19:17–23. https://doi.org/10.1007/s003000050211

Desvignes T, Le François NR, Goetz LC et al (2019) Intergeneric hybrids inform reproductive isolating barriers in the Antarctic icefish radiation. Sci Rep 9:5989. https://doi.org/10.1038/s41598-019-42354-z

Desvignes T, Lauridsen H, Valdivieso A et al (2022) A parasite outbreak in notothenioid fish in an Antarctic fjord. iScience 25:104588. https://doi.org/10.1016/j.isci.2022.104588

Devine J, Péron C (2023) 2023 Ross Sea shelf survey results.

Evans CW, Tupmongkol K (2014) X-cell disease in Antarctic fishes. Polar Biol 37:1261–1269. https://doi.org/10.1007/s00300-014-1518-6

Evans CW, Patel S, Matzke NJ, Millar CD (2023) Cryoxcellia borchgrevinki gen. nov., sp. Nov., a new parasitic X-cell species in an Antarctic nototheniid fish, the bald notothen Trematomus borchgrevinki. Polar Biol. https://doi.org/10.1007/s00300-023-03132-w

Faltýnková A, Kudlai O, Salganskiy OO et al (2022) Trematodes from Antarctic teleost fishes off Argentine islands, west Antarctica: molecular and morphological data. Syst Parasitol 99:491–523. https://doi.org/10.1007/s11230-022-10041-9

Freeman MA (2009) X-cell parasites in the European dab Limanda limanda are related to other X-cell organisms: a discussion on the potential identity of this new group of parasites. Parasitology 136:967–980. https://doi.org/10.1017/S0031182009006507

Freeman M, Eydal M, Yoshimizu M et al (2011) Molecular identification and transmission studies of X-cell parasites from Atlantic cod Gadus morhua (Gadiformes: Gadidae) and the northern black flounder pseudopleuronectes obscurus (pleuronectiformes: pleuronectidae). Parasit Vectors 4:15. https://doi.org/10.1186/1756-3305-4-15

Freeman MA, Fuss J, Kristmundsson Á et al (2017) X-cells are globally distributed, genetically divergent fish parasites related to perkinsids and dinoflagellates. Curr Biol 27:1645-1651.e3. https://doi.org/10.1016/j.cub.2017.04.045

Hillis DM, Dixon MT (1991) Ribosomal DNA: molecular evolution and phylogenetic inference. Q Rev Biol 66:411–453. https://doi.org/10.1086/417338

Kalyaanamoorthy S, Minh BQ, Wong TKF et al (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. Nat Methods 14:587–589. https://doi.org/10.1038/nmeth.4285

Karlsbakk E, Nystøyl CF, Plarre H, Nylund A (2021) A novel protist parasite, Salmoxcellia vastator n. gen., n. sp. (Xcelliidae, Perkinsozoa), infecting farmed salmonids in Norway. Parasit Vectors 14:431. https://doi.org/10.1186/s13071-021-04886-0

Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Brief Bioinform 20:1160–1166. https://doi.org/10.1093/bib/bbx108

Klimpel S, Kuhn T, Mehlhorn H (eds) (2017) Biodiversity and evolution of parasitic life in the southern ocean. Springer International Publishing, Cham

Kraberger S, Austin C, Farkas K et al (2022) Discovery of novel fish papillomaviruses: from the Antarctic to the commercial fish market. Virology 565:65–72. https://doi.org/10.1016/j.virol.2021.10.007

Lee SR, Choi S-G, Chung S et al (2022) Geographical differences in the diet of Dissostichus mawsoni revealed by metabarcoding. Front Mar Sci. https://doi.org/10.3389/fmars.2022.888167

Matsuoka K, Skoglund A, Roth G et al (2021) Quantarctica, an integrated mapping environment for Antarctica, the southern ocean, and sub-Antarctic islands. Environ Model Softw 140:105015. https://doi.org/10.1016/j.envsoft.2021.105015

Metz S, Itoïz S, Obiol A et al (2023) Global perspective of environmental distribution and diversity of Perkinsea (Alveolata) explored by a meta-analysis of eDNA surveys. Sci Rep 13:20111. https://doi.org/10.1038/s41598-023-47378-0

Minh BQ, Schmidt HA, Chernomor O et al (2020) IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. Mol Biol Evol 37:1530–1534. https://doi.org/10.1093/molbev/msaa015

O'Brien KM, Crockett EL, Adams BJ et al (2022) The time is right for an Antarctic biorepository network. Proc Natl Acad Sci 119:e2212800119. https://doi.org/10.1073/pnas.2212800119

Oguz MC, Tepe Y, Belk MC et al (2015) Metazoan parasites of Antarctic fishes. Turk J Parasitol 39:174–178. https://doi.org/10.5152/tpd.2015.3661

Parker E, Jones CD, Arana PM et al (2020) Infestation dynamics between parasitic Antarctic fish leeches (Piscicolidae) and their crocodile icefish hosts (Channichthyidae). Polar Biol. https://doi.org/10.1007/s00300-020-02670-x

Rubtsova NY, Chaudhary A, Glotov S, Kuzmina TA (2024) Description of Pseudobenedeniella johnstoni sp. n. (Monogenea: Capsalidae) from the gills of Antarctic black rockcod, Notothenia coriiceps Richardson in coastal waters of west Antarctica. Helminthologia 61:327–344. https://doi.org/10.2478/helm-2024-0037

Smeele ZE, Ainley DG, Varsani A (2018) Viruses associated with Antarctic wildlife: from serology based detection to identification of genomes using high throughput sequencing. Virus Res 243:91–105. https://doi.org/10.1016/j.virusres.2017.10.017

Utevsky A, Utevsky S, Cichocka JM et al (2023) Return of the prodigal son: morphology and molecular phylogenetic relationships of a new Antarctic fish leech (Hirudinea: Piscicolidae) imply a bipolar biogeographic pattern. Syst Biodivers 21:2246476. https://doi.org/10.1080/14772000.2023.2246476

Van Doorslaer K, Kraberger S, Austin C et al (2018) Fish polyomaviruses belong to two distinct evolutionary lineages. J Gen Virol 99:567–573. https://doi.org/10.1099/jgv.0.001041

Vanstreels RET, Palma RL, Mironov SV (2020) Arthropod parasites of Antarctic and Subantarctic birds and pinnipeds: a review of host-parasite associations. Int J Parasitol Parasites Wildl 12:275–290. https://doi.org/10.1016/j.ijppaw.2020.03.007