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RESEARCH ARTICLE

First identification of mycobacteriosis in Atlantic mackerel (*Scomber scombrus*)

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Abstract

Mycobacterium infection in fish is a well-known disease problem globally, mainly in the farming of ornamental fish or fish for food. Less is known about the prevalence, distribution and the effects such infections have on wild fish species. Presumptive mycobacteriosis has previously been observed in Atlantic mackerel (*Scomber scombrus*). Since 2018, there has been an increase in reports of granulomatous kidney disease in Atlantic mackerel with the suspicion of this being mycobacteriosis. A total of six individuals were sent to the Institute of Marine Research for further examination. They were caught in the Nordic Sea by either commercial fishing vessels or during the International Ecosystem Summer Survey in the Nordic Seas (IESSNS research cruise) between 2018 and 2020. Samples for both histological and molecular analysis were collected. Here, we detect a likely novel *Mycobacterium* species in tissue samples from Atlantic mackerel with this condition, on the basis of rDNA and protein gene sequences. The same unnamed bacterium seems to have been found in some Pacific marine fishes. The macroscopic and histological manifestation of the disease is described. Over the past years, there has been an increase in reports of mycobacteriosis worldwide and climate change has been suggested as one of the driving forces as these bacteria prefer warm water.

KEYWORDS
DNA sequences, emerging disease, histopathology, *Mycobacterium*, wild fish

1 | INTRODUCTION

Mycobacteriosis, caused by Gram-positive bacteria from the genus *Mycobacterium* sensu lato, include several well-known chronic diseases affecting aquatic and terrestrial animals. The known fish hosts for *Mycobacterium* spp. infections include a range of both wild and farmed fish in fresh, brackish and marine waters (Davidovich, Morick, et al., 2020; Gauthier & Rhodes, 2009; Jacobs et al., 2009). The infection is usually systemic, and all tissues of the fish may be affected. External signs of mycobacteriosis are variable and non-specific; however, typical signs are emaciation, exophthalmia, skin lesions and ulcerations. Internally, swollen haematopoietic organs and whitish nodules and granulomas in organs (spleen, kidney, heart) and muscles are often observed (Austin & Austin, 2007; Davidovich, Pretto, et al., 2020; Gauthier & Rhodes, 2009). Histopathological examination of affected tissue samples typically shows defined spherical-shaped granulomas containing acid-fast bacterial colonies and /or a necrotic core (Davidovich, Morick, et al., 2020; Ortega et al., 2014).

Lately, *Mycobacterium* infections have caused concern as emerging diseases (Davidovich, Morick, et al., 2020; Mugetti et al., 2020). It has been suggested that climate change and global warming may facilitate the spread of these bacteria, many of which thrive in warm water (Davidovich, Morick, et al., 2020). Most of what is known about mycobacteriosis in fish relate to the aquaculture industries and ornamental fish trade, less to the impact mycobacteriosis has on wild fish stocks. However, there is an increasing number of species, strains and isolates of mycobacteria originating from wild fish on a global scale (Jacobs et al., 2009).

Over the last few years, there has been an increase in reports of a granulomatous kidney disease in Atlantic mackerel (*Scomber scombrus*). Deep frozen individuals were received at the institute of Marine research in Bergen for further examination, and some of the lesions resembled *Mycobacterium* sp. infections. We therefore aimed at examining the samples for acid-fast bacteria, and molecularly test the tissues for mycobacteria, obtain sequences and identify the agent.

2 | MATERIALS AND METHODS

All fish examined were caught by either commercial fishing vessels or during the International Ecosystem Summer Survey in the Nordic Seas (IESSNS research cruise). Thus, no additional approval for collecting samples was needed.

2.1 | Fish and tissue sampling

The six mackerel individuals studied were caught between 2018 and 2020. Three were caught by commercial fishing vessels south of the Shetlands in October 2018 (ID-MOL4-6) and North of Scotland in January 2019 (ID-MOL11, ID-MOL12). From the time of capture to arrival on shore, the fish was kept in RSW tanks (refrigerated sea water) at a temperature of −1°C. At the fish processing factory, it was noticed that some individuals displayed granulomas in the kidney when it was cut in half. These fish were then immediately frozen at −20°C and sent to IMR for further examination. At IMR, the fish was thawed at room temperature, and all samples were collected before the organs were completely tawed. Tissue samples of organs with visible granulomas (kidney and pylorus) were collected for histological examination and PCR analysis.

Three individuals were captured during the IESSNS research cruise, by IMR participants in the Northern part of the Norwegian Sea, two (ID-MOL8, ID-MOL9) in July 2019 and one (ID-MOL31) in July 2020. These individuals were also selected because of the observed granulomas in the kidney.

Samples of the heart, liver, kidney and skin/muscle from fish caught during the IESSNS research cruise, were collected from freshly caught fish for both histological examination and PCR analysis.

2.2 | Ziehl-Neelsen staining

Tissue samples for histology were fixed in 10% neutral phosphate-buffered formalin (VWR), dehydrated in ethanol, cleared in xylene and embedded in paraffin. Sections (3 μm) were stained with Ziehl-Neelsen (ZN) AFB-colour staining kit (cold staining) (Merck). Both methyl blue (Sigma) and haematoxylin (Shandon Instant Haematoxylin, Thermo Fisher Scientific) were, respectively, used for counterstaining.

2.3 | DNA extraction, PCR amplification and sequencing

DNA was extracted using DNeasy Tissue kit (Qiagen) from tissue samples stored in ethanol and dried (60°C) before extraction. PCR amplification was performed with Hot-StartTaq DNA polymerase (Qiagen). The samples were first screened with primers Myco-F/Myco-R (Phung et al., 2013) and Tb11/Tb12 (Telenti et al., 1993). In positive samples, 16S rDNA-ITS fragments were amplified using the primer pairs: T39/Roc1R, Roc1F/T13, 16SC-F/Rev-16C, MycoITS 1F/MycoITS 1R and Myco 16S-1/Myco16S-2, hsp65 gene sequences with the primers Mycohsp-1/Mycohsp-2 and rpoB gene sequences with the primers MycorpoB-1/MycorpoB-2 (Table 1). PCR products were purified and sequenced directly with the PCR primers in both directions, using Sanger's method using an ABI 3730XL analyser performed at the Sequencing laboratory at the University of Bergen. Sequences are deposited in GenBank, with accession no's OQ342862-78.

3 | RESULTS

3.1 | Gross pathology

External examination of these individuals revealed no signs of disease, and they seemed overall in good condition. However, internally there were extensive changes to the internal organs, especially the kidney, with large amounts of whitish nodules of various sizes (Figure 1a–d). Granulomas in the kidney were in most individuals evenly distributed throughout the whole organ (Figure 1a–c). No other macroscopic signs of disease were observed in any of the examined individuals. Four of the individuals were females between 9 and 11 years old, from the year-classes 2008 and 2010. The length of the individuals was between 32.2 and 41.0 cm and with an average of 36.5 ± 3.85 cm.

3.2 | Histopathology

Histological examination of tissue samples from internal organs of all fish shows numerous spherical-shaped granulomas containing ZN-positively stained bacteria (Figure 2a–f). The granulomas were

TABLE 1 Primers used to amplify *Mycobacterium* sp. genes or markers.

Primer name	Sequence (5′-3′)	Target	Reference
Myco-F	GCTGGATCACCTCC TTTCTA	ITS rDNA	Phung et al. (2013)
Myco-R	AGATGCTCGCAACCACTAT	ITS rDNA	Phung et al. (2013)
T39	CGAACGGGTGAGTA ACACG	16S rRNA gene	Whipps et al. (2003)
T13	TGCACACAGGCCAC AAGGGA	16S rRNA gene	Whipps et al. (2003)
Roc 1F	CGTTGTCCGGAATTACTG	16S rRNA gene	Whipps et al. (2003)
Roc 1R	CCACCTACGAGCTC TTTACG	16S rRNA gene	Whipps et al. (2003)
16SC-F	CGATGCAACGCGAAGAAC	16S rRNA gene	Whipps et al. (2003)
Rev16C	GCGATTCATCTGCT GTTGTG	16S rRNA gene	Whipps et al. (2003)
Myco16S-1	ACACATGCAAGTCGAAC GGAAAGG	16S rRNA gene	Stine (2008)
Myco16S-2	TGCGGGACTTAACCCAA CATCTCA	16S rRNA gene	Stine (2008)
MycoITS1F	GACGAAGTCGTAACAAGG	ITS rDNA	Whipps et al. (2003)
MycoITS1R	ATGCTCGCAACCAC TATCCA	ITS rDNA	Whipps et al. (2003)
Tb11	ACCAACGATGGTGT GTCCAT	HSP65 gene	Telenti et al. (1993)
Tb12	CTTGTCGAACCGCA TACCCT	HSP65 gene	Telenti et al. (1993)
MycoHSP-1	GATCCGGAGGAATCACT TCGCAAT	HSP gene	Stine (2008)
MycoHSP-2	TCGTCCTTGGTGATGAC GACCTT	HSP gene	Stine (2008)
MycorpoB-1 MF	CGACCACTTCGGCAACCG	rpoB gene	Kim et al. (1999)
MycorpoB-1 MF	TCGATCGGGCACATCCGG	rpoB gene	Kim et al. (1999)

of different sizes and differed in the thickness of the connective tissue capsules. Necrosis in the cores was also observed. In the heart, a high density of inflammatory cells was observed near the granulomas, especially in the epicardium (Figure 2a). No evidence for an inflammatory response was observed elsewhere or in any other examined organs. Histopathological examination of all kidney samples revealed evenly distributed granulomas throughout the whole tissue sample (Figure 2c). Examination of samples from the liver showed a more uneven distribution of granulomas (Figure 2e). Only occasionally granulomas containing ZN-positively stained bacteria were observed in muscle samples (Figure 2f).

The tissue samples taken from the frozen fish were not well suited for describing histopathological changes in the tissue. However, intact granulomas containing ZN-positively stained bacteria were observed in all individuals.

3.3 | Sequences

Mycobacterium sp. HSP65 gene sequences were obtained from all six mackerel studies. These sequences were identical, except for one substitution in Mol8 (415nt compared). Four were extended to 940nt, but no further divergence was seen. The closest relative in Genbank (13 Jan 2023) was the HSP65 sequence of a *Mycobacterium* sp. (EU619914) from a marine fish in Chesapeake Bay, USA (96.8% identity, 839 positions compared). The closest identified sequence was the *Mycobacterium lentiflavum* type strain (CP092423) (96.3% identity, 947 positions compared) isolated from a human.

rpoB sequences were obtained from five of the *Mycobacterium* sp. infected mackerels. All these were identical (327nt compared) and showed the highest identity (94.2%) with the type strain of *Mycobacterium stomatepiae* rpoB gene sequence (AP022587), a bacterium isolated from a freshwater ornamental fish (*Stomatepia mariae*).

ITS rDNA sequences were obtained from all six mackerel. There were two polymorphic sites in the 190 positions aligned (99%–100% identity), one sequence (Mol8) differing from the others at these sites. In GenBank, the ITS sequences showed 99%–100% identity to the ITS sequence of *Mycobacterium* sp. YM-12 (AF541924) from a Pacific rockfish (*Sebastes alutus*) and an identical sequence (KT896749) from rainbow trout (*Oncorhynchus mykiss*) in freshwater in Montana. *Mycobacterium* sp. partial 16S rDNA sequences

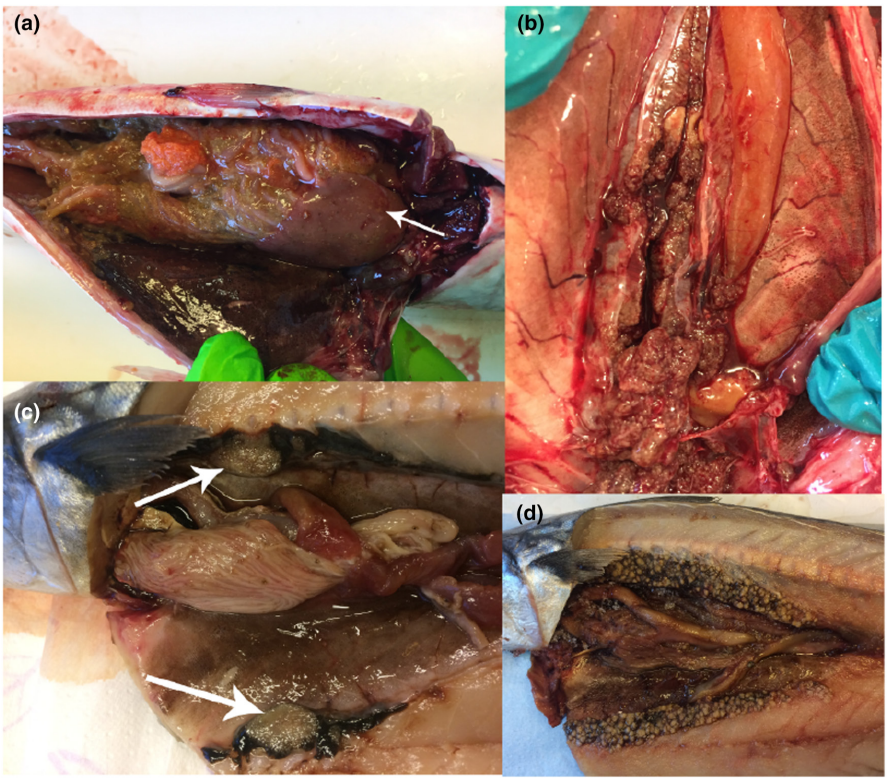

FIGURE 1 (a–d) Gross pathology of Atlantic mackerel showing nodules in viscera. All diagnosed with mycobacteriosis. (a) Nodules around intestine and on liver (arrow) (ID-MOL31). (b) Smaller nodules in kidney (ID-MOL8). (c) White arrows pointing at one large tumour-like growth cut in half (ID-MOL4-6). (d) Extensive occurrence of nodules in kidney and visera in ID-MOL12.

(1437nt) from five fish were identical, except for a single substitution in Mol8 (99.9%–100.0% identity). In GenBank, the 16S sequences showed the highest identity (99.9%–100.0%) to the 16S sequence of *Mycobacterium* sp. YM-12 (AF541924) from a Pacific rockfish. The closest identified sequence was of *Mycobacterium montefiorense* (AF330038.2) (99.3% identity), a bacterium isolated from skin lesions of a moray eel (*Gymnothorax funebris*) in Florida.

The relationship between the 16s-ITS sequences of *Mycobacterium* sp. from mackerel and similar sequences deposited in GenBank is shown in Figure 3.

4 | DISCUSION

This is to our knowledge the first confirmed observation of mycobacteriosis in Atlantic mackerel.

The condition has been observed before in mackerel in British waters (Bucke, 1980; Hastings et al., 1982; MacKenzie, 1988), and it has been demonstrated that the nodules could contain acid-fast bacteria (Murchelano et al., 1986). In all cases, these findings were considered likely mycobacteriosis (Murchelano et al., 1986). However, *Nocardia* spp. can cause similar lesions, and with the recent splitting of genus *Mycobacterium* into five genera, the fish mycobacteria now belong to the genera *Mycobacterium* sensu stricto, *Mycobacteroides* and *Mycolicibacterium* (Gupta et al., 2018). Based on the mycobacterium-like sequences obtained here, the infections in mackerel represent a single species of bacterium in the genus *Mycobacterium*. Since there are no related sequences from characterized and named species, it is likely undescribed. Based on sequence identity, the same species seems to have been detected by Whipps et al. (2003) in granulomas occurring in certain Pacific rockfishes, *Sebastes alutus* and *Sebastes reedi*. In that study, *Mycobacterium* spp. culture attempts were unsuccessful, so the bacterial sequences were also obtained from infected tissues.

Apparently then, the same bacterium causes mycobacteriosis in unrelated fish species in the Atlantic and Pacific Oceans. However, a surprising finding was that the same bacterium (as judged from ITS rDNA sequences) also infect wild rainbow trout in the Missouri River, Montana (Terrazas, 2016). In the Pacific rockfishes, the prevalence of the mycobacterial granulomas ranged from 2.0% to 6.6%, while *Ichthyophonus* sp. infections occurred in 48%–51% (Kent et al., 2001). *Ichthyophonus* sp. infections are also prevalent in northeast Atlantic mackerel (Storesund et al., 2022), but in the present case, only one of the studied fishes was found to harbour such a coinfection. Both pathogens cause granulomatous lesions (Murchelano et al., 1986), that can macroscopically be confused.

Our gross and histopathological observations are consistent with findings in Atlantic horse mackerel (*Trachurus trachurus*) suffering from mycobacteriosis with granulomas in different internal organs and histopathological observations of spherical-shaped granulomas containing acid-fast bacteria (Ortega et al., 2014) The observed different size and the difference in the thickness of the connective tissue capsule, indicate that the granulomas are at different developmental stages. This has also been described from turbot (*Scophthalmus maximus*) suffering from mycobacteriosis (dos Santos et al., 2002). As reviewed by Gauthier and Rhodes (2009)

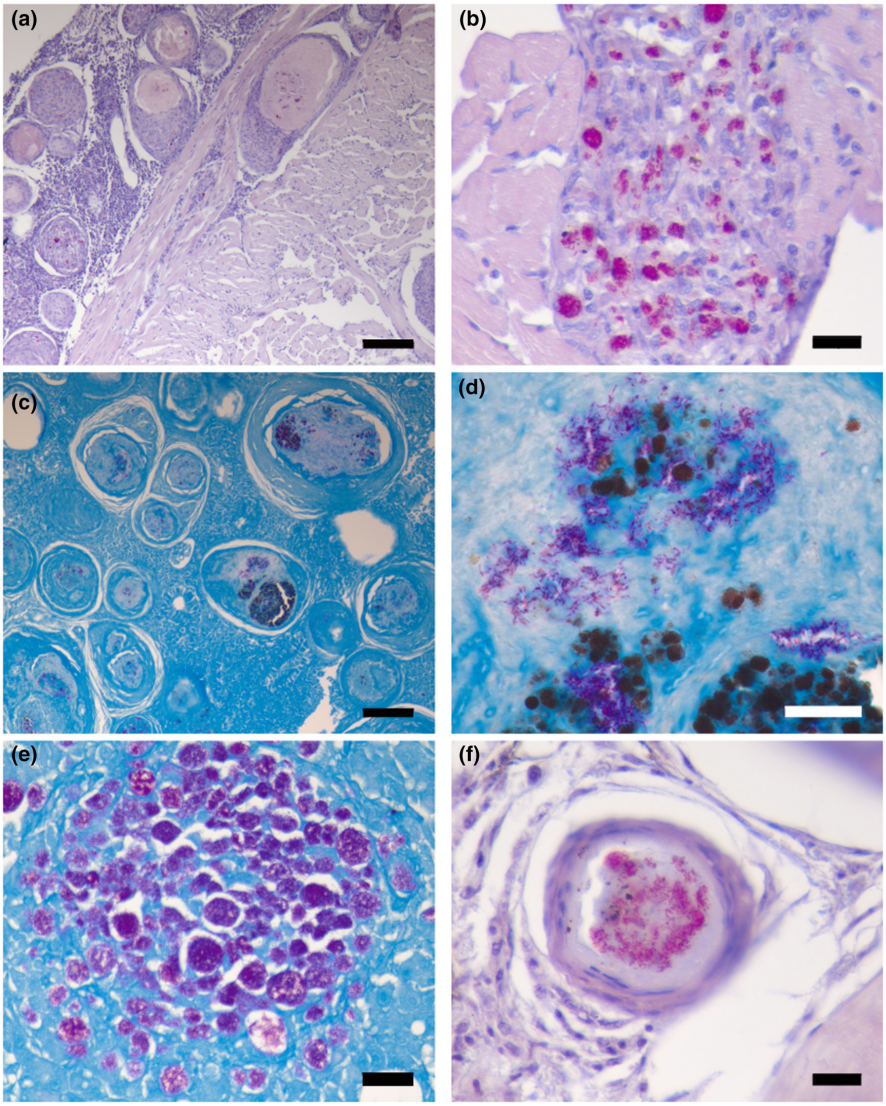

FIGURE 2 (a–f) Histopathology based on tissue samples from fresh mackerels; Ziehl-Neelsen staining, (a, b, f) hematoxyline counterstaining and (c–e) methyl blue as counterstaining. Mycobacteria are stained bright pink/purple. (a) Severe granulomatous epicarditis of ID-MOL31, scale bar 100 μm. (b) Staining of mycobacteria in granuloma in myocardium (ID-MOL31), scale bar 15 μm. (c) Granulomas in kidney (ID-MOL31), scale bar 100 μm. (d) Enlargement of centre granuloma in (c) showing free *mycobacteria* cells, scale bar 15 μm. (e) Aggregates of mycobacteria in liver of ID-MOL9, scale bar 25 μm. (f) Muscle with granuloma containing mycobacteria (ID-MOL31), scale bar 10 μm.

calcification of the granuloma core may be observed. No such observation was made during our examinations. The number of analysed individuals and tissue samples are limited in this study. However, the kidney was the overall most affected organ. Even though these individuals show signs of a severe developing chronic infection, no external signs of disease were observed.

The reasons for an increase in observations of mycobacterial infections over the past decade are not known. Transmission of mycobacteria is not fully understood (Jacobs et al., 2009). Apparent transmission through feeding (eating of infected fish) has been seen in aquaculture, and horizontal transmission may also occur through contaminated prey, contact or water (Hashish et al., 2018; Jacobs et al., 2009). Results from studies of vertical or transovarian transmission have been inconclusive (Jacobs et al., 2009). Mackerels are schooling fish living in dense cohorts, feeding on plankton or small fish. Such high densities of hosts may facilitate transmission between individuals in the schools. A recent shift to a more northerly and eastly distribution of mackerel (ICES, 2022), may also contribute to the spread of pathogens to new areas. Environmental changes such as climate change might play a part in areas with rising water temperatures as *Mycobacterium* spp. are warm water species. Mycobacteriosis are emerging diseases in southern European aquaculture (Mugetti et al., 2020), and attention should be made to natural reservoirs of the bacteria in wild fish.

Understanding the impact of disease on wild fish stocks is fundamentally difficult due to the complexity of all interactions that may occur. The present observations are a basis that can facilitate further work, particularly molecular studies on both epizootiology and host–parasite interactions.

Strains of several *Mycobacterium* spp. are known for their potential of infecting both fish and humans, thus precaution should always be taken when dealing with these bacteria. Whether the Mycobacterium species infecting mackerel is zoonotic is unknown. Therefore, it is important that the Mycobacterium species infecting Atlantic mackerel and Pacific rockfishes is cultured and phenotypically characterized, so the zoonotic potential can be assessed.

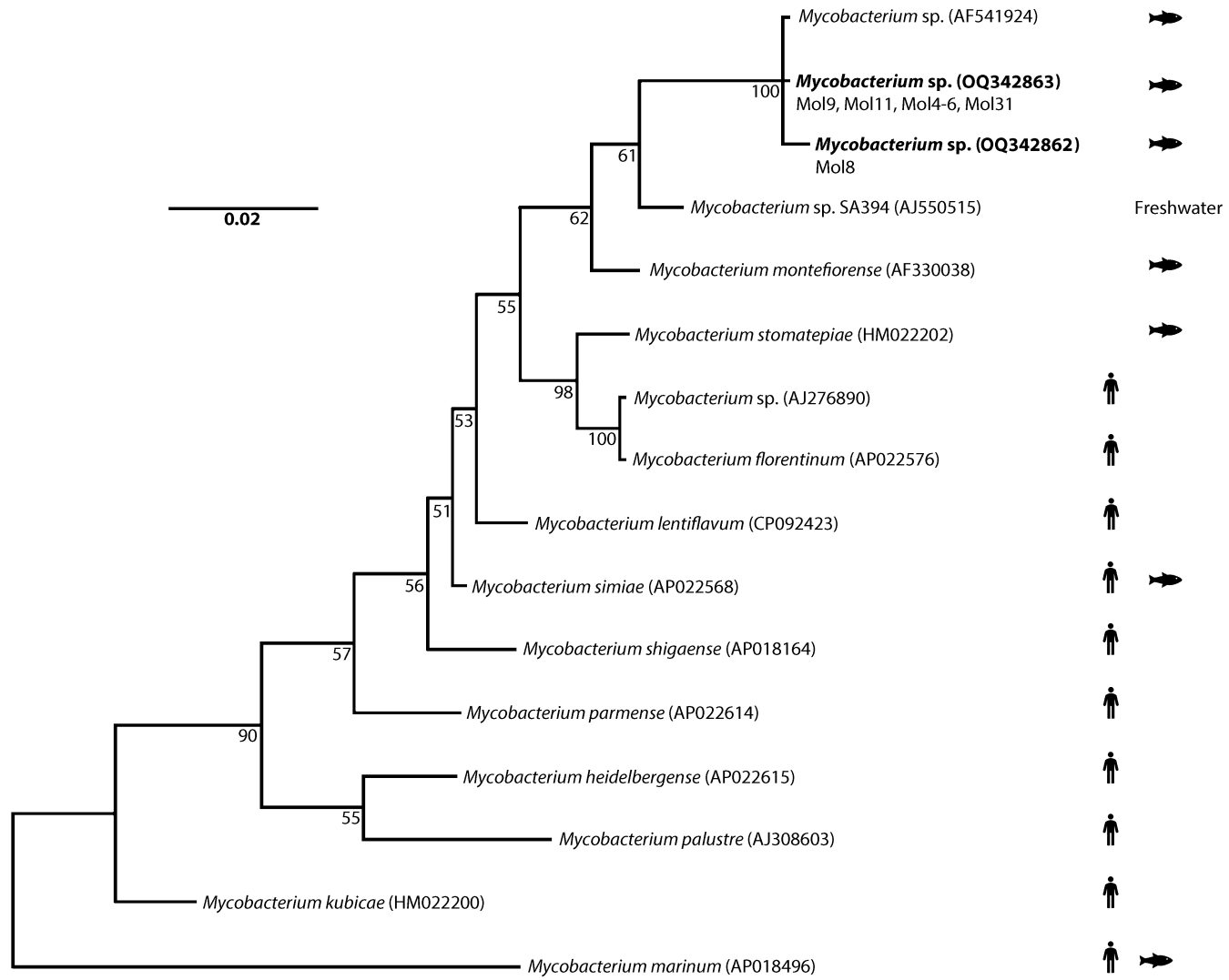

FIGURE 3 Relationship between the 16srDNA-ITS sequences of *Mycobacterium* sp. from mackerel and similar sequences deposited in GenBank. Bayesian inference (MrBayes) 1611 positions, 16 taxa, invgamma model, rooted with *Mycobacterium marinum*. Numbers at nodes posterior probabilities (%). The known hosts are indicated, as fishes or humans. However, the species reported from humans have in some cases been isolated also from other mammals.

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CONFLICT OF INTEREST STATEMENT

The authors confirm that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data are available from the corresponding author upon reasonable request.

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