Journal of Aquatic Animal Health, 2025, **37**, 170–183
https://doi.org/10.1093/jahafs/vsaf010
Advance access publication: October 3, 2025
Article

First molecular identification, biological diversity, and infection features of myxozoan parasites in Whiting *Merlangius merlangus* along the Turkish coast of the Black Sea

Cem Tolga Gürkanlı[1], Sevilay Okkay[2,*], Yılmaz Çiftçi[1], and Ahmet Özer[3]

[1]Department of Fisheries Technology Engineering, Fatsa Faculty of Marine Science, Ordu University, Fatsa-Ordu, Türkiye
[2]Department of Biology, Faculty of Arts and Science, Kocaeli University, Kocaeli, Türkiye
[3]Faculty of Fisheries and Aquatic Sciences, Sinop University, Sinop, Türkiye

*Corresponding author: Sevilay Okkay. Email: sevilay.okkay@kocaeli.edu.tr.

ABSTRACT

Objective: Myxosporean parasites are worldwide-distributed cnidarians that infect the organs and tissues of marine and freshwater organisms, primarily fish. Based on morphological peculiarities, two myxosporean species, *Myxidium gadi* and *Ceratomyxa merlangi*, from the gallbladder content of Whiting *Merlangius merlangus* inhabiting four sampling localities (Kocaeli, Sinop, Ordu, and Trabzon) along the Black Sea coast of Türkiye have been identified.

Methods: Concordant with the morphological data, the first phylogenetic analyses on the nucleotide sequences of 18S ribosomal DNA confirmed our *Myxidium* specimens to be *M. gadi*. This study also provided the first molecular data on *C. merlangi*, which appeared to be the closest species to *C. cretensis* and *C. arcuata* on the phylogenetic trees. The infection prevalence (%) and density values of each parasite species were calculated according to season and sampling localities of Whiting.

Results: *Ceratomyxa merlangi* had a higher overall prevalence value (39.6%) than *M. gadi* (25.7%). The density values of both parasite species ranged between 2+ and 3+ in all fish samples. When the infection indices in sampling localities were compared for both parasite species, *C. merlangi* and *M. gadi* had the highest infection prevalence values in Sinop samples (66.3%); the highest density of infection (3+) was recorded in Sinop samples for *C. merlangi* and in Ordu samples for *M. gadi*.

Conclusions: This study provides the first molecular data on *M. gadi* and *C. merlangi*, revealing their phylogenetic positions. In addition, seasonal and regional infection data for these species in the southern Black Sea region are reported for the first time, and it has been determined that both species can occur together.

KEYWORDS: Black Sea, *Ceratomyxa*, climate change, *Merlangius merlangus*, *Myxidium*, myxozoa

LAY SUMMARY

This study reveals the prevalence and distribution of two fish parasites in the southern Black Sea. The results of the study help to understand when and where these parasites infect fish, contributing to fish health monitoring and marine ecosystem protection.

INTRODUCTION

The Whiting *Merlangius merlangus* is a member of the family Gadidae and is the only valid species in the genus *Merlangius* (Froese & Pauly, 2023). Based on morphological features, previous literature presumed that there were two subspecies, namely *M. merlangus merlangus*, which is distributed in the North Atlantic Ocean (Iceland), southwest Barents Sea, western Baltic Sea, and northern shores of Portugal; and *M. merlangus euxinus*, which is distributed in the Adriatic Sea, Aegean Sea, Sea of Marmara, Azov Sea, and Black Sea. A recent molecular study conducted by Şalcıoğlu et al. (2020) indicated no clear distinction between the two presumed subspecies. From an economic point of view, the Whiting is one of the most important demersal fish species in Türkiye, and the total

Received: January 10, 2025. **Revised:** June 12, 2025. **Editorial decision:** June 24, 2025

amount of the catch was 10,379.9 metric tons in 2022, most of which (10,025.3 metric tons) was obtained from the southern Black Sea (Özer et al., 2015; TÜİK, 2021, 2022). Up to now, many studies concerning infections by different parasite taxa, including myxozoan parasites in Black Sea Whiting, have been published or presented, and details are provided in a checklist by Özer (2021). It is known that parasitic infections, together with unfavorable abiotic and biotic ecological factors, may have negative impacts on fish health and fish populations; thus, more comprehensive and comparable studies on fish parasites, including myxosporeans and their infections in Whiting, are needed due to their significance for fisheries and human health.

Members of the class Myxozoa represent a lineage of the phylum Cnidaria that diverged from free-living and evolutionarily Medusozoa-related cnidarian ancestors at some distant time, ultimately to become parasitic (Jiménez-Guri et al., 2007; Okamura et al., 2015). Through the evolutionary process of their complex parasitic lifestyle, they developed a two-host life cycle strategy in which they infect an invertebrate (annelids and freshwater bryozoans) as the first host and a vertebrate (usually fishes, but rarely amphibians, reptiles, and even birds) as the second host in freshwater environments (Bartholomew et al., 1997, 2006; Markiw & Wolf, 1983; Székely et al., 2014). On the other hand, the current knowledge of their life strategies in marine environments is limited; members of some genera have a direct fish-to-fish infection strategy (Diamant, 1997; Yasuda et al., 2002), whereas others display a two-host life cycle strategy for infections (Rocha et al., 2019, 2020). As can be expected from an early diverged taxon, Myxozoa reveals a great biological diversity, with about 2,600 binomial species, comprising one-fifth of the whole phylum Cnidaria. So far, three myxozoan species—*Myxidium sphaericum*, *Myxidium finnmarchicum*, and *Myxobolus aeglefini*—have been reported as the parasites infecting Whiting (i.e., the presumed subspecies *M. merlangus merlangus*) in the northeast Atlantic (Dethlefsen et al., 1996; MacKenzie & Kalavati, 1995; MacKenzie et al., 2010). On the other hand, *Leptotheca informis* (only one report is available), *Myxidium incurvatum* (probably *Myxidium gadi* according to our evaluation), *Ceratomyxa merlangi*, and *M. gadi* have been reported as myxozoan parasites infecting Whiting (i.e., the presumed subspecies *M. merlangus euxinus*) in the Black Sea (Özer et al., 2015, 2017; Özkan, 2015; Skuratovskaya et al., 2013; Yurakhno, 1997, 2004, 2008, 2009a, 2009b, 2013; Yurakhno & Naidenova, 2000). However, most of the studies of Black Sea Whiting focused on myxozoan parasites inhabiting the northern Black Sea coast around Sevastopol, Kerch Strait, Tarkhankut, the southern coast of Crimea, Caucasia, and the northwestern part of the Black Sea, whereas a limited number of studies examined Whiting populations collected from the southern Black Sea, mostly from a single location (the Sinop coast of Türkiye). Thus, there is a need for comprehensive studies on the myxozoan fauna and their infection levels in Black Sea Whiting inhabiting the entire southern coast of the Black Sea to fill the information gap.

In this context, the present study focused on overcoming this significant issue by conducting comparative and comprehensive studies on the biological diversity and ecology of myxozoan parasites infecting the Whiting that inhabit the southernmost Black Sea coast at four sampling localities with seasonal distribution through morphological and molecular approaches for the first time.

METHODS

Fish sampling and parasitological investigation

In total, 280 Whiting samples (11.2–20.5 cm in total length) were collected from local fishermen in the Ordu (41°06′34.2″N, 37°32′02.0″E) and Trabzon (41°02′27.5″N, 39°49′46.7″E) provinces, which are located along the eastern Black Sea coast of Türkiye; and the Kocaeli (41°09′52.6″N, 30°00′02.9″E) and Sinop (42°05′27.7″N, 35°06′39.5″E) provinces, located along the western Black Sea coast of Türkiye (Figure 1). Fish sampling was performed twice in the present study: once in the summer period (July–August 2021; $n = 152$) and again in the winter period (December 2021–January 2022; $n = 128$). Microscopic investigations of myxosporean parasites were performed in the skin, fins, gills, heart, liver, gallbladder, stomach, intestine, kidney, urinary bladder, and gonads of fish samples using an Olympus BX51 microscope (equipped with an Olympus DP50 digital camera) and a Carl Zeiss Primostar FN 18 light microscope. Morphological identifications of myxosporean parasites from 20 fresh spores were conducted according to Jameson (1929) and Lom and Dyková (1992). The prevalence of infection (%) and density values of parasites were calculated according to Bush et al. (1997). Sterne's exact 95% confidence limits were calculated for prevalence using Quantitative Parasitology (QPweb) software (Reiczigel & Rózsa, 2020). Differences in prevalence values between four fish populations from the four sampling localities and between the two sampling seasons were determined by the exact unconditional test that maintains the prescribed type I error rate, which has a higher statistical power for a small sample size ($N < 100$). Differences in prevalence values between sampling localities and seasons were determined using Fisher's exact test. All statistical tests were performed at a significance level of 0.05. The density values of infection were scaled from one plus, representing the lowest density (+), and six pluses, representing the highest density (++++++), according to a methodology modified from 200× magnification by Gürkanl et al. (2018; + = 1–9; ++ = 10–19; +++ = 20–29; ++++ = 30–39; +++++ = 40–49; ++++++ > 50). All infection indices were calculated for each myxozoan species as well as for co-infections.

Molecular analyses

Genomic DNA extractions from myxozoan-infected Whiting tissues were performed using an Invitrogen PureLink Genomic DNA Mini Kit (Invitrogen, USA). The extracted genomic DNA was then stored at −20°C before use. To construct phylogenies, the small subunit of ribosomal DNA (hereafter, "18S rDNA") was used as the genetic marker. The PCR amplifications for the gene were performed using the primer set MyxospecF (Fiala, 2006) and 18r (Whipps et al., 2003) with the protocol described by Okkay et al. (2020). Ingredients for a 50-µL reaction mixture were as follows: 5 µL of 10× PCR buffer, 0.8 mM dNTP mix (Thermo Scientific, USA), 1.5 mM $MgCl_2$, 0.5 pmol (final concentration) of each primer (Oligomer Biyoteknoloji, Türkiye), 1.25 U of *Taq* polymerase (Invitrogen), genomic DNA (~50 ng) and double-distilled H_2O (up to 50 µL in

Figure 1. Map of sampling localities for Whiting throughout the southern Black Sea (numbers in circles correspond to the sampling localities in Türkiye; 1 = Kocaeli; 2 = Sinop; 3 = Ordu; 4 = Trabzon) (Adapted from d-maps, https://d-maps.com/carte.php?num_car=4446&lang=en).

final volume). The PCR amplifications were performed using a Techne TC-Plus thermal cycler. Afterward, the products were electrophoresed on a 1% agarose gel (prepared in 1× tris–borate–EDTA buffer) and were visualized with a photo-print imaging system (Vilber Lourmat). Nucleotide sequencing analyses were performed commercially by Macrogen-Europe BV (Amsterdam, Netherlands) from both strands. Geneious version 4.8.2 (Kearse et al., 2012)was used to edit and assemble the nucleotide sequences. The data sets for phylogenetic analyses were constructed according to the available molecular-based studies as well as the Basic Local Alignment Search Tool (BLAST; https://blast.ncbi.nlm.nih.gov/Blast.cgi) search results for the new 18S rDNA nucleotide sequences obtained in the study (Tables 1, 2). The software ClustalX version 2.1 (Thompson et al., 1997) was employed for multiple nucleotide sequence alignments of the data sets, and BioEdit version 7.2.5 (Hall, 1999) was used to check and edit the alignment files manually. To determine the evolutionary model(s) that provided the best fit to our data sets, Akaike's information criterion (AIC; Akaike, 1974) and Bayesian information criterion (BIC) tests were applied with jModelTest version 0.1 (Guindon & Gascuel, 2003; Posada, 2008). To determine the phylogenetic relationships among 18S rDNA nucleotide sequences, maximum likelihood (ML), neighbor-joining (NJ; Saitou & Nei, 1987), and maximum parsimony (MP; Eck & Dayhoff, 1966; Fitch, 1977) algorithms were used. Maximum likelihood analysis was performed using PhyML version 3.0 (Guindon & Gascuel, 2003). The NJ and MP analyses, on the other hand, were conducted using PAUP* version 4.0 beta 10 (Swofford, 1998). Additionally, a heuristic search approach using the Tree Bisection and Reconnection (TBR) swapping algorithm (with 10 random repetitions) was performed for MP analysis. To test the topological robustness of the phylogenetic trees, bootstrap tests (Efron, 1982; Felsenstein, 1985) were conducted with 10,000 replicates for NJ analysis and 1,000 replicates for MP and ML analyses. The similarities between nucleotide sequences were determined using MEGA version 10.4 (Kumar et al., 2018). All new 18S rDNA nucleotide sequences obtained in this study have been deposited in GenBank under accession numbers PV726994–PV727001 (Tables 1, 2).

RESULTS

The gallbladder of the investigated Whiting specimens was the only organ infected by myxozoan parasites. Initial microscopic observations of spore morphologies revealed that these parasite individuals belonged to the genera *Myxidium* and *Ceratomyxa*. Of the 280 investigated Whiting individuals, 72 fish (25.7%) were found to be infected with *Myxidium* sp-1 spores in the gallbladder, with an overall density ranked as 2+ per microscopic field. The infection prevalence and density values of *Ceratomyxa* sp-1 in Whiting were 39.6% (111 of 280 fish) and 3+, respectively. Moreover, in 56 of the 280 Whiting examined, *Myxidium* sp-1 and *Ceratomyxa* sp-1 coexisted in the host gallbladder, with infection prevalence and density values of 20.0% and 3+, respectively.

Morphology and phylogeny of myxozoan parasites

The spores of *Myxidium* sp-1 individuals were fusiform and equal-sized, with two polar capsules (pyriform in shape with pointed ends) located at the opposite ends, and the suture line divided the spores into two equal parts (Figure 2A; Table 1). In addition to the homogeneity in spore morphology, the detailed measurements of spore structures also indicated that all belonged to the same species, *Myxidium* sp-1 (Table 1).

Table 1. Comparative description of *Ceratomyxa merlangi* and *Myxidium gadi*, their morphologically similar species, and their hosts. Abbreviations: SL = spore length (μm), SW = spore width/spore thickness (μm), PCL = polar capsule length (μm), PCW = polar capsule width (μm), and PF = polar filament (μm).

Species	SL	SW	PCL	PCW	PF	Host fish	Reference
***Myxidium* species**							
M. gadi	13.8 (13.0–14.7)[a]	6.3 (6.0–6.9)[a]	4.9 (4.3–5.2)[a]	2.6 (2.5–2.7)[a]	–	Whiting	This study
M. gadi	13.9 (12.9–14.6)[a]	5.7 (5.3–6.0)[a]	5.1 (4.8–5.3)[a]	2.7 (2.5–2.8)[a]	–	Whiting	Özkan (2015)
M. gadi	11.3 ± 0.1[b]	5.3 ± 0.2[b]	3.4 ± 0.5[b]	2.8 ± 0.7[b]	–	Shorthorn Sculpin *Myoxocephalus scorpius*	Kodádková et al. (2014)
M. gadi	12.0–15.0[c]	5.0–7.5[c]	3.9 ± 0.42[c]	3.23 ± 0.54[c]	–	Saithe *Pollachius virens*	MacKenzie and Kalavati (1995)
***Ceratomyxa* species**							
C. merlangi	6.0 (5.8–6.4)[a]	33.8 (30.1–36.2)[a]	2.7 (2.5–3.0)[a]	2.0 (1.8–2.6)[a]	–	Whiting	This study
C. merlangi	5.5 (5.0–5.8)[a]	32.2 (27.6–34.79)[a]	2.7 (2.4–2.9)[a]	2.2 (1.9–2.3)[a]	–	Whiting	Özkan (2015)
C. merlangi	6.0–8.0[c]	30.0–53.7[c]	2.8–3.6[c]	1.6–2.0[c]	–	Whiting	Zaika (1966)
C. arcuata	5–8[c]	20–30[c]	–	–	–	Three-bearded Rockling *Gaidropsarus vulgaris*, Corkwing Wrasse *Symphodus melops*, Blackspot Seabream *Pagellus bogaraveo*	Thélohan (1895)
C. arcuata	5.5–6.0[c]	25–31[c]	3.5–4.0[c]	–	2–5	–	Parisi (1912)
C. arcuata	6.8 ± 0.9 (6.0–9.0)[d]	36.2 ± 2.7 (32.5–40.0)[d]	3.7 ± 0.7 (2.5–5.0)[d]	3.0 ± 0.2 (2.5–4.0)[d]	4–5	Whiting	Kalavati and MacKenzie (1999)
C. arcuata	7.25 (5–8)[a]	23.5 (20–30)[a]	2.75[e]	2.5[e]	–	Black Scorpionfish *Scorpaena porcus*	Lubat et al. (1989)
C. arcuata	7.5 ± 0.4 (7–9)[d]	35.6 ± 3.3 (30–40)[d]	3.3 ± 0.4 (3–4)[d]	3 ± 0.4 (2.5–3.5)[d]	4–5	Salema Porgy *Sarpa salpa*	Laamiri (2014)
C. cretensis	6.7 ± 0.1 (5.5–8.9)[d]	30.7 ± 0.5 (21.5–38.9)[d]	2.3 ± 0.1 (1.9–2.9)[d]	2.3 ± 0.1 (1.9–2.8)[d]	3–4	Atlantic Lizardfish *Synodus saurus*	Kalatzis et al. (2013)

[a]Mean, with range in parentheses
[b]Mean ± SD
[c]Range
[d]Mean ± SD, with range in parentheses
[e]Mean

Among them, one sample from each sampling locality (AO-68, AO-72, AO-73, and AO-80) was selected as a representative for molecular analyses. Subsequently, approximately 1,400 bp of the 18S rDNA gene of these specimens were amplified, sequenced, and subjected to phylogenetic analyses. As a result, all *Myxidium* sp-1 specimens showed the same 18S rDNA nucleotide sequence, and the BLAST result suggested that *M. gadi* (GQ890675, DQ377707, and DQ377711) was the closest species, with 99.63–100% sequence identities. Thus, a data set using 18S rDNA nucleotide sequences of *M. gadi* and allied species was formed (Table 2). Phylogenetic analyses were performed using 1,218 aligned nucleotides containing 321 variable sites (430 mutations). The AIC and BIC tests suggested the GTR + I + G (I [proportion of invariable sites] = 0.556; G [gamma distribution] = 0.587) and TIM3ef + I + G (I = 0.557; G = 0.590) evolutionary models, respectively. However, the ML and NJ trees created using the GTR + I + G model were preferred in the study since they showed higher bootstrap values. Maximum parsimony analysis, which was conducted using 244 synapomorphic sites, suggested a single most parsimonious tree with 773 steps (consistency index [CI] = 0.556274; retention index [RI] = 0.322448; homoplasy index [HI] = 0.443726). In Figure 3, an ML tree is given, and bootstrap values obtained from ML, NJ, and MP analyses are stated on each related node. On the phylogenetic tree, *Myxidium* sp-1 specimens showed the same 18S rDNA nucleotide sequence with *M. gadi* specimens GQ890675 (from Whiting in the United Kingdom; MacKenzie et al., 2010) and DQ377711 (from Saithe in Scotland, the North Sea; Fiala, 2006). Additionally, *M. gadi* specimens DQ377707 (from Haddock in the North Sea; Fiala, 2006) appeared as a sister with 99.6% nucleotide sequence similarity. This relationship was supported with 99, 97, and 100% bootstrap values in the ML, NJ, and MP trees, respectively. In addition to the nucleotide sequences used in phylogenetic analyses, there were some other *M. gadi* 18S rDNA nucleotide sequences in GenBank that were extracted from Atlantic Cod *Gadus morhua* in Norway (GQ890673, GQ890674, and GQ890676; MacKenzie et al., 2010), but they were not added to the data set for analyses since they were too short. However, they all showed the same 18S rDNA sequence as *Myxidium* sp-1. On the tree, *Zschokkella*

Table 2. GenBank accession numbers and source information for *Myxidium* and *Ceratomyxa* specimens obtained in this study and allied myxozoan and *Ceratomyxa* species obtained from GenBank.

Species	Host fish	Target organ	Locality	GenBank accession number	Reference
AO-68 (*Myxidium gadi*)	Whiting	Gallbladder	Türkiye	PV726994	This study
AO-72 (*M. gadi*)	Whiting	Gallbladder	Türkiye	PV726995	This study
AO-73 (*M. gadi*)	Whiting	Gallbladder	Türkiye	PV726996	This study
AO-80 (*M. gadi*)	Whiting	Gallbladder	Türkiye	PV726997	This study
Zschokkella neopomacentri	Miry's Demoiselle *Neopomacentrus miryae*	Gallbladder	Israel	DQ516379	Diamant and Palenzuela (2005)
Ellipsomyxa syngnathi	Nilsson's Pipefish *Syngnathus rostellatus*	Gallbladder	Denmark	GQ229234	Køie and Karlsbakk (2009)
Ellipsomyxa gobii	Common Goby *Pomatoschistus microps*	–	Denmark	AY505126	Køie et al. (2004)
Coccomyxa colurodontidis	*Colurodontis paxmani*	–	Australia	HM037790	Heiniger et al. (2011)
Zschokkella bergense	Blackbelly Rosefish *Helicolenus dactylopterus*	Gallbladder	North Atlantic	DQ377702	Fiala (2006)
Auerbachia pulchra	Roundnose Grenadier *Coryphaenoides rupestris*	Gallbladder	North Atlantic	DQ377703	Fiala (2006)
M. gadi	Haddock *Melanogrammus aeglefinus*	Gallbladder	Scotland	DQ377707	Fiala (2006)
M. gadi	Saithe	Gallbladder	North Sea	DQ377711	Fiala (2006)
Myxidium incurvatum	Dragonet *Callionymus lyra*	Gallbladder	North Sea	DQ377708	Fiala (2006)
Myxidium lapipiscis	*Gobius* sp.	–	Australia	MG562499	Miller et al. (2018)
Sigmomyxa sphaerica	Garfish *Belone belone*	–	Denmark	JN033225	Karlsbakk and Køie (2012)
Myxidium laticurvum	Greater Weever *Trachinus draco*	–	Denmark	JN033230	Karlsbakk and Køie (2012)
Ellipsomyxa nigropunctatis	Blackspotted Puffer *Arothron nigropunctatus*	Gallbladder	Australia	KF179050	Heiniger and Adlard (2014)
Myxidium scomberomori	Broadbarred King Mackerel *Scomberomorus semifasciatus*	Gallbladder	Australia	KF179052	Heiniger and Adlard (2014)
Myxidium milleri	Schultz's Pipefish *Corythoichthys schultzi*	Gallbladder	Australia	KF179053	Heiniger and Adlard (2014)
Myxidium maxi	Peacock Rockskipper *Istiblennius meleagris*	Gallbladder	Australia	KF179054	Heiniger and Adlard (2014)
Myxidium queenslandicus	Scissortail Sergeant *Abudefduf sexfasciatus*	–	Australia	EU440379	Gunter and Adlard (2008)
Myxidium finnmarchicum	Black Sea Turbot *Scophthalmus maeoticus*	Gallbladder	Türkiye	MZ130192	Özer et al. (2022)
Myxidium parvum	Peacock Blenny *Salaria pavo*	Gallbladder	Türkiye	MZ087785	Gürkanlı et al. (2022)
Ellipsomyxa mugilis	Mugilidae	Bile	Spain	AF411336	Palenzuela et al. (2002)
Kudoa trifolia	Golden Gray Mullet *Liza aurata*	Various organs	Spain	AM183300	Holzer et al. (2006)
Kudoa yasuganai	Olive Flounder *Paralichthys olivaceus*	Brain	Japan	AY302741	Whipps et al. (2004)
AO-66 (*Ceratomyxa merlangi*)	Whiting	Gallbladder	Türkiye	PV726998	This study
AO-67 (*C. merlangi*)	Whiting	Gallbladder	Türkiye	PV726999	This study
AO-69 (*C. merlangi*)	Whiting	Gallbladder	Türkiye	PV727000	This study
AO-70 (*C. merlangi*)	Whiting	Gallbladder	Türkiye	PV727001	This study
Ceratomyxa arabica	Twobar Seabream *Acanthopagrus bifasciatus*	Gallbladder	Saudi Arabia	KJ631533	Al-Qahtani et al. (2015)
Ceratomyxa arcuata	Anglerfish *Lophius piscatorius*	Gallbladder	North Sea, off Scotland	KJ419344	Fiala et al. (2015)
C. arcuata	Whiting	Gallbladder	North Sea, off Scotland	KM273023	Fiala et al. (2015)
Ceratomyxa cretensis	Atlantic Lizardfish	Gallbladder	Greece	JX869942	Kalatzis et al. (2013)
Ceratomyxa filamentosi	Yellowfin Aulopus *Aulopus filamentosus*	Gallbladder	Greece	JX869943	Kalatzis et al. (2013)
Ceratomyxa draconis	Greater Weever	Gallbladder	Tunisia	MF540151	Azizi et al. (2020)
Ceratomyxa saurida	Slender Lizardfish *Saurida elongata*	Gallbladder	China	MT808644	Yang et al. (2023)
Ceratomyxa truncata	European Pilchard *Sardina pilchardus*	Gallbladder	Tunisia	MT935658	Mansour et al. (2022)
Ceratomyxa mehlhorni	Golden Trevally *Gnathanodon speciosus*	Bile	Saudi Arabia	KR086362	Mansour et al. (2015)

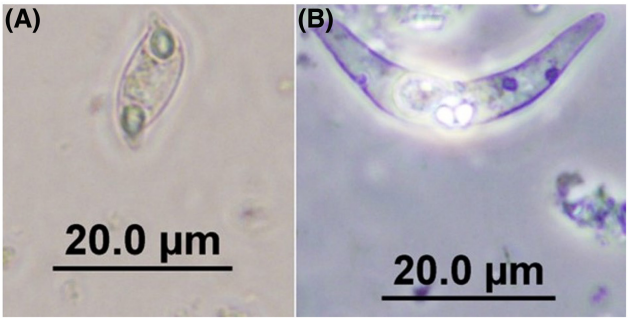

Figure 2. Light microscopic images of myxosporean species in the gallbladder of Whiting: (A) an individual spore of *Myxidium* sp-1 and (B) an individual spore of *Ceratomyxa* sp-1.

bergense (DQ377702) and *M. finnmarchicum* (MZ130192) appeared as sister species to the *M. gadi* lineage (Figure 3).

The spores belonging to *Ceratomyxa* sp-1 in the present study were crescent-shaped, with a blunt, rounded shape towards the ends. Two polar capsules were located almost in the middle of the spore (Figure 2B). Moreover, detailed morphometric measurements also supported that all *Ceratomyxa* specimens in this study were the same species, *Ceratomyxa* sp-1 (Table 1). For phylogenetic analyses, one *Ceratomyxa* sp-1 specimen (AO-66, AO-67, AO-69, and AO-70) was selected from each locality (Table 2). Approximately 1,400 bp of the 18S rDNA gene were sequenced, and three different nucleotide sequences were determined out of four selected *Ceratomyxa* sp-1 specimens. The 18S rDNA nucleotide sequence similarities among *Ceratomyxa* sp-1 specimens were higher than 99.8%, thus supporting the hypothesis that these specimens all belonged to the same species (*Ceratomyxa* sp-1). The BLAST results suggested *Ceratomyxa arcuata* (KJ419344) as the closest species to our new 18S rDNA nucleotide sequences. Based on this information, a data set composed of species related to *C. arcuata* was constituted for constructing phylogenies (Table 2). Phylogenetic analyses were conducted over 1,253 aligned nucleotides with 291 variable sites (353 mutations). The AIC and BIC tests suggested the GTR + G (G = 0.246) and TIM2G (G = 0.247) evolutionary models, respectively. In this study, the GTR + G model was preferred for ML and NJ analyses because the bootstrap values suggested by this model were higher than those suggested by the TIM2 + G model. Maximum parsimony analysis was conducted over 208 synapomorphic sites and revealed a single most parsimonious tree with 402 steps (CI = 0.878109; RI = 0.874680; HI = 0.121891). An ML tree is shown in Figure 4, and bootstrap values obtained from the ML, NJ, and MP analyses are stated on each related node. On the phylogenetic trees created using the ML, NJ, and MP algorithms, our three new *Ceratomyxa* sp-1 18S rDNA nucleotide sequences (AO-67, AO-70, and AO-66/AO-69) formed a lineage, and *C. arcuata* (KM273023 from Whiting and KJ419344 from Anglerfish in the North Sea; Fiala et al., 2015) appeared as the sister species to this lineage. The nucleotide sequence similarities between *Ceratomyxa* sp-1 and the *C. arcuata* specimens were between 98.8% and 99.1%. *Ceratomyxa cretensis* was the third species in the lineage as a sister to the species mentioned earlier. The relationships between these three species were supported with sufficient bootstrap values in ML and NJ trees (≥54%). In the MP analysis, on the other hand, the bootstrap tree did not support these relationships with significant values, although the topology of the MP tree was the same as the topology of the ML and NJ trees (Figure 4).

The distribution of *Myxidium* sp-1 and *Ceratomyxa* sp-1 concerning sampling locality and season

The overall infection prevalence and density values of our *Myxidium* sp-1 and *Ceratomyxa* sp-1, as well as their coexistence in Whiting, concerning their locality-based and seasonal results, are presented in Table 3. Moreover, detailed seasonal infection prevalences and density values observed at the study localities are also presented in Table 4. When the infection prevalence of *Myxidium* sp-1 was evaluated in the sampling localities, Sinop samples had the maximum value, followed by the Kocaeli, Ordu, and Trabzon samples (Table 4). Both *Ceratomyxa* sp-1 and co-infections of *Myxidium* sp-1 and *Ceratomyxa* sp-1 also followed the pattern in the prevalence values of infections (Table 3). Infection prevalence values of each individual parasite species and their co-existence at all four sampling localities had statistically significant differences ($P < 0.05$; Table 5). However, when the individual parasite species and their prevalence values at individual sampling localities were compared, some had statistically significant differences, whereas others did not ($P > 0.05$; Table 5).

The overall infection prevalence values of both individual parasite species and their co-infection during two sampling seasons were also determined (Table 3). The infection prevalence of *Ceratomyxa* sp-1 and the co-existing parasites was higher in summer, but prevalence was higher in winter for *Myxidium* sp-1, without any statistically significant difference ($P > 0.05$; Table 5). When the seasonal locality-based prevalence of infection was considered, summer samples at Kocaeli and Ordu, contrary to Sinop samples, had slightly higher infection prevalence and density values than winter samples, without any statistically significant differences ($P > 0.05$; Tables 3, 5). In Trabzon samples, however, a statistically significant difference was determined only for *Ceratomyxa* sp-1, which was found in both seasons ($P < 0.05$), while *Myxidium* sp-1 and the co-existing parasites were found only in summer samples (Tables 4, 5).

When the mean density of infection was examined, a homogeneous level of densities ranking either 2+ or 3+ was determined for each individual parasite and for the co-existing parasites at all four sampling localities as well as both overall and in locality-based sampling seasons, without any statistically significant differences ($P > 0.05$; Tables 3–5).

DISCUSSION

Morphology and molecular phylogeny

In the present study, 280 Whiting individuals were investigated for myxosporean fauna in the summer and winter seasons, year-round, from four sampling localities representing the whole southern Turkish coast of the Black Sea for the first time. This study is also the first investigation on the molecular approach to provide exact species identification of the previously morphologically identified myxosporean parasites that infect Whiting. Microscopic observations revealed that only two myxosporean species, which belonged to the genera *Myxidium*

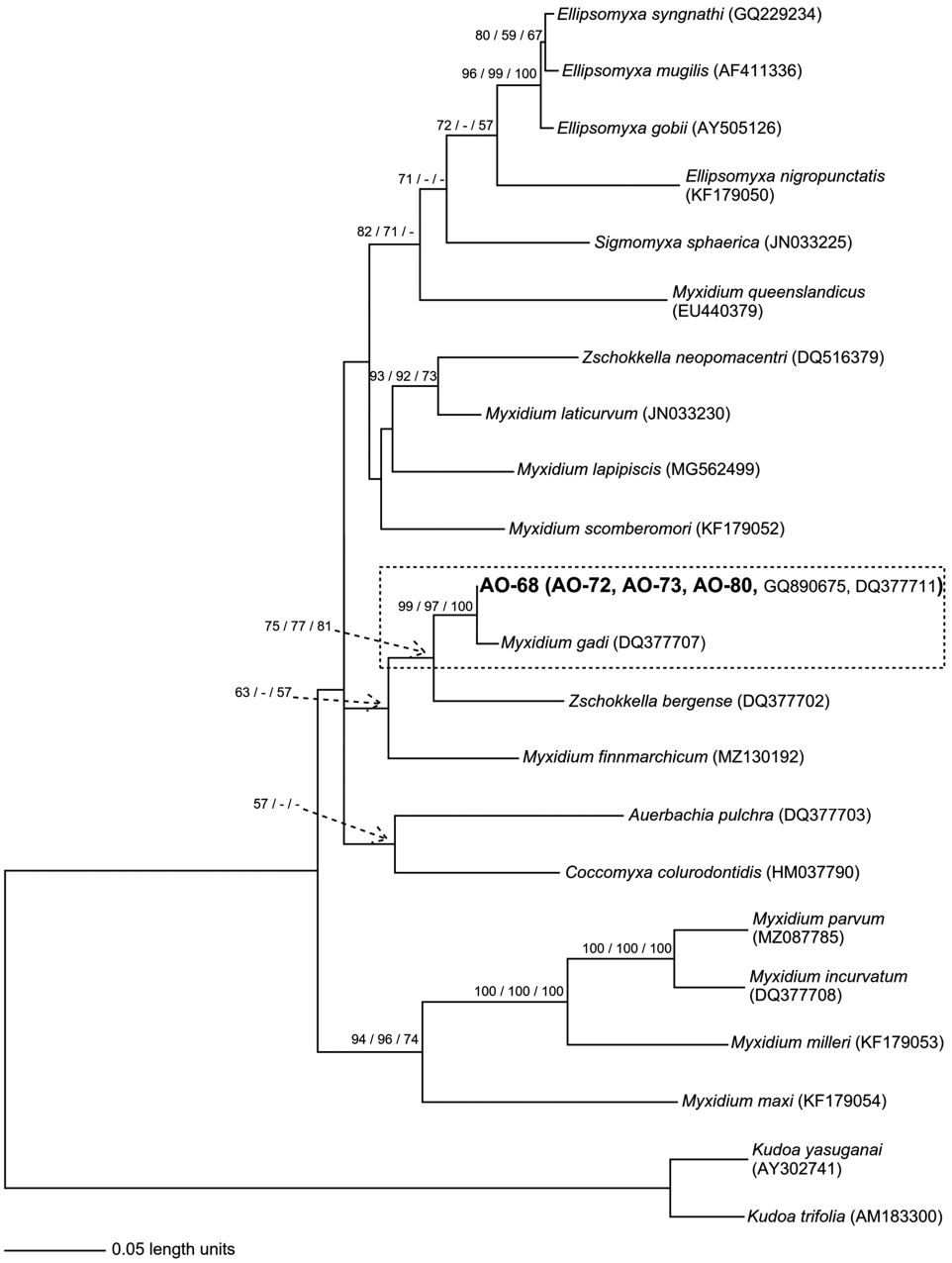

Figure 3. Maximum likelihood tree based on 18S ribosomal DNA (rDNA) nucleotide sequences. *Myxidium* sp-1 18S rDNA nucleotide sequences obtained in this study are shown in bold. The 18S rDNA nucleotide sequences of related *Myxidium* species obtained from GenBank are provided, with GenBank accession numbers shown in parentheses (Table 2). The tree was rooted using *Kudoa trifolia* and *K. yasuganai*. The bootstrap values (≥50%) obtained from maximum likelihood, neighbor joining, and maximum parsimony analyses are stated on each related node in the given order.

and *Ceratomyxa*, were present in all infected fish in accordance with previous reports on the myxosporean parasites of Whiting in the Black Sea.

Morphological and morphometric data on myxospores showed that some individuals (*Myxidium* sp-1) in this study (Figure 3; Table 2) were identical to previously reported *M. gadi* except for the length of the polar capsules. Polar capsule lengths of *Myxidium* sp-1 in this study were much larger than those of the *M. gadi* specimens reported from Shorthorn Sculpin *Myoxocephalus scorpius* in the Svalbard Archipelago and from Saithe *Pollachius virens* in the North Sea (Kodádková et al., 2014; MacKenzie & Kalavati, 1995), but they were quite similar to the data given for *M. gadi* from Whiting in the southern Black Sea (Özkan, 2015). Concordant with these data, Ben-David et al. (2016) indicated that minimal differences may be observed in polar capsules as the parasite exhibits contractile dynamics due to infection adaptation in different hosts. In the present study, phylogenetic analyses based on the nucleotide sequences of the 18S rDNA gene of selected specimens from the four sampling localities also indicated that *Myxidium* sp-1 was related to the same species indicated by Georgévitch (1916). In this context, in light of the morphological and

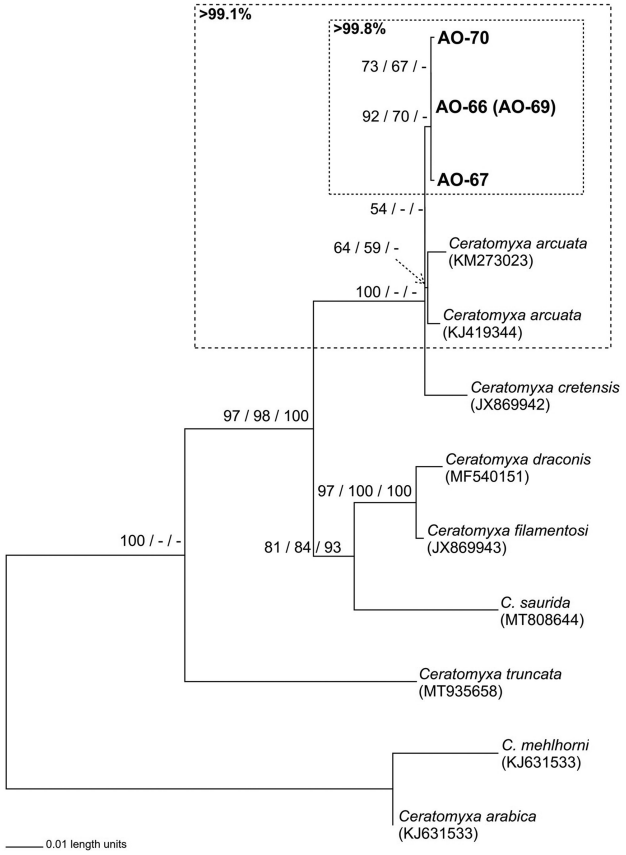

Figure 4. Maximum likelihood tree based on 18S ribosomal DNA (rDNA) nucleotide sequences. *Ceratomyxa* sp-1 18S rDNA nucleotide sequences obtained in this study are shown in bold. The 18S rDNA nucleotide sequences of related *Ceratomyxa* species obtained from GenBank are provided, with GenBank accession numbers shown in parentheses (Table 2). The tree was rooted using *Ceratomyxa mehlhorni* and *C. arabica*. The bootstrap values (≥50%) obtained from maximum likelihood, neighbor-joining, and maximum parsimony analyses are stated on each related node in the given order.

molecular phylogenetic data obtained in this study, we assigned our *Myxidium* sp-1 specimens to *M. gadi*, which was originally described by Georgévitch (1916) from Pollack *Pollachius pollachius* and Common Sole *Solea solea* sampled along the Atlantic coast of France. Since the first identification, *M. gadi* has been reported from the following host fishes and localities: Atlantic Cod in the Baltic Sea/Russia, in the White Sea, and on the Atlantic coast of Canada (Khan et al., 1986; Petrushevskii, 1932; Shulman & Shulman-Albova, 1953); Haddock along the Atlantic coast of Canada and in the Barents Sea (Fantham et al., 1940; Polyanskii, 1966); Saithe in the Barents Sea and the North Sea (Feist, 1995; Feist & Bucke, 1992; MacKenzie & Kalavati, 1995; Polyanskii, 1966); European Flounder *Platichthys flesus* in the Baltic Sea/Russia (Petrushevskii, 1932); and Common Sole in the Adriatic Sea (Lubat et al., 1989). *Myxidium gadi* has also been reported from the Black Sea, where, different from the other localities, it was primarily observed in Whiting and only two exceptional records were from European Flounder, reported by Okkay and Özer (2018) and Yurakhno (1997). *Myxidium gadi* was first recorded from Whiting and European Flounder off the Crimean coast of the Black Sea (Yurakhno, 1987). Subsequently, it was reported from Whiting inhabiting nearly all of the northern Black Sea, including Russia, Ukraine, and Georgia (Özer et al., 2015, 2017; Skuratovskaya et al., 2013; Yurakhno, 1988, 1997, 2004, 2008, 2009a, 2009b, 2010, 2013; Yurakhno & Naidenova, 2000).

Microscopic observations of bile from the gallbladder of Whiting samples (39.6%) in the present study revealed a second myxozoan species corresponding to members of the genus *Ceratomyxa*. Detailed morphological and morphometric data on the myxospores revealed that all *Ceratomyxa* specimens from the four sampling localities belonged to the same species (*Ceratomyxa* sp-1). Moreover, when morphological and morphometric data obtained from *Ceratomyxa* sp-1 were compared with data describing *C. merlangi*, which is the common myxozoan parasite of Black Sea Whiting, it was not surprising that they were well fitting (Table 1). *Ceratomyxa merlangi* is an endemic myxozoan species of the Black Sea, which so far has been observed only from the gallbladder of Whiting. On the other hand, our BLAST results of 18S rDNA sequences pointed to two other species, *C. arcuata* and *C. cretensis*; however, phylogenetic relationships and nucleotide sequence similarities did not support unambiguously assigning *Ceratomyxa* sp-1 specimens to one of those species. Morphological and morphometric data were also concordant with this inference. First of all, *Ceratomyxa* sp-1 differs from *C. arcuata* with its myxospore morphology, which is relatively semicircular and narrows towards the ends, with a cylindrical or rounded terminal. Moreover, although spore lengths were quite similar, other myxospore morphometrics (spore thickness, polar capsule length, and polar capsule width) differed in one or more parameters (see Table 2) when compared with *C. arcuata* from different hosts in earlier studies (Kalavati & MacKenzie, 1999; Laamiri, 2014; Lubat et al., 1989; Parisi, 1912; Thélohan, 1895). The other phylogenetically close species, *C. cretensis* from Atlantic Lizardfish, has a larger suture length than that of *Ceratomyxa* sp-1 (see Table 2). In addition, the ratio of polar capsule length to polar capsule width is quite low. Polar capsules of this species differ from *Ceratomyxa* sp-1 by having a more rounded shape (Kalatzis et al., 2013). Unfortunately, because the 18S rDNA nucleotide sequence of *C. merlangi* was not available in databases, we could not phylogenetically compare *Ceratomyxa* sp-1 with *C. merlangi*. However, based on the presence of highly similar morphological and morphometric data, we assigned our *Ceratomyxa* sp-1 specimens to *C. merlangi*. Common ecological niches (geographical distribution, host fish selection, and tissue selection) of *Ceratomyxa* sp-1 and *C. merlangi* also support this inference since some myxozoan parasites have host and tissue selectivity (Atkinson et al., 2015; Eszterbauer, 2004; Fiala, 2006; Gunter & Adlard, 2010; Holzer et al., 2004). Thus, we have provided the first molecular results (18S rDNA nucleotide sequences) of *C. merlangi* as new data for science. Since its first identification by Zaika (1966) off Sevastopol–Russia, *C. merlangi* has been reported from Whiting inhabiting nearly the whole northern Black Sea, including Russia, Ukraine, and Georgia (Özer et al., 2015, 2017; Yurakhno, 1988, 1997,

Table 3. Overall infection prevalence (%) and density values of *Ceratomyxa merlangi*, *Myxidium gadi*, and co-existing *C. merlangi* + *M. gadi* in Whiting sampled at different localities and during different seasons (*N* = number of fish examined; CI = 95% confidence interval based on Sterne's exact score limit [CI given in parentheses]; **P* < 0.05). Infection density codes are defined in the *Methods*.

Category	Species, locality, or season	*N*	Fish length (cm) ± SD	Prevalence (%) and CI	Mean density of infection
Species	*C. merlangi*	280	15.1 ± 1.8	39.6 (33.9–45.5)	3+
	M. gadi	280	15.1 ± 1.8	25.7 (20.9–31.2)	2+
	C. merlangi + *M. gadi*	280	15.1 ± 1.8	20.0 (15.7–25.2)	3+
Locality	*C. merlangi*				
	Kocaeli	56	15.2 ± 1.8	33.9 (22.1–47.3)	2+
	Sinop	95	15.6 ± 1.8	61.0 (50.5–70.6)	3+
	Ordu	55	14.8 ± 1.4	21.8 (12.4–34.5)	2+
	Trabzon	74	14.7 ± 1.8	29.7 (20.1–41.2)	3+
	M. gadi				
	Kocaeli	56	15.2 ± 1.8	37.5 (25.8–50.9)	3+
	Sinop	95	15.6 ± 1.8	41.0 (31.5–51.6)	2+
	Ordu	55	14.8 ± 1.4	12.7 (6.1–24.4)	2+
	Trabzon	74	14.7 ± 1.8	6.7 (2.7–15.3)	2+
	C. merlangi + *M. gadi*				
	Kocaeli	56	15.2 ± 1.8	21.4 (12.2–33.8)	3+
	Sinop	95	15.6 ± 1.8	34.7 (25.7–44.9)	2+
	Ordu	55	14.8 ± 1.4	10.9 (4.9–22.5)	2+
	Trabzon	74	14.7 ± 1.8	6.7 (2.7–15.3)	3+
Season	*C. merlangi*				
	Summer	152	15.4 ± 1.5	42.8 (34.9–51.0)	3+
	Winter	128	14.8 ± 2.0	35.9 (28.1–44.9)	3+
	M. gadi				
	Summer	152	15.4 ± 1.5	24.3 (18.0–31.9)	2+
	Winter	128	14.8 ± 2.0	27.3 (20.2–35.9)	3+
	C. merlangi + *M. gadi*				
	Summer	152	15.4 ± 1.5	20.4 (14.6–27.6)	2+
	Winter	128	14.8 ± 2.0	19.5 (13.4–27.3)	3+

2004, 2008, 2009a, 2009b, 2010, 2013). With this study, the presence of *C. merlangi* throughout nearly the entire southern coast of the Black Sea has now been validated.

Effects of sampling locality and season on parasite infections

Among the studies mentioned above, reports on the infection indices of both *M. gadi* and *C. merlangi* in Whiting inhabiting the northern coast of the Black Sea are very limited in old studies, with the infection prevalence ranging between 10% and 70% (Yurakhno, 1994, 1997 , 2008). However, Özer et al. (2015, 2017) reported more comprehensive data for both parasite species in Black Sea Whiting from Sevastopol in the north and Sinop in the south. The present study provides the first data on the existence of *M. gadi* in Whiting inhabiting nearly the whole southern coast of the Black Sea in Türkiye, with seasonal occurrences. The overall infection prevalence and density values of *M. gadi* obtained from the four sampling localities throughout the southern Black Sea were 25.7% and 2+ per microscopic field in the present study, and these values were 41.0% and 2+ per microscopic field at the locality of Sinop. Moreover, the seasonal prevalence of infection of *M. gadi* increased from 0.0% in summer to 23.6% in spring at Sinop and from 10.0% in summer to 40.0% in winter within Balaklava Bay (Özer et al., 2017); prevalence was 36.9% in summer and 44.8% in winter at Sinop in the present study. *Myxidium gadi* has also been reported from the same host in the southern Black Sea off Sinop, with infection prevalences between 6.7% and 63.0% with the intensities of numerous developing and mature spores (Özer et al., 2015) and a prevalence and density of 18.6% and 4+ (Özer et al., 2017). These data show that the results obtained in the present study were intermediate between the results reported from the northern coast and were higher than those of previous reports on *M. gadi* infections in Whiting from the southern Black Sea coast, namely Sinop.

Ceratomyxa merlangi, the other species in the present study, has also been reported from Whiting inhabiting the northern coast of the Black Sea (Yurakhno, 1994, 1997, 2008) and off Sinop in the southern Black Sea (Özer et al., 2015, 2017; Özkan, 2015), with infection prevalence values of 7–47% and 6.7–77.8%, respectively. In the present study, the overall infection prevalence and density values of *C. merlangi* obtained from the four sampling localities throughout the southern Black Sea were 39.6% and 3+ per microscopic field, and these values were 61.0% and 3+ per microscopic field in the locality of Sinop. The data obtained for *C. merlangi* from both sides of the Black Sea fell within the previously reported ranges. When the infection indices for both myxosporean species in four sampling localities were compared, the Sinop and Kocaeli samples (representing the central and western parts of the Black Sea) had higher infection prevalence values than the Ordu and Trabzon samples (representing the eastern part of the Black Sea), with statistically significant differences. The infection density values, on the other hand, were very similar at the four sampling localities,

Table 4. Seasonal infection prevalence (%) and density values of *Ceratomyxa merlangi*, *Myxidium gadi*, and their co-infections in Whiting *Merlangius merlangus* (N = number of fish examined; CI = 95% confidence interval based on Sterne's exact score limit [CI given in parentheses]; $^*P < 0.05$). Infection density codes are defined in the *Methods*.

			C. merlangi			*M. gadi*			Co-infection (*M. gadi* + *C. merlangi*)		
Locality	Season	*N*	Infected fish	Prevalence (%) and CI	Mean density	Infected fish	Prevalence (%) and CI	Mean density	Infected fish	Prevalence (%) and CI	Mean density
Trabzon	Summer (22.1–25.9°C)	47	20	42.5 (28.5–57.5)	3+	5	10.6 (4.3–23.2)	2+	5	10.6 (4.3–23.2)	3+
	Winter (7.5–14.1°C)	27	2	7.4 (1.3–23.7)	3+	0	0.0	0	0	0.0	0
Ordu	Summer (24.6–27.1°C)	30	7	23.3 (11.2–41.6)	2+	4	13.3 (4.7–29.8)	2+	3	10.0 (2.8–26.3)	2+
	Winter (6.1–14.4°C)	25	5	20.0 (8.2–39.8)	3+	3	12.0 (3.4–30.3)	2+	3	12.0 (3.4–30.3)	2+
Sinop	Summer (23.4–26.7°C)	46	26	56.5 (41.2–70.8)	3+	17	36.9 (23.7–52.2)	2+	16	40.0 (22.2–50.0)	3+
	Winter (8.8–13.8°C)	49	32	65.3 (51.0–77.8)	3+	22	44.8 (31.5–59.3)	2+	17	34.7 (22.2–49.0)	2+
Kocaeli	Summer (23.1–26.2°C)	29	12	41.4 (24.6–60.5)	2+	11	37.9 (22.1–57.0)	2+	7	24.1 (11.5–43.0)	2+
	Winter (7.9–12.6°C)	27	7	25.9 (12.4–46.2)	3+	10	37.0 (20.2–57.0)	4+	5	18.5 (7.0–36.0)	3+

with some statistically significant differences. Concordant with the available literature, we also observed both *M. gadi* and *C. merlangi* either separately or as co-infections in the gallbladder of Whiting hosts. Co-infections followed similar patterns in infection prevalence values and densities, both in the present study and in previous reports by Özer et al. (2015 , 2017).

The obtained locality- and season-based differences and similarities could have resulted from several factors, such as life cycle strategies, the availability of alternate hosts, water temperatures, fish stock differences, and the depth of sampling localities. Similar evaluations were made for both parasite species in a previous study by Özer et al. (2017). Currently, it is not known how the infection processes of *C. merlangi* and *M. gadi* are completed: either alternate with the two-host life cycle (one vertebrate host [fish] and one invertebrate host [annelids]) or direct fish-to-fish transmission. Previous studies have indicated that both life cycle strategies are possible, as was seen for *Ceratomyxa* and *Parvicapsula* species using polychaetes as alternate hosts (Bartholomew et al., 1997, 2006; Køie et al., 2004, 2008) and fish-to-fish transmission for some marine myxosporean species (Diamant, 1997; Redondo et al., 2002). Co-infections of both parasite species, along with the individual infections determined here, have also been reported in previous studies (Özer et al., 2017; Yurakhno, 1997). Based on current data, we can assume that both parasite species have the same life cycle strategies—either alternate or fish-to-fish transmission.

Climate change is an increasing concern all over the world, and the physical and chemical properties of the global ocean have been substantially affected by warming as the most significant stressor on marine life by resulting in an overall increase of 1°C over the past decade (Kennedy et al., 2019; Rutterford et al., 2023). Increases in water temperatures strongly impact and cause changes in the composition of fish assemblages, leading to increased abundances at higher temperatures for some fish species, including Whiting (Fossheim et al., 2015). Water temperature is also one of the key factors in myxosporean infections, along with specific physical, chemical, and biological conditions that are necessary for the successful development of parasites (Rocha et al., 2011). Even though the life cycle strategies of both myxosporean species are currently unknown, the determined higher infection prevalence values in the present study relative to those previously reported by Özer et al. (2017) at Sinop and Sevastopol for both parasite species might have resulted from higher water temperatures yielding higher abundances in fish hosts and facilitating host-to-host interactions in the same sampling localities. Impacts of water temperature values on the viability of actinosporean stages—the second alternate stage in invertebrates during the myxozoan life cycle—have also been reported, with a range of 3–25 d at different water temperatures (Markiw, 1992; Özer & Wootten, 2002; Xiao & Desser, 2000; Yokoyama et al., 1993). Thus, if the life cycle strategy involves invertebrate hosts for two parasite species, the minimum viability of 3 d at 22°C reported by Özer and Wootten (2002) for an actinosporean stage could be enough for successful infections in Whiting, leading to the higher infection prevalences in the present study.

Conclusions

The significant findings and their scientific importance in the present study are as follows: (1) Current knowledge on two myxosporean parasite species, *M. gadi* and *C. merlangi*, based solely on the morphological and morphometric data, has been expanded by providing new data from new sampling localities along with the first molecular data. (2) *Myxidium gadi* and *C. merlangi* have been reported as the only myxozoan parasites of Whiting that inhabit nearly the entire southern Black Sea. Thus,

Table 5. Comparative statistical differences (*P*-values) in the prevalence and density of *Ceratomyxa merlangi*, *Myxidium gadi*, and coexisting *C. merlangi* + *M. gadi* between locality samples and seasons (*$P < 0.05$; NA = not applicable).

	C. merlangi		*M. gadi*		*C. merlangi* + *M. gadi*	
Locality or season comparison	**Prevalence (%)**	**Mean density**	**Prevalence (%)**	**Mean density**	**Prevalence (%)**	**Mean density**
Locality						
Kocaeli–Sinop	0.001*	0.156	0.300	0.031*	0.092	0.437
Kocaeli–Ordu	0.183	0.888	0.002*	0.031*	0.146	0.179
Kocaeli–Trabzon	0.300	0.343	0.000*	0.034*	0.016*	0.959
Sinop–Ordu	0.000*	0.238	0.000*	0.400	0.001*	0.275
Sinop–Trabzon	0.000*	0.999	0.000*	0.347	0.001*	0.423
Ordu–Trabzon	0.300	0.362	0.283	0.876	0.300	0.177
Kocaeli–Sinop–Ordu–Trabzon	0.000*	0.383	0.000*	0.027*	0.000*	0.336
Season						
Kocaeli summer–winter	0.243	0.384	0.300	0.061	0.300	0.202
Sinop summer–winter	0.300	0.392	0.300	0.202	0.300	0.845
Ordu summer–winter	0.300	0.530	0.300	0.999	0.300	0.400
Trabzon summer–winter	NA	NA	NA	NA	NA	NA
Overall summer–winter	0.252	0.212	0.300	0.206	0.300	0.572

the missing geographical part of the southern Black Sea coast's myxozoan fauna infecting the Black Sea Whiting has been completed. Together with the data from earlier studies, these two species appeared to be the myxozoan parasites infecting Whiting in the whole Black Sea. (3) The first molecular records (18S rDNA nucleotide sequences) of *C. merlangi* for the scientific world have been provided, and the phylogenetic position of *C. merlangi* has been revealed. Additionally, robust genetic information has been provided for the precise identification of this species as needed in future studies. (4) The first molecular records (18S rDNA nucleotide sequences) of *M. gadi* from the Black Sea have been provided, and these data will contribute to future studies concerning the genetic borders of this species. (5) The first comprehensive infection indices for two myxozoan species infecting Whiting in relation to season and at different localities have been provided for the southern Black Sea.

DATA AVAILABILITY

The DNA sequence data have been deposited in GenBank, and alcohol samples of myxosporean parasites are preserved in the parasitology laboratory collection. The generated data sets for infection indices during the current study are stored on the personal computers of the authors and are open to everyone who needs them upon request.

ETHICS STATEMENT

No studies involving laboratory animals or invasive techniques were conducted. The parasite samples were obtained from slaughtered fish in fishing nets; hence, ethical approval was not required.

FUNDING

This study was financially supported by the Scientific Research Projects Coordination Unit of Ordu University in Ordu, Türkiye, with Project Number D-2106.

CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

ACKNOWLEDGMENTS

Author contributions are as follows: C. T. Gürkanlı, S. Okkay, and A. Özer provided support for the fieldwork of the study, including purchasing fish, their transportation, dissections, and parasitological examinations. For molecular work, C. T. Gürkanlı and Y. Çiftçi generated DNA sequence data from parasite samples and conducted all phylogenetic analyses. For statistical analysis, A. Özer conducted all necessary calculations. C. T. Gürkanlı and S. Okkay prepared the first draft of the manuscript. A. Özer oversaw all subsequent revisions of the manuscript and wrote the final text. All authors reviewed the manuscript and provided edits on the final version.

REFERENCES

Akaike, H. (1974). A new look at statistical model identification. *IEEE Transactions on Automatic Control*, *19*, 716–723. https://doi.org/10.1109/TAC.1974.1100705

Al-Qahtani, H. A., Mansour, L., Al-Quraishy, S., & Abdel-Baki, A. A. (2015). Morphology, phylogeny and seasonal prevalence of *Ceratomyxa arabica* n. sp. (Myxozoa: Myxosporea) infecting the gallbladder of *Acanthopagrus bifasciatus* (Pisces: Sparidae) from the Arabian Gulf, Saudi Arabia. *Parasitology Research*, *114*, 465–471. https://doi.org/10.1007/s00436-014-4204-2

Atkinson, S. D., Bartosova-Sojkova, P., Whipps, C. M., & Bartholomew, J. L. (2015). Approaches for characterising myxozoan species. In B. Okamura, A. Gruhl, & J. L. Bartholomew (Eds.), *Myxozoan evolution, ecology and development* (pp. 111–123). Springer International Publishing.

Azizi, R., Yemmen, C., Rangel, L. F., Santos, M. J., & Bahri, S. (2020). Morphology, seasonality and molecular characterization of *Ceratomyxa draconis* n. sp. parasite of *Trachinus draco* (L.) from the Bay of Bizerte, Tunisia. *Parasitology Research*, *119*, 2431–2438. https://doi.org/10.1007/s00436-020-06664-w

Bartholomew, J. L., Atkinson, S. D., & Hallet, S. L. (2006). Involvement of *Manayunkia speciosa* (Annelida: Polychaeta: Sabellidae) in the life cycle of *Parvicapsula minibicornis*, a myxozoan parasite of Pacific salmon. *Journal of Parasitology*, *92*, 742–748. https://doi.org/10.1645/GE-781R.1

Bartholomew, J. L., Whipple, M. J., Stevens, D. G., & Fryer, J. (1997). The life cycle of *Ceratomyxa shasta*, a myxosporean parasite of salmonids, requires a freshwater polychaete as an alternative host. *Journal of Parasitology*, *83*, 859–868. https://doi.org/10.2307/3284281

Ben-David, J., Atkinson, S. D., Pollak, Y., Yossifon, G., Shavit, U., Bartholomew, J. L., & Lotan, T. (2016). Myxozoan polar tubules display structural and functional variation. *Parasites & Vectors*, *9*, Article 549. https://doi.org/10.1186/s13071-016-1819-4

Bush, A. O., Lafferty, K. D., Lotz, J. M., & Shostak, A. W. (1997). Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology*, *83*, 575–583. https://doi.org/10.2307/3284227

Dethlefsen, V., Söffker, K., Büther, H., & Dam, U. (1996). Organochlorine compounds in marine organisms from the international North Sea incineration area. *Archive of Fishery and Marine Research*, *44*, 215–242.

Diamant, A. (1997). Fish-to-fish transmission of a marine myxosporean. *Diseases of Aquatic Organisms*, *30*, 99–105. https://doi.org/10.3354/dao030099

Diamant, A., & Palenzuela, O. (2005, September 11–16). Myxidium *or* Zschokkella? *A systematic dilemma illustrated by a new myxosporean parasite of* Neopomacentrus miryae *(Pomacentridae) from the northern Red Sea* [Paper presentation]. EAFP 12th international conference, Copenhagen, Denmark.

Eck, R. V., & Dayhoff, M. O. (1966). *Atlas of protein sequence and structure*. National Biomedical Research Foundation.

Efron, B. (1982). *The jackknife, the bootstrap and other resampling plans* (CBMS-NSF MA, Monograph 38). Society for Industrial and Applied Mathematics.

Eszterbauer, E. (2004). Genetic relationship among gill-infecting *Myxobolus* species (Myxosporea) of cyprinids: Molecular evidence of importance of tissue-specificity. *Diseases of Aquatic Organisms*, *58*, 35–40. https://doi.org/10.3354/dao058035

Fantham, H. B., Porter, A., & Richardson, L. R. (1940). Some more Myxosporidia observed in Canadian fishes. *Parasitology*, *32*, 333–353. https://doi.org/10.1017/S0031182000015821

Feist, S. W. (1995). Ultrastructural aspects of *Myxidium gadi* (Georgévitch, 1916) (Myxozoa: Myxosporea) infections in Pollack (*Pollachius pollachius* L.) and Saithe (*P. virens* L.). *European Journal of Protistology*, *31*, 309–317. https://doi.org/10.1016/S0932-4739(11)80095-7

Feist, S. W., & Bucke, D. (1992). *Myxidium gadi* Georgévitch, 1916 infections in Saithe *Pollachius virens* L. from the North Sea. *Bulletin of the European Association of Fish Pathologists*, *12*, 211–214.

Felsenstein, J. (1985). Confidence limits on phylogenies: An approach using the bootstrap. *Evolution; International Journal of Organic Evolution*, *39*, 783–791. https://doi.org/10.2307/2408678

Fiala, I. (2006). The phylogeny of Myxosporea (Myxozoa) based on small subunit ribosomal RNA gene analysis. *International Journal for Parasitology*, *36*, 1521–1534. https://doi.org/10.1016/j.ijpara.2006.06.016

Fiala, I., Hlavničková, M., Kodádková, A., Freeman, M. A., Bartošová-Sojková, P., & Atkinson, S. D. (2015). Evolutionary origin of *Ceratonova shasta* and phylogeny of the marine myxosporean lineage. *Molecular Phylogenetics and Evolution*, *86*, 75–89. https://doi.org/10.1016/j.ympev.2015.03.004

Fitch, W. (1977). On the problem of discovering the most parsimonious tree. *The American Naturalist*, *111*, 223–257. https://doi.org/10.1086/283157

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, *5*, 673–677. https://doi.org/10.1038/nclimate2647

Froese, R., & Pauly, D. (2023). *FishBase: World wide web electronic publication*. http://www.fishbase.org

Georgévitch, J. (1916). Note sur les myxosporidies des poissons de la baie de Vilefranche et de Monaco. *Bulletin de l'Institut Océanographique de Monaco*, *322*, 1–7.

Guindon, S., & Gascuel, O. (2003). A simple, fast and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology*, *52*, 696–704. https://doi.org/10.1080/10635150390235520

Gunter, N. L., & Adlard, R. D. (2008). Bivalvulidan (Myxozoa: Myxosporea) parasites of damselfishes with description of twelve novel species from Australia's Great Barrier Reef. *Parasitology*, *135*, 1165–1178. https://doi.org/10.1017/S0031182008004733

Gunter, N., & Adlard, R. (2010). The demise of *Leptotheca* Thélohan, 1895 (Myxozoa: Myxosporea: Ceratomyxidae) and assignment of its species to *Ceratomyxa* Thélohan, 1892 (Myxosporea: Ceratomyxidae), *Ellipsomyxa* Køie, 2003 (Myxosporea: Ceratomyxidae), *Myxobolus* Bütschli, 1882 and *Sphaerospora* Thélohan, 1892 (Myxosporea: Sphaerosporidae). *Systematic Parasitology*, *75*, 81–104. https://doi.org/10.1007/s11230-009-9227-1

Gürkanlı, C. T., Okkay, S., Çiftci, Y., & Özer, A. (2022). Molecular and morphological description of *Myxidium parvum* (Cnidaria) from *Salaria pavo* (Blenniidae) in the Black Sea. *Parasitology International*, *87*, Article 102520. https://doi.org/10.1016/j.parint.2021.102520

Gürkanlı, C. T., Okkay, S., Çiftci, Y., Yurakhno, V., & Özer, A. (2018). Morphology and molecular phylogeny of *Ortholinea mullusi* sp. nov. (Myxozoa) in *Mullus barbatus* from the Black Sea. *Diseases of Aquatic Organisms*, *127*, 117–124. https://doi.org/10.3354/dao03192

Hall, T. A. (1999). BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, *41*, 95–98.

Heiniger, H., & Adlard, R. D. (2014). Relatedness of novel species of *Myxidium* Bütschli, 1882, *Zschokkella* Auerbach, 1910 and *Ellipsomyxa* Køie, 2003 (Myxosporea: Bivalvulida) from the gall bladders of marine fishes (Teleostei) from Australian waters. *Systematic Parasitology*, *87*, 47–72. https://doi.org/10.1007/s11230-013-9454-3

Heiniger, H., Gunter, N. L., & Adlard, R. D. (2011). Re-establishment of the family Coccomyxidae and description of five novel species of *Auerbachia* and *Coccomyxa* (Myxosporea: Bivalvulida) parasites from Australian fishes. *Parasitology*, *138*, 501–515. https://doi.org/10.1017/S0031182010001447

Holzer, A. S., Blasco-Costa, I., Sarabeev, V. L., Ovcharenko, M. O., & Balbuena, J. A. (2006). *Kudoa trifolia* sp. n.—Molecular phylogeny suggests a new spore morphology and unusual tissue location for a well-known genus. *Journal of Fish Diseases*, *29*, 743–755. https://doi.org/10.1111/j.1365-2761.2006.00770.x

Holzer, A., Sommerville, C., & Wootten, R. (2004). Molecular relationships and phylogeny in a community of myxosporeans and actinosporeans based on their 18S rDNA sequences. *International Journal for Parasitology*, *34*, 1099–1111. https://doi.org/10.1016/j.ijpara.2004.06.002

Jameson, P. (1929). Myxosporidia from Californian fishes. *Journal of Parasitology*, *16*, 59–68. https://doi.org/10.2307/3271910

Jiménez-Guri, E., Okamura, B., & Holland, P. W. (2007). Origin and evolution of a myxozoan worm. *Integrative and Comparative Biology*, *47*, 752–758. https://doi.org/10.1093/icb/icm026

Kalatzis, P. G., Kokkari, C., & Katharios, P. (2013). Description and relationships of two novel species of *Ceratomyxa* Thélohan, 1892 infecting the gallbladders of Aulopiformes: Atlantic Lizardfish *Synodus saurus* Linnaeus, 1758 and Royal Flagfin *Aulopus filamentosus* Bloch, 1792 from Cretan Sea, Greece. *Parasitology Research*, *112*, 2055–2061. https://doi.org/10.1007/s00436-013-3366-7

Kalavati, C., & MacKenzie, K. (1999). The genera *Ceratomyxa* Thélohan, 1892, *Leptotheca* Thélohan, 1895 and *Sphaeromyxa* Thélohan, 1892 (Myxosporea: Bivalvulida) in gadid fish of the northeast Atlantic. *Systematic Parasitology*, *43*, 209–216. https://doi.org/10.1023/A:1006144721096

Karlsbakk, E., & Køie, M. (2012). The marine myxosporean *Sigmomyxa sphaerica* (Thélohan, 1895) gen. n., comb. n. (syn. *Myxidium*

sphaericum) from Garfish (*Belone belone* (L.)) uses the polychaete *Nereis pelagica* L. as invertebrate host. *Parasitology Research*, *110*, 211–218. https://doi.org/10.1007/s00436-011-2471-8

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P., & Drummond, A. (2012). Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, *28*, 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Kennedy, J. J., Rayner, N. A., Atkinson, C. P., & Killick, R. E. (2019). An ensemble data set of sea surface temperature change from 1850: The Met Office Hadley Centre HadSST.4.0.0.0 data set. *Journal of Geophysical Research: Atmospheres*, *124*, 7719–7763. https://doi.org/10.1029/2018JD029867

Khan, R. A., Bowering, W. R., Burgeois, C., Lear, H., & Pippy, J. H. (1986). Myxosporean parasites of marine fish from the continental shelf off Newfoundland and Labrador. *Canadian Journal of Zoology*, *64*, 2218–2226. https://doi.org/10.1139/z86-336

Kodádková, A., Dyková, I., Tyml, T., Ditrich, O., & Fiala, I. (2014). Myxozoa in high Arctic: Survey on the central part of Svalbard Archipelago. *International Journal for Parasitology: Parasites and Wildlife*, *3*, 41–56. https://doi.org/10.1016/j.ijppaw.2014.02.001

Køie, M., & Karlsbakk, E. (2009). *Ellipsomyxa syngnathi* sp. n. (Myxozoa, Myxosporea) in the pipefish *Syngnathus typhle* and *S. rostellatus* (Teleostei, Syngnathidae) from Denmark. *Parasitology Research*, *105*, 1611–1616. https://doi.org/10.1007/s00436-009-1598-3

Køie, M., Karlsbakk, E., & Nylund, A. (2008). The marine herring myxozoan *Ceratomyxa auerbachi* (Myxozoa: Ceratomyxidae) uses *Chone infundibuliformis* (Annelida: Polychaeta: Sabellidae) as invertebrate host. *Folia Parasitologica*, *55*, 100–104. https://doi.org/10.14411/fp.2008.013

Køie, M., Whipps, C. M., & Kent, M. L. (2004). *Ellipsomyxa gobii* (Myxozoa: Ceratomyxidae) in the Common Goby *Pomatoschistus microps* (Teleostei: Gobiidae) uses *Nereis* spp. (Annelida: Polychaeta) as invertebrate hosts. *Folia Parasitologica*, *51*, 14–18. https://doi.org/10.14411/fp.2004.002

Kumar, S., Stecher, G., Li, M., Knyaz, C., & Tamura, K. (2018). MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution*, *35*, 1547–1549. https://doi.org/10.1093/molbev/msy096

Laamiri, S. (2014). New observations on Myxozoa of the Goldline Sea Bream *Sarpa salpa* L. 1758 (Teleostei: Sparidae) from the Mediterranean coast of Tunisia. *Zootaxa*, *3887*, 157–190. https://doi.org/10.11646/zootaxa.3887.2.3

Lom, J., & Dyková, I. (1992). *Protozoan parasites of fishes*. Elsevier.

Lubat, V., Radujkovic, B., Marques, A., & Bouix, G. (1989). Parasites des poissons marins du Montenegro: Myxosporidies. *Acta Adriatica*, *30*, 31–50.

MacKenzie, K., Collins, C., Chaganti, K., & Hemmingsen, W. (2010). *Myxidium finnmarchicum* n. sp. (Myxosporea: Myxidiidae) from the gall bladder of Whiting *Merlangius merlangus* (L.) (Pisces: Teleostei) in north Norway. *Zootaxa*, *2673*, 56–64. https://doi.org/10.11646/zootaxa.2673.1.3

MacKenzie, K., & Kalavati, C. (1995). Species in the genus *Myxidium* Bütschli, 1882 (Myxosporea: Bivalvulida) parasitizing the gall bladders of gadid fish in the northeast Atlantic. *Journal of Natural History*, *29*, 851–863. https://doi.org/10.1080/00222939500770291

Mansour, L., Abdel-Baki, A. A., Al-Qahtani, H. A., & Al-Quraishy, S. (2015). Morphological and molecular aspects of *Ceratomyxa mehlhorni* n. sp., a parasite of the Golden Trevally *Gnathanodon speciosus* in the Arabian Gulf off the Saudi Arabian coast, with data on its seasonal prevalence. *Parasitology Research*, *114*, 3783–3789. https://doi.org/10.1007/s00436-015-4608-7

Mansour, L., Thabet, A., Al-Tamimi, J., Nahdi, S., Alomar, S., & Abdel-Baki, A. S. (2022). Morphological redescription and phylogenetical position of *Ceratomyxa truncata* Thélohan (1895) and *Coccomyxa morovi* Léger and Hesse, 1907 (Myxozoa: Myxosporea) infecting the gall bladder of *Sardina pilchardus* (Walbaum) from Tunisian coast. *Acta Parasitologica*, *67*, 288–297. https://doi.org/10.1007/s11686-021-00462-9

Markiw, M. E. (1992). Experimentally induced whirling disease II: Determination of longevity of the infective triactinomyxon stage of *Myxobolus cerebralis* by vital staining. *Journal of Aquatic Animal Health*, *4*, 44–47. https://doi.org/10.1577/1548-8667(1992) 0042.3.CO;2

Markiw, M., & Wolf, K. (1983). *Myxosoma cerebralis* (Myxozoa: Myxosporea) etiologic agent of salmonid whirling disease requires tubificid worm (Annelida: Oligochaete) in its life cycle. *The Journal of Protozoology*, *30*, 561–564. https://doi.org/10.1111/j.1550-7408.1983.tb01422.x

Miller, T., Barnett, S., Seymour, J., Jenkins, T., McNamara, M., & Adlard, R. D. (2018). Biliary tract-infecting myxosporeans from estuarine and reef stonefish (Scorpaeniformes: Synanceiidae) off eastern Australia, with descriptions of *Sphaeromyxa horrida* n. sp. and *Myxidium lapipiscis* n. sp. (Myxosporea: Bivalvulida). *Journal of Parasitology*, *104*, 254–261. https://doi.org/10.1645/17-79

Okamura, B., Gruhl, A., & Bartholomew, J. L. (2015). *An introduction to Myxozoan evolution, ecology and development*. Springer.

Okkay, S., Gürkanlı, C. T., Çiftci, Y., Yurakhno, V., & Özer, A. (2020). Morphological and molecular descriptions of *Sphaeromyxa sevastopoli* (Cnidaria) from host fishes from Sinop on the Black Sea coast. *Parasitology Research*, *119*, 2463–2471. https://doi.org/10.1007/s00436-020-06740-1

Okkay, S., & Özer, A. (2018). Myxozoan parasites of some teleost fishes in the Black Sea. In A. Y. Sönmez, S. Bilen, E. Terzi, & A. E. Kadak (Eds.), *International congress on engineering and life science, proceeding book* (pp. 80–82). Kastamonu University.

Özer, A. (2021). *Checklist of marine, freshwater, and aquarium fish parasites in Turkey*. Turkish Marine Research Foundation.

Özer, A., Gürkanlı, C. T., Okkay, S., Çiftci, Y., & Yurakhno, V. (2022). Molecular and morphological description of *Ceratomyxa scophthalmi* sp. nov. (Cnidaria, Myxozoa) infecting *Scophthalmus maeoticus* and first report of *Myxidium finnmarchicum* in the Black Sea. *Diseases of Aquatic Organisms*, *151*, 85–96. https://doi.org/10.3354/dao03693

Özer, A., Kornyychuk, Y. M., Öztürk, T., & Yurakhno, V. (2015). Comparative study on parasite fauna of the Whiting *Merlangius merlangus* in the northern and southern zones of the Black Sea. *Turkish Journal of Fisheries and Aquatic Sciences*, *15*, 285–294. https://doi.org/10.4194/1303-2712-v15_2_10

Özer, A., & Wootten, R. (2002). Biological characteristics of some actinosporeans. *Journal of Natural History*, *36*, 2199–2209. https://doi.org/10.1080/00222930110089175

Özer, A., Yurakhno, V., Öztürk, T., & Kornyychuk, Y. M. (2017). Myxosporean parasites of *Ceratomyxa merlangi* and *Myxidium gadi* in Whiting *Merlangius merlangus*: A comparative epizootiological analysis based on samples from two localities off southern and northern coasts of the Black Sea. *Parasitology Research*, *116*, 2463–2469. https://doi.org/10.1007/s00436-017-5550-7

Özkan, H. (2015). *Determination of the myxozoan parasite fauna of some fishes inhabiting the Black Sea* [Master's thesis, Sinop University]. (In Turkish.)

Palenzuela, O., Redondo, M. J., & Alvarez-Pellitero, P. (2002). Description of *Enteromyxum scophthalmi* gen. nov., sp. nov. (Myxozoa), an intestinal parasite of Turbot (*Scophthalmus maximus* L.) using morphological and ribosomal RNA sequence data. *Parasitology*, *124*, 369–379. https://doi.org/10.1017/s0031182001001354

Parisi, B. (1912). Primo contributo alla distribuzione geografica dei Missosporidi in Italia. *Atti Della Societa Italiana di Scienze Naturali Milano*, *50*, 283–299.

Petrushevskii, G. K. (1932). Zur systemafik und cytologie der Myxosporidia aus einigen fischen des Weissen Meeres. *Archiv fur Protistenkunde*, *78*, 543–556.

Polyanskii, Y. I. (1966). *Parasites of the fish of the Barents Sea*. Israel Program for Scientific Translations.

Posada, D. (2008). jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, *25*, 1253–1256. https://doi.org/10.1093/molbev/msn083

Redondo, M. J., Palenzuela, O., Riaza, A., Macías, Á., & Álvarez-Pelliterro, P. (2002). Experimental transmission of *Enteromyxum*

scophthalmi (Myxozoa), an enteric parasite of turbot *Scophthalmus maximus*. *Journal of Parasitology*, *88*, 482–488. https://doi.org/10.1645/0022-3395(2002)088[0482:ETOESM]2.0.CO;2

Reiczigel, J., & Rózsa, L. (2020). *Quantitative Parasitology (QPweb)* [Computer software]. https://www2.univet.hu/qpweb/qp10/index.php

Rocha, S., Alves, Â., Antunes, C., Azevedo, C., & Casal, G. (2019). Molecular data infers the involvement of a marine aurantiactinomyxon in the life cycle of the myxosporean parasite *Paramyxidium giardi* (Cnidaria, Myxozoa). *Parasitology*, *146*, 1555–1563. https://doi.org/10.1017/S0031182019000866

Rocha, S., Casal, G., Matos, P., Matos, E., Dkhıl, M., & Azevedo, C. (2011). Description of *Triangulamyxa psittaca* sp. nov. (Myxozoa: Myxosporea), a new parasite in the urinary bladder of *Colomesus psittacus* (Teleostei) from the Amazon River, with emphasis on the ultrastructure of plasmodial stages. *Acta Protozoologica*, *50*, 327–338. https://doi.org/10.4467/16890027AP.11.030.0067

Rocha, S., Rangel, L. F., Casal, G., Azevedo, C., Rodrigues, P., & Santos, M. J. (2020). Involvement of sphaeractinomyxon in the life cycle of mugiliform-infecting *Myxobolus* (Cnidaria, Myxosporea) reveals high functionality of actinospore morphotype in promoting transmission. *Parasitology*, *147*, 1320–1329. https://doi.org/10.1017/S0031182020001043

Rutterford, L. A., Simpson, S. D., Bogstad, B., Devine, J. A., & Genner, M. J. (2023). Sea temperature is the primary driver of recent and predicted fish community structure across northeast Atlantic shelf seas. *Global Change Biology*, *29*, 2510–2521. https://doi.org/10.1111/gcb.16633

Saitou, N., & Nei, M. (1987). The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution*, *4*, 406–425. https://doi.org/10.1093/oxfordjournals.molbev.a040454

Şalcıoğlu, A., Gubili, C., Krey, G., Sönmez, Y. A., & Bilgin, R. (2020). Phylogeography and population dynamics of the eastern Mediterranean Whiting (*Merlangius merlangus*) from the Black Sea, the Turkish Straits system, and the North Aegean Sea. *Fisheries Research*, *229*, Article 105614. https://doi.org/10.1016/j.fishres.2020.105614

Shulman, S. S., & Shulman-Albova, R. E. (1953). *Parasites of the White Sea fishes*. Izdatelstvo Akademia Nauk SSSR.

Skuratovskaya, E. N., Yurakhno, V. M., & Zavyalov, A. V. (2013). The influence of parasitic infection on the Black Sea Whiting *Merlangius merlangus euxinus* (Gadidae) morphophysiological and biochemical parameters. *Vestnik Zoologii*, *47*, 309–317. https://doi.org/10.2478/vzoo-2013-0032

Swofford, D. L. (1998). *PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4 beta 10*. Sinauer Associates.

Székely, C., Borkhanuddin, M. H., Cech, G., Kelemen, O., & Molnar, K. (2014). Life cycles of three *Myxobolus* spp. from cyprinid fishes of Lake Balaton, Hungary involve triactinomyxon-type actinospores. *Parasitology Research*, *113*, 2817–2825. https://doi.org/10.1007/s00436-014-3942-5

Thélohan, P. (1895). Recherches sur les Myxosporidies. *Bulletin Biologique de la France et de la Belgique*, *5*, 100–394.

Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F., & Higgins, D. G. (1997). The ClustalX–Windows interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, *25*, 4876–4882. https://doi.org/10.1093/nar/25.24.4876

TÜİK. (2021). *Fishery production statistics*. https://biruni.tuik.gov.tr/medas/?kn=97&locale=tr

TÜİK. (2022). *TÜİK news bulletin 45745*. https://data.tuik.gov.tr/Bulten/Index?p=Su-Urunleri-2021-45745

Whipps, C. M., Adlard, R. D., Bryant, M. S., Lester, R. J., Findlay, V., & Kent, M. L. (2003). First report of three *Kudoa* species from eastern Australia: *Kudoa thyrsites* from Mahi Mahi (*Coryphaena hippurus*), *Kudoa amamiensis* and *Kudoa minithyrsites* n. sp. from Sweeper (*Pempheris ypsilychnus*). *The Journal of Eukaryotic Microbiology*, *50*, 215–219. https://doi.org/10.1111/j.1550-7408.2003.tb00120.x

Whipps, C. M., Grossel, G., Adlard, R. D., Yokoyama, H., Bryant, M. S., Munday, B. L., & Kent, M. L. (2004). Phylogeny of the Multivalvulidae (Myxozoa: Myxosporea) based on comparative ribosomal DNA sequence analysis. *Journal of Parasitology*, *90*, 618–622. https://doi.org/10.1645/GE-153R

Xiao, C., & Desser, S. S. (2000). The longevity of actinosporean spores from oligochaetes of Lake Sasajewun, Algonquin Park, Ontario, and their reaction to fish mucus. *Journal of Parasitology*, *86*, 193–195. https://doi.org/10.1645/0022-3395(2000)086[0193:TLOASF]2.0.CO;2

Yang, C., Huang, Y., Atkinson, S. D., Bartholomew, J. L., Ma, H., & Zhao, Y. (2023). Morphological and genetic analysis of *Ceratomyxa saurida* Zhao *et al.* 2015 and *Ceratomyxa mai* sp. nov. (Myxozoa: Ceratomyxidae) from the East China Sea. *International Journal of Systematic and Evolutionary Microbiology*, *73*, Article 005662. https://doi.org/10.1099/ijsem.0.005662

Yasuda, H., Ooyama, T., Iwata, K., Tun, T., Yokoyama, H., & Ogawa, K. (2002). Fish-to-fish transmission of *Myxidium* spp. (Myxozoa) in cultured Tiger Puffer suffering from emaciation disease. *Fish Pathology*, *37*, 29–33. https://doi.org/10.3147/jsfp.37.29

Yokoyama, H., Ogawa, K., & Wakabayashi, H. (1993). Some biological characteristics of actinosporeans from the oligochaete *Branchiura sowerbyi*. *Diseases of Aquatic Organisms*, *17*, 223–228. https://doi.org/10.3354/dao017223

Yurakhno, V. M. (1987). The myxosporean fauna of the Sevastopol bays fish. *Annotirovanniy spisok dokadov Vsesoyuznoy nauchnoy conferencii molodih uchenih-komsomoltcev, Vklad molodih uchenih-komsomoltcev v resheniye sovremennih problem oceanologii i hydrobiologii, Sevastopol*. (In Russian.)

Yurakhno, V. M. (1994). *Myxosporea of the Black Sea fish: Systematics, fauna, ecology, zoogeography* [Doctoral dissertation]. Sevastopol. (In Russian.)

Yurakhno, V. M. (1988). On fish myxosporeans of Sevastopol bays. III Vsesoyuznaya conferenciya po morskoy biologii (Sevastopol, 1988). *Abstract Kiev*, *2*, 91–92. (In Russian.)

Yurakhno, V. M. (1997). Influence of environmental factors on myxosporean infestation of Black Sea fish in coastal waters. *Oceanological and Hydrobiological Studies*, *1*, 75–85.

Yurakhno, V. M. (2004). The fauna of myxosporeans (Protozoa: Myxosporea) of fishes in the Black Sea and its seasonal and interannual aspects of variability. In C. M. Nigmatullin (Ed.), *Sovremenny je problemy parazitologii, zoologii i ekologii* (pp. 160–171). Kaliningrad State Technical University. (In Russian.)

Yurakhno, V. M. (2008). Peculiarities of the Black Sea Whiting myxosporean infestation depending on its size, age and sexual characteristics in various areas of the Black Sea. *Ekologiya Morya*, *75*, 48–52. (In Russian.)

Yurakhno, V. M. (2009a). The origin of the Black Sea fish myxosporean (Myxozoa, Myxosporea) fauna. *Vestnik Zoologii*, *23*, 199–207. (In Russian.)

Yurakhno, V. M. (2009b). The Black Sea and the Sea of Azov fish diseases induced by myxosporeans (Myxozoa: Myxosporea). *Ekologiya Morya*, *77*, 33–37. (In Russian.)

Yurakhno, V. M. (2010). Prevalence of myxosporeans in the Black Sea fish from the results of two voyages 1988. *Naukovi Zapysky Ternopilskogo Naysionalnogo Pedagogichnogo Universitetu im. V. Gnatyuka. Seriya: Biologiya. Specialniy Vipusk: Hydroecologiya*, *3*, 327–331. (In Russian.)

Yurakhno, V. M. (2013). The nature protection aspect of the Black Sea fish myxosporean studies. *Vestnik Zoologii*, *47*, 62–70. https://doi.org/10.2478/vzoo-2013-0056

Yurakhno, V. M., & Naidenova, N. N. (2000, July 1–7). *On pathogenic effect of* Myxidium gadi *(Cnidospora, Myxosporea) on gall bladder of* Merlangius merlangus euxinus *in the Black Sea* [Paper presentation]. Ecological parasitology on the turn of millennium: International symposium, St. Petersburg, Russia.

Zaika, B. E. (1966). *The fauna of protozoa-parasites of fish of the Black Sea*. Ukrainian Academy of Sciences.