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Biodiversity and Parasitological Characteristics of Myxozoa (Cnidaria) Infecting European Seabass, *Dicentrarchus labrax* (Linnaeus, 1758) In the Aegean Sea Coasts of Türkiye

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Abstract

In this study, diversity and parasitological features of Myxozoan parasites infecting *Dicentrarchus labrax* (Linnaeus, 1758) grown in sea cages located in the coasts of İzmir and Muğla districts of Türkiye were investigated. For this aim, a total of 240 host specimens were examined and 147 of them (61.25%) determined to be infected by Myxozoan parasites. Based on the morphology of the myxospores examined, the presence of one species belonging to the genus *Kudoa* Meglitsch, 1947 and two different species within the genus *Ceratomyxa* Thélohan, 1892 were determined. Depending on phylogenetic relationships obtained from 18S rDNA nucleotide sequence data, *Kudoa* specimens were assigned to *K. dicentrarchi* Sitjà-Bobadilla & Álvarez-Pellitero, 1992 and *Ceratomyxa* species were assigned to *C. diplodae* Lubat, Radujkovic, Marques & Bouix, 1989 and *C. labracis* Sitjà-Bobadilla & Álvarez-Pellitero, 1993.

The *K. dicentrarchi* specimens were found in the gallbladder and gonads of the European seabass with 38.75% prevalence of infection. *Ceratomyxa diplodae* and *C. labracis* were only found in the bile with 37.92% and 2.5% prevalence of infections, respectively.

This study presents the first record of *C. diplodae* and *C. labracis* in *D. labrax* from the Turkish marine environment. Moreover, this research contributes the initial molecular record for *K. dicentrarchi* identified in *D. labrax* from the Turkish coastline.

Introduction

Myxozoa, one of the six classes of the Cnidaria phylum, is composed of aquatic endoparasite species infecting both vertebrates (particularly fish) and invertebrates (Hartigan et al., 2016; Koch & Grimmelikhuijzen, 2020). Currently, more than 2600 myxozoan species have been identified which are classified within 64 genera and 17 families (Fiala et al., 2015a; Li et al., 2023). Although most of the myxozoa species are harmless or minimally damage the host tissues, some species are extremely pathogenic (Okamura et al., 2015; Rocha et al., 2015; Schmidt-Posthaus & Wahli, 2015). For instance, Ceratomyxosis (*Ceratomyxa shasta* Noble, 1950), Whirling disease (*Myxobolus cerebralis* Höfer, 1903) and Enteromyxosis (*Enteromyxum leei* Diamant, Lom & Dykova, 1994 and *E. scophthalmi* Palenzuela, Redondo & Alvarez-Pellitero, 2002) are some of the most important fish diseases caused by myxozoa species (Hallett & Bartholomew, 2012; Sitjà-Bobadilla & Palenzuela, 2012). Moreover, some species including *Kudoa septempunctata* Matsukane, Sato, Tanaka, Kamata & Sugita-Konishi, 2010 causes food poisoning in humans by consuming infected fish raw (Lee, 2017).

Dicentrarchus labrax Linnaeus, 1758 (European seabass), the host fish considered in this study, is the most economically important farmed fish species in Türkiye with approximately 157 000 tons of annual production. The fish farms in the Aegean Sea compass approximately 94% of this annual production (Çöteli, 2022; TUIK 2023). Moreover, Türkiye is the largest producer of European seabass with 52.21% of global output (Özden et al., 2024). So far, eight myxozoa species have been reported infecting various organs and tissues including seminal fluid, gallbladder, intestine, kidney, gonads, spleen, liver, pancreas and urinary system of the European seabass. These species are, *Sphaerospora testicularis*, *Ceratomyxa diplodae*, *C. labracis*, *Enteromyxum leei*, *Kudoa iwatai*, *K. dicentrarchi*, *Ortholinea labracis* (Egusa & Shiomitsu, 1983; Lubat et al., 1989; Sitjà-Bobadilla & Álvarez-Pellitero, 1990; Sitjà-Bobadilla & Álvarez-Pellitero, 1992; Sitjá-Bobadilla & Álvarez-Pellitero, 1993a; Diamant et al., 1994; Rangel et al., 2017; Birincioğlu et al., 2023)

From Türkiye, mostly from fishes inhabiting off the Black Sea, 30 myxozoa taxa (23 binomial species and 7 in genus level) have been reported so far (Özer, 2020). These species belong to the following genera; *Kudoa* Meglitsch, 1947 (3 species), *Ortholinea* Shulman, 1962 (4 species), *Ceratomyxa* Thélohan, 1892 (5 species), *Henneguya* Thélohan, 1892 (1 species), *Myxobolus* Bütschli, 1882 (7 species), *Sphaeromyxa* Thélohan, 1892 (1 species) and *Myxidium* Bütschli, 1882 (2 species) (Özer, 2020). Out of these species, only three were from the Aegean Sea waters off the Turkish coast: *Kudoa dicentrarchi* and *Ceratomyxa* sp., isolated from European seabass, and *Myxobolus exiguus* Thélohan, 1895, extracted from *Mugil cephalus* (Altunel, 1983; Özer & Öztürk, 2011; Birincioğlu et al., 2023).

Despite the significant importance of European seabass production in the Aegean Sea for Türkiye and the world, there is notable deficiency in data regarding the myxozoan fauna infecting this fish species. The main goal of this study is to complete this deficiency. To accomplish this aim, we focused on the İzmir and Muğla districts which are the most intense locations in the meaning of aquaculture activities in the Aegean Sea, and examined European seabass specimens from fish farms in these two locations for myxozoan infections using both conventional (morphological) and molecular phylogenetic approaches.

Materials & Methods

Sample Collection and Parasitological Investigations

European seabass specimens measuring 28-39 cm in total body length and 280-600 gr in weight were collected from local fish farms located on the coastline of Muğla (37°01’49”N, 28°30’23”E) and İzmir (38°25’60’’N, 27°9’0’’E) provinces. From each of the two locations, 10 fish samples were collected monthly (a total of 240 fish samples) between July 2019 and June 2020. Parasitological investigations were conducted on fin, gallbladder, bile, gill, gonad, intestine, kidney, liver, skin, muscle tissues and urinary bladder samples from the collected fish using a Nikon Eclipse 80i (Nikon Instruments Inc., Japan) microscope equipped with a digital camera Nikon DS-Fi 1 (DP50). For microscopic examination, each organ sample was carefully separated and placed between microscope slides. Additionally, no staining method was applied to the preparations. Measurements were conducted on at least 30 fresh spores and were evaluated according to Lom & Arthur (1989), Lom & Dyková (1992), Bush et al. (1997), Heiniger et al. (2008) and Yurakhno & Ovcharenko (2014).

Molecular and Phylogenetic Analyses

From each morpho-type determined, representative myxozoa specimens were selected considering sampling locality and season, for molecular analyses. Total genomic DNA isolations from myxozoan infected tissues were performed using a PureLink® Genomic DNA kit (Invitrogen, USA) according to the manufacturer’s instructions. Primer set MyxospecF (Fiala, 2006) / 18R (Whipps et al., 2003) was used for amplification of small subunit ribosomal DNA (18S rDNA here after) locus which is the most common genetic marker used for the identification of myxozoan isolates. Amplifications were performed with a Techne (TC-Plus, Staffordshire, UK) thermal cycler using the PCR mixture and condition explained in Okkay et al. (2018) and Okkay et al. (2021), respectively. Both the genomic DNA and the PCR products were electrophoresed on 1% agarose gels which were prepared in 1X TBE buffer. Visualization of the ethidium bromide-stained gels was performed using the Photo-print imaging system (Vilber Lourmat, France). Nucleotide sequencings of amplified 18S rDNA fragments were performed commercially by Macrogen-Europe BV (Amsterdam, The Netherlands) using the same primer set mentioned earlier.

The sequences from both strands were assembled using the program BioEdit (Hall, 1999). Data sets for phylogenetic analyses were conducted according to BLAST (Basic Local Alignment Search Tool - https://blast.ncbi.nlm.nih.gov/Blast.cgi) results and available literature (Supplementary Table 1 and Supplementary Table 2). ClustalX (Thompson et al., 1997) was used to align the homolog bases of genotypes in the data sets. Akaike information criterion (AIC / Akaike, 1974) and Bayesian information criterion (BIC) tests were applied using jModelTest v. 0.1 software to determine the best fitting substitution model(s) to the data sets (Guindon & Gascuel, 2003; Posada, 2008). Maximum-likelihood (ML), Neighbor-Joining (NJ / Saitou & Nei, 1987) and Maximum-Parsimony (MP / Eck & Dayhoff, 1966; Fitch, 1977) algorithms were used for phylogenetic reconstructions. PhyML 3.0 (Guindon & Gascuel, 2003) was utilized for ML analysis, while PAUP* v. 4.0b10 (Swofford, 1998) was used for NJ and MP

analyses. A heuristic search method utilizing the TBR swapping algorithm with 10 random repeats was carried out for MP analysis. Bootstrap tests (Efron, 1982; Felsenstein, 1985) were conducted with 1000 replicates for MP and ML analyses and 10000 replicates for NJ analyses to determine the robustness of the phylogenetic trees. All new SSU genotypes obtained in this study have been deposited in GenBank under accession numbers PP788707-PP788714 (Supplementary Table 1, 2).

Results

Morphological Identification of Myxozoan Parasites

A total of 240 European seabass specimens that were seasonally obtained from fish farms in two different localities of the Aegean Sea (Muğla and İzmir) were parasitologically investigated for myxozoan infection. As a result, the bile and/or gonads of 147 fish samples were determined to be infected by myxozoan specimens. Initial microscopic observations of the myxospores revealed three distinct morphotypes associated with the genera *Kudoa* (one morphotype identified as *Kudoa* sp.-1) and *Ceratomyxa* (two morphotypes identified as *Ceratomyxa* sp.-1 and *Ceratomyxa* sp.-2) (Figure 1A-C).

Specimens of the *Kudoa* morphotype were observed both in the gallbladder and gonads of European seabasses collected from İzmir and Muğla provinces. Additionally, no cyst-like formations were observed in the tissues infected *Kudoa* specimes. The spores of this parasite exhibit a pear-like spherical shape with two identical valves. Additionally, two pyriform, spherical and nearly equally sized polar capsules were observed in all specimens. Moreover, the parasite sporoplasm covers almost the entire parasite (Figure 1A). The basic morphometric measurements of myxospores including average, standart deviation, minimum and maximum values, were as follows; 5.52±0.51 (4.41-6.48) µm in spore length, 5.30±0.60 (4.19-6.71) µm in spore thickness, 1.65±0.37 (1.14-2.69) µm in polar capsule length and 1.55±0.36 (0.94-2.36) µm in polar capsule width (Table 1). According to similar myxospore morphologies and morphometries, all *Kudoa* specimens observed were considered as specimens of the same species, *Kudoa* sp.-1.

As mentioned, specimens of the genus *Ceratomyxa* observed in this study revealed two basic morphotypes. Specimens from both of these morphotypes were observed scattered in the bile of the European seabasses obtained from both localities. The myxospores of the first *Ceratomyxa* morphotype were observed as curled in the shape of a crescent and containing two polar capsules. The polar capsules were round in shape and located close to each other in the middle of the spore. Parasite sporoplasm was observed to cover almost the entire parasite (Figure 1B). The basic morphometric measurements of this morphotype including average, standart deviation, minimum and maximum values were as follows; 6.69±1.49 (3.62-8.88) µm in spore length, 22.00±5 (9.83-27.97) µm in spore thickness, 1.60±0.3 (0.94-2.69) µm in polar capsule length and 1.60±0.4 (1.02-4.41) µm in polar capsule width (Table 2). According to similar myxospore morphologies and morphometries, specimens of the first *Ceratomyxa* morphotype were considered as specimens of the same species, *Ceratomyxa* sp.-1.

Specimens of the second *Ceratomyxa* morphotype, however were determined only from 6 fish samples. Myxospores of this morphotype were curved shaped and had two spherical polar capsules in the middle that were roughly the same sized. But different from the first morphotype, tail-like valve extensions excisted on both

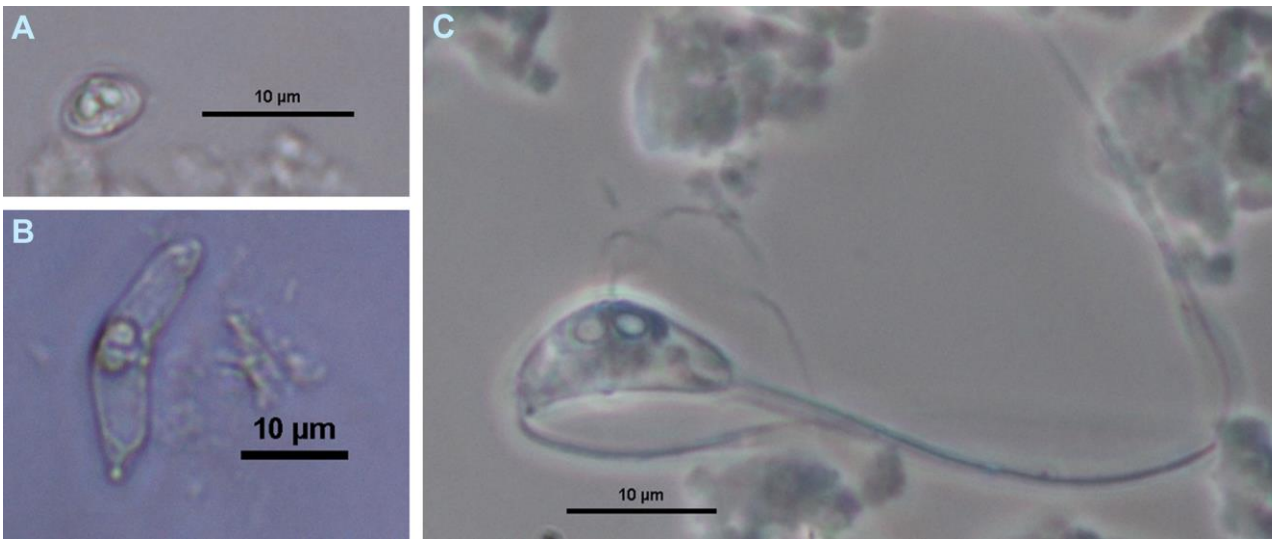

Figure 1 Light microscope image of; **A)** Sutural view of *Kudoa dicentrarchi* (*Kudoa* sp.-1); **B)** Sutural view of *Ceratomyxa diplodae* (*Ceratomyxa* sp.-1); **C)** Sutural view of *Ceratomyxa labracis* (*Ceratomyxa* sp.-2).

Table 1. Comparison of source informations and descriptive characteristics of *Kudoa dicentrarchi* specimens obtained in this study with those given in existing literature.

Species	Host	Locality	Spore Lenght (µm)	Spore Width (µm)	Spore Thickness (µm)	PolarCapsule Length (µm)	PolarCapsule Width (µm)	Site of Infections	Infection Prevalence %	Source
***Kudoa* sp.-1**	*D. labrax*	Türkiye	5.52±0.51	-	5.30±0.60	1.65±0.37	1.55±0.36	Gallbladder / Gonads	38.75	**This study**
(*K. dicentrarchi*)			(4.41-6.48)		(4.19-6.71)	(1.14-2.69)	(0.94-2.36)			
K. dicentrarchi	*D. labrax*	Spain	4.5±0.51	3.9±0.22	5.30±0.48	1.78±0.3	1.4±0.29	Gut / Gallbladder /	52.2	Sitjà-Bobadilla &
			(3.5-6)	(3.5-4.0)	(4.6-8)	(1-2.6)	(0.7-2)	Kidney		Álvarez-Pellitero (1992)
K. dicentrarchi	*D. labrax*	Portugal	4.9±0.2	3.4±0.2	5.3±0.3	1.8±0.2	1.3±0.1	-	-	Rangel et al. (2016)
			(4.5-5.4)	(3.1-3.6)	(4.9-5.8)	(1.4-2.1)	(1.1-1.5)			

Table 2. Comparison of source informations and descriptive characteristics of *Ceratomyxa diplodae* and *C. labracis* specimens obtained in this study with those given in existing literature.

Species	Host	Locality	Spore Lenght (µm)	Spore Thickness (µm)	Polar Capsule Length (µm)	Polar Capsule Width (µm)	Valve Extension	Site of Infections	Infection Prevalence (%)	Source
***Ceratomyxa* sp.-1**	*D. labrax*	Türkiye	6.69±1.49	22.00±5	1.6±0.3	1.6±0.4	-	Bile	37.92	**This study**
(*C. diplodae*)			(3.62-8.88)	(9.83-27.97)	(0.94-2.69)	(1.02-4.41)				
C. diplodae	*Diplodus annularis*	Montenegro	6.0 (5.0-7.0)	20.0 (18.0–22.0)	2.2	2.0	-	Gallbladder	-	Lubat et al. (1989)
C. diplodae	*D. labrax*	Spain	6.2±0.4 (5.0–7.5)	20.9±2.8 (17.0–27.0)	3.0±0.3 (2.5–3.8)	2.8±0.4 (2.0–3.8)	-	Gallbladder	-	Sitjà-Bobadilla and Álvarez-Pellitero (1993a)
C. diplodae	*Diplodus puntazzo*	Greece	6.6 ± 0.5	24.0 ± 0.8	2.7 ± 0.2	2.7 ± 0.2	-	Gallbladder	100	Katharios et al. (2007)
C. diplodae	*D. labrax*	Portugal	5.7 ± 0.5 (4.8–6.7)	20.0±2.5 (16.3–24.0)	2.9±0.3 (2.5–3.4)	2.9±0.3 (2.5–3.4)	-	Gallbladder	7.1	Rocha et al. (2016)
***Ceratomyxa* sp.-2**	*D. labrax*	Türkiye	6.67±0.9	15.70±2.37	2.40±0.46	2.41±0.5	61.19±11	Bile	2.5	**This study**
(*C. labracis*)			(5.65-9.42)	(13.37-22.97)	(1.80-3.59)	(1.57-3.93)	(33-80)			
C. labracis	*D. labrax*	Spain	6.2±0.4 (5-8)	12.4±1.5 (10-15)	3.1±0.6 (2-4)	2.7±0.5 (2-3.5)	66.1±20.6 (30-120)	Bile and Gallbladder	-	Sitjá-Bobadilla and Álvarez-Pellitero (1993a)

sides of the spores (Figure 1C). The basic morphometric measurements of this morpho-type covering average, standart deviation, minimum and maximum values were as follows; 6.67±0.9 (5.65-9.42) µm in spore length, 15.70±2.37 (13.37-22.97) µm in spore thickness, 2.40±0.46 (1.80-3.59) µm in polar capsule length, 2.41±0.5 (1.57-3.93) µm in polar capsule width and 61.19±11 (33-80) µm in valve extension (Table 2). Accordingly specimens of this *Ceratomyxa* morphotype were considered as in the same species, *Ceratomyxa* sp.-2.

Molecular Phylogenetic Analyses

From each morphotype, following myxozoan specimens were selected for molecular identifications; DAIG-1, DTIG-1, DEBG-3, DEIS-3, DTBG-5, DEIG-6 (*Kudoa* sp.-1), DTIS-2, DEBS-4 (*Ceratomyxa* sp.-1) and all six *Ceratomyxa* sp.-2 specimens. Approximately 1330 bp. of 18S rDNA gene was obtained from *Kudoa* sp.-1 and *Ceratomyxa* sp.-1 specimens mentioned above, however, no result was obtained from non of the *Ceratomyxa* sp.-2 specimens.

Among six *Kudoa* sp.-1 specimens, a total of four different 18S rDNA genotypes with nucleotide sequence similarities between 100-99.8% were determined. For all genotypes, the BLAST result suggested *Kudoa dicentrarchi* (KT970638 and KT970639) as the closest species (100-99.85%). Accordingly, a data set that composed of *K. dicentrarchi* and closely related *Kudoa* species was conducted for phylogenetic analyses. To obtain a more accurate tree, some distantly related species to our genotypes that represent the main lineages of the genus *Kudoa* have also been added to the data set (Supplementary Table 1). The aligned data set was 1221 bases long with 293 segregated sites. The AIC and BIC tests suggested GTR+I+G (I: 0.567, G: 0.483) and TPM3uf+I+G (I: 0.571, G: 0.487) substitution models, respectively. MP analysis was performed over 219 synapomorphic characters and revealed 120 most parsimonious trees (786 steps, CI: 0.480916, RI: 0.722449, HI: 0.519084). Because of the higher bootstrap values and topological consistency, the ML and NJ trees that created using GTR+I+G model is preferred in this study. Additionally, the bootstrap values obtained from ML, NJ and MP analyses are given on each related node. On the tree, all *Kudoa* sp.-1 genotypes appeared within the same lineage together with *K. dicentrarchi* genotypes, KT970638 (extracted from *D. labrax* in Portugal) and KT970639 (extracted from *Capitella* sp. in Portugal) (Rangel et al., 2016). More over, specimens DAIG-1, DEIS-3 and DTIG-1, DTBG-5 showed exactly the same 18S rDNA nucleotide sequences with *K. dicentrarchi* genotypes KT970638 and KT970639, respectively (Figure 2). The nucleotide sequence similarities within this lineage were higher than 99.8%. Isolate VMY02 ex. from *Moolgarda cunnesius* in Vietnam (Yurakhno et al., 2022) was the closest species to the lineage mentioned above with nucleotide sequence similarities between 97.8-97.9%. This relationship was supported with 86%, 77% and 59% bootstrap values in ML, NJ and MP trees, respectively. *Kudoa eugerres* was the last species in the lineage and was sister to the lineage mentioned above with 98%, 99% and 99% bootstrap values in ML, NJ and MP trees, respectively (Figure 2).

The representative specimens (DTIS 2 and DEBS 4) for *Ceratomyxa* sp.-1 showed two distinct genotypes with 99.8% nucleotide sequence similarity. BLAST results pointed to *Ceratomyxa diplodae* (KX099691) as the most similar species with nucleotide sequence identities higher than 99.3%. Accordingly, a data set was constructed with 18S rDNA genotypes of *C. diplodae* and allied *Ceratomyxa* species (Supplementary Table 2). The aligned data set was 1170 bp (excluding all gaps) long with 230 segregated sites. The TIM3+I+G (I:0.433, G:0.294) and the TrN+I+G (I:0.428, G:0.288) substitution models were suggested by the AIC and BIC tests, respectively. However, the ML and NJ trees created using the TIM3+I+G model were considered in the study since they had higher bootstrap values than the ones created with the TrN+I+G model. The MP analysis that performed using 166 synapomorphic characters suggested the two most parsimonus trees with 1282 steps (CI: 0.574883, RI: 0.564696, HI: 0.425117). The Figure 3 shows the ML tree that was created using the TIM3+I+G model, and on each node bootstrap values obtained from ML, NJ, and MP analyses were shown.

In all trees created using ML, NJ and MP algorithms, our new genotypes (DEBS-4 and DTIS-2) appeared in the same lineage with; *C. scorpaeni* (MW377576), *Ceratomyxa* sp.-1 LFR-2017 (MF540150), *Ceratomyxa* sp. ex. *Sparus aurata* (JF820292), *Ceratomyxa* sp. 2 ex. *Sparus aurata* (JF820293), *C. sparusaurati* (AF411471), *Ceratomyxa* sp. ex. *Diplodus annularis* (JF820291), *C. puntazi* (JF820290) and *C. diplodae* (KX099691) (Figure 3). Although the phylogentic position of *C. puntazzi* was slightly different at ML, NJ and MP trees, the other relationships were consistent in all trees and were supported with sufficient bootstrap values (>50). Within this lineage, our new genotypes appeared as sisters to *C. diplodae* with nucleotide sequence similarities higher than 99.4%. This relationship was supported with 77% and 51% bootstrap values in the ML and NJ trees, respectively (Figure 3).

As mentioned earlier, we were not able to amplify the 18S rDNA locus from non of the *Ceratomyxa* sp.-2 specimens, thus only morphological and morphometric data are available for them.

Parasitological Characteristics

Kudoa sp.-1 specimens in this study were observed in the gallbladder and gonads of the European seabass specimens that were collected from both İzmir and Muğla districts. The annual infection prevalence of this parasite was calculated as 40% in İzmir samples, reached

its peak in September with a prevalence of 100%, while in Muğla samples it was 37.5%, with a peak at 90% prevalence in August. Additionally, the total infection prevalence averaged at 38.75%. In general, the infection prevalence of *Kudoa* sp.-1 increased with the begining of summer and reached its highest levels in August and September. However, little to no infections were observed in most winter and early spring fish samples (Figure 4, Supplementary Table 3).

The second parasite, *Ceratomyxa* sp.-1, defined in this study observed only in the bile of the host fishes collected from both locations. However, the infection periods with *Ceratomyxa* sp.-1 specimens differed significantly between the two locations. In İzmir fish samples, infection with *Ceratomyxa* sp.-1 specimens were determined during winter, spring and summer (except for june), with a fluctuating prevalence of infection. Remarkably, peaks in infection rates were noted in January and September, reaching prevalences of 70% and no infections were observed during fall period (September-November). Additionally, the annual infection prevalence was calculated as 28.3%. Conversely, in Muğla fish samples, infections with this parasite occurred throughout the year (except for July), with peaks observed in September and October, reaching prevalences of 90%. And the annual infection prevalence was calculated as 47.5% (Figure 4, Supplementary Table 3).

Specimens of *Ceratomyxa* sp.-2, on the other hand were, observed in the bile of only six European seabass individuals collected from both locations. The annual infection prevalence of this parasite was calculated as 0.8% in İzmir samples, with a single fish showing infection in April, corresponding to a prevalence of 10%.

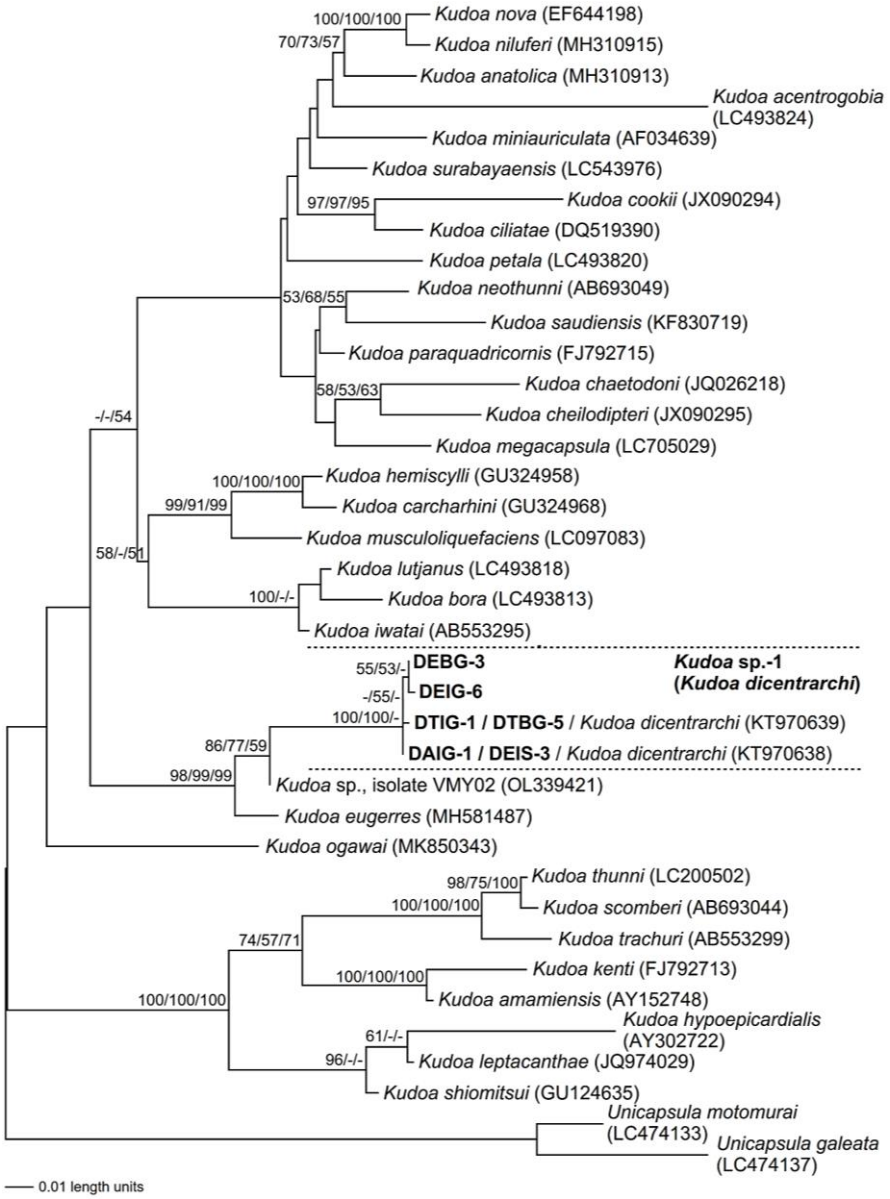

Figure 2. ML tree showing the phylogenetic relationships of new *Kudoa* 18S rDNA genotypes obtained in this study **(stated in bold)** and genotypes of different *Kudoa* species (obtained from GenBank, see Supp. Table 1) representing main lineages of the genus *Kudoa*. The tree was rooted with *Unicapsula motomurai*, *U. galeata* and the bootstrap values (≥50%) obtained from ML, NJ and MP analyses were stated on each related node with the given order.

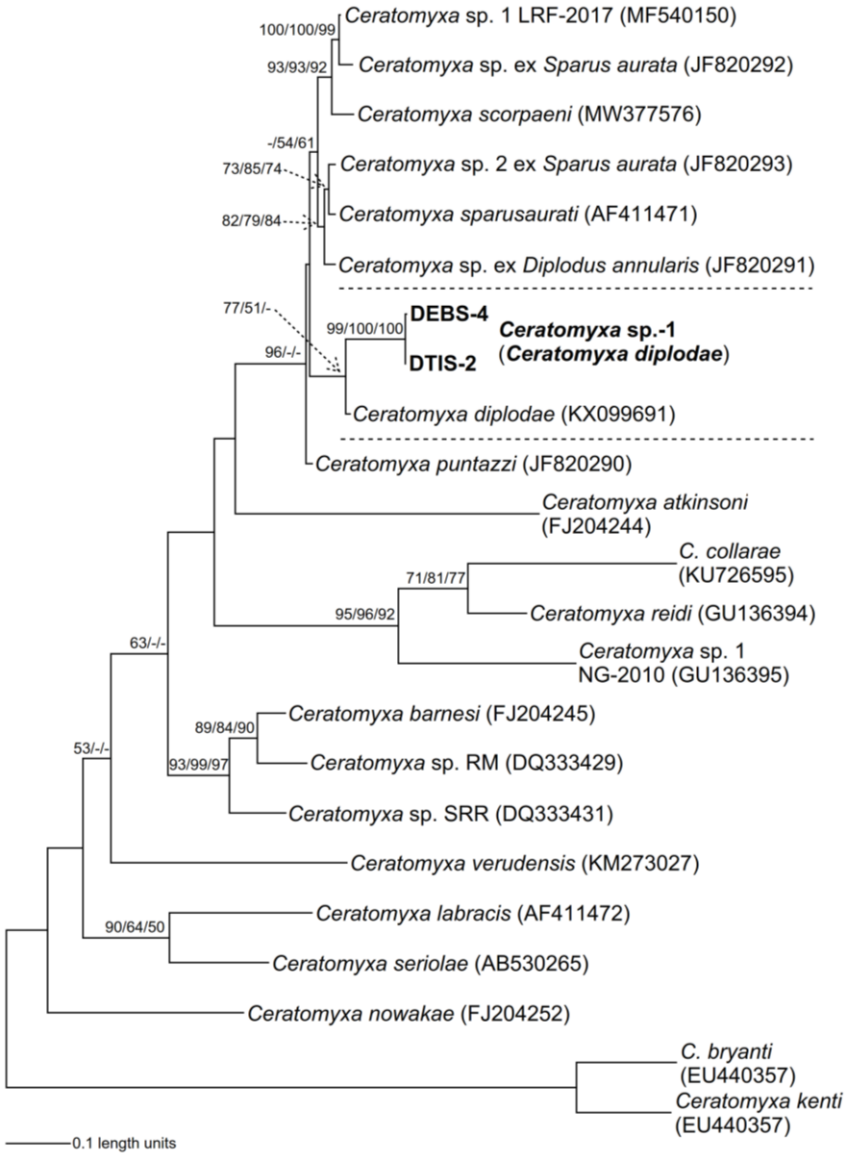

Figure 3. ML tree depending on 18S rDNA nucleotide sequences. *Ceratomyxa* sp.-1 18S rDNA genotypes obtained in this study are **stated in bold**. And the 18S rDNA genotypes of related *Ceratomyxa* species obtained from GenBank have given with the GenBank accession numbers (Supp. Table 2). The tree was rooted using *Ceratomyxa bryanti* and *C. kenti*. The bootstrap values (≥50%) obtained from ML, NJ and MP analyses were stated on each related node with the given order.

In Muğla samples, it was 4.2%, with peaks of 20% prevalence observed in February and May. The total annual infection prevalence, however, stood at 2.5%. The infections were observed in winter and spring fish samples, with no infection determined during summer and fall periods (Figure 4, Supplementary Table 3).

Discussion

In this study, the biological diversity and parasitological characteristics of myxozoan parasite species infecting *Dicentrarchus labrax* (Linnaeus, 1758) (European seabass), one of the most commonly produced fish in the Aegean Sea region of Türkiye, were investigated. Samples were collected from Muğla and İzmir provinces which are the most significant localities in the meaning of aquaculture activities. A total of 240 European seabass individuals were examined and 147 of them were found to be infected with myxozoan parasites. Initial microscopic examinations showed that these parasites are belonging to one *Kudoa* (*Kudoa* sp.-1) and two different *Ceratomyxa* (*Ceratomyxa* sp.-1 and *Ceratomyxa* sp.-2), species.

Phylogenetic analyses depending on nucleotide sequences of the 18S rDNA gene clearly related the genotypes of *Kudoa* sp.-1 with *Kudoa dicentrarchi* (Figure 2). Significantly high sequence similarities (100%≥x≥99.7%) between *Kudoa* sp.-1 genotypes and *K. dicentrarchi* genotypes (KT970638 and KT970639) also supported this relationship. Additionally, a comparison of morphometric data obtained from *Kudoa* sp.-1 specimens with the original description of *K. dicentrarchi* (Sitjà-Bobadilla & Álvarez-Pellitero, 1992) verified this relationship (Figure 1A, Table 1). As a result, depending on data from myxospore morphology and phylogenetic analyses depending on 18S rDNA

nucleotide sequences we assign *Kudoa* sp.-1 specimens to *Kudoa dicentrarchi*. This species was first described from European seabass in Spain as *Sphaerospora dicentrarchi* (Sitjà-Bobadilla & Álvarez-Pellitero, 1992). However, this species was later transferred to the genus *Kudoa* and named *K. dicentrarchi* due to molecular data provided by Casal et al. (2019). So far, *K. dicentrarchi* has been reported in Italy (*Dicentrarcus labrax*), Spain (*D. labrax*), Portugal (*D. labrax*, *D. punctatus*) and the northern Black Sea (*Mugil cephalus*, *Paramugil parmatus*, *Valamugil speigleri*, *V. formosae*) (Sitjà-Bobadilla & Álvarez-Pellitero, 1993b; Fioravanti et al., 2004; Xavier et al., 2013; Rangel et al., 2016; Yurakhno & Thi, 2019). Recently Birincioğlu et al. (2023) reported *K. dicentrarchi* from *D. labrax* cultivated in the fish farms in the Aegean coast of Türkiye. Nevertheless, this study primarily relies on morphological data, thus lacking molecular insights. In this context, our study presents the first molecular records of *K. dicentrarchi* from Eastern Mediterranean, encompassing the Turkish coasts. *Kudoa dicentrarchi* has been reported to infect various tissues and organs of its hosts, including the gonads, bladder, gallbladder, intestines, stomach, kidneys, spleen, liver-pancreas and serosa. Similarly, in this study *K. dicentrarchi* specimens were detected in the gallbladder and gonads of the European seabass. This finding is concordant with the available literature, revealing the tissue specificity (connective tissue) of this parasite without a specific target organ (Sitjà-Bobadilla & Álvarez-Pellitero, 1993b; Fioravanti et al., 2004; Xavier et al., 2013; Rangel et al., 2016; Yurakhno & Thi, 2019).

The annual prevalence of *Kudoa dicentrarchi* in cultured European seabass was determined as 38.75% in this study (Supplementary Table 3). The current infection rate appears to be relatively lower in comparison to the documented cases in fish farms along the European coasts of the Atlantic Ocean (Portugal), and the western Mediterranean basin encompassing Spain and Italy. Existing literature suggests infection rates ranging between 40% and 95% in these regions (Sitjà-Bobadilla & Álvarez-Pellitero 1992; Fioravanti et al. 2004, 2006; Castro et al. 2018). Furthermore,

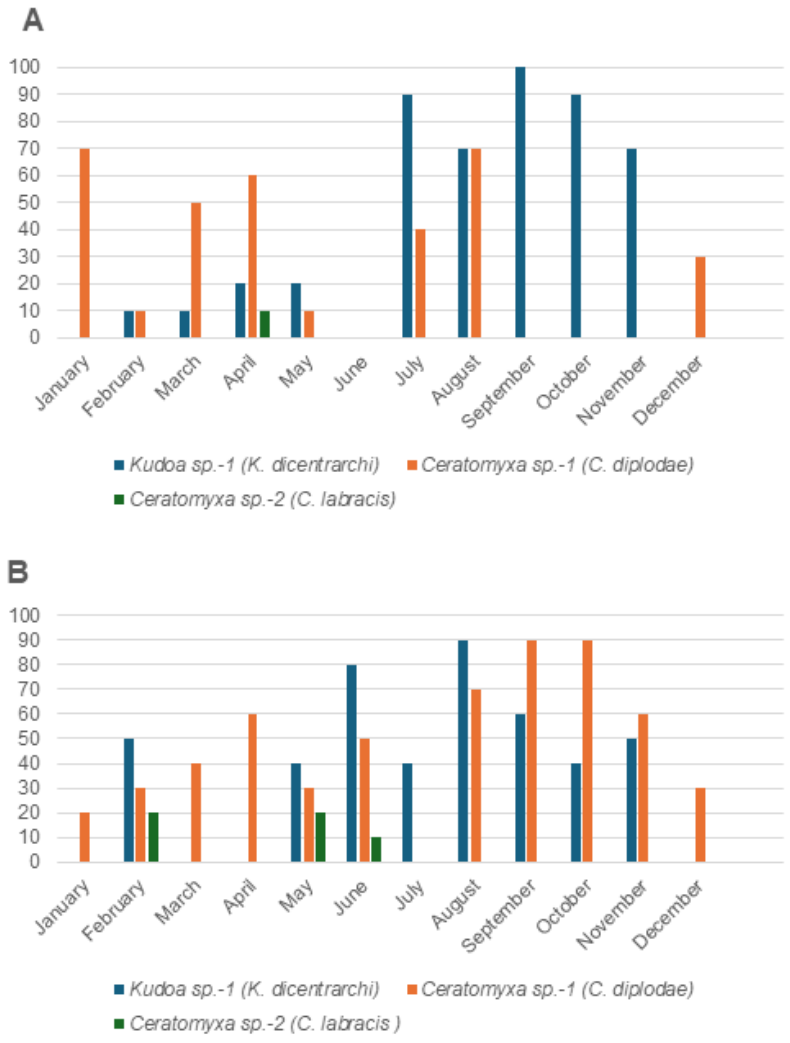

Figure 4. The bar chart showing the monthly variations in infection prevalences of *D. labrax* specimens obtained from sea cages located in İzmir (A) and Muğla (B). In the graphics each color is representing one of the three (*Kudoa dicentrarchi*, *Ceratomyxa diplodae* and *C. labracis*) parasites detected in this study.

Birincioğlu et al. (2023) reported infection prevalence ranging between 34% and 90%, varying according to the sizes of the fish, from different fish farms located in the Aegean Sea. The lower infection prevalence rates observed in this study may be attributed to ecological factors or to some anthropogenic factors such as unfavorable cultivation conditions as mentioned in previous studies.

Phylogenetic analysis of 18S rDNA genotypes belonging to *Ceratomyxa* sp.-1 specimens (DEBS-4 and DTIS-2) revealed the close relationship of these specimens with *Ceratomyxa diplodae* (Figure 3). This close phylogenetic relationship is also supported with significant (≥99.4%) 18S rDNA nucleotide sequence similarities. Moreover, myxospore morphology and morphometric data of these specimens fit well with the original description data of *C. diplodae* (Figure 1B, Table 2) (Lubat et al., 1989). According to these results we designate *Ceratomyxa* sp.-1 specimens to *C. diplodae*. *Ceratomyxa diplodae* was first described from the gallbladder of *Diplodus annularis* in the Adriatic Sea (Montenegro) (Lubat et al., 1989). Subsequently, this species was reported in other countries such as Spain (*D. labrax*), Italy (*D. labrax*), Greece (*Diplodus puntazzo*) and Portugal (*D. labrax*) (Lubat et al., 1989; Sitjà-Bobadilla & Álvarez-Pellitero, 1993a; Fioravanti et al., 2006; Katharios et al., 2007; Rocha et al., 2016). In Türkiye, five different parasite species belonging to the *Ceratomyxa* genus have been identified including, *Ceratomyxa belonea* Lubat, Radujkovic, Marques & Bouix, 1989 (*Belone belone* Linnaeus, 1760), *C. merlangi* (*M. merlangus*), *C. scorpaeni* Garbouj, Rangel, Castro, Hmissi, Santos & Bahri, 2016 (*Scorpaena porcus* Linnaeus, 1758), *C. scophthalmi* Özer, Gürkanlı, Okkay, Çiftçi & Yurakhno, 2022 (*Scophthalmus maeoticus* Pallas 1814) and one potentially new *Ceratomyxa* species from the gallbladder of *Solea solea* (Özer & Yurakhno, 2013; Özer et al., 2017; Yurakhno et al., 2017; Eiras, 2006; Eiras et al., 2018; Özer et al., 2022). However, there have been no records of *C. diplodae* reported from Türkiye thus far. Therefore, this study presents the first record of *C. diplodae* from *D. labrax* grown in fish farms in Türkiye and also Eastern Mediterranean.

In this study, the annual prevalences of *C. diplodae* were calculated as 28.3% and 47.5% from fish samples obtained from fish farms in İzmir and Muğla, respectively (Figure 4, Supplementary Table 3). The disparity in these rates may be attributed to the high density of aquaculture activities in Muğla district, leading to unfavorable ecological conditions. Moreover, fish-to-fish transmissions in intensive sea cages have shown in some myxozoan genera like *Myxidium* (Diamant 1997; Yasuda *et al*., 2002). Additionally, in general these rates were notably higher than the data provided in available literature from Italy and Portugal, where infection rates are reported to be less than 10% (Fioravanti et al., 2006; Rocha et al., 2016). However, one exception was reported by Castro et al. (2018), with a prevalence of infection ranging between 11.6% and 46.5% in Portugal. Similarly, the significant differences in prevalence rates observed in this study compared to other countries may be due to the fact that aquaculture activities in the Aegean Sea are conducted in confined areas, in contrast to their counterparts in other regions.

As previously noted, no molecular data was obtained for *Ceratomyxa* sp.-2 specimens in this study, Nonetheless, based on the unique myxospore morphology, satisfying similarities in morphometric data of myxospores, and host fish data, we assigned *Ceratomyxa* sp.-2 specimens to *Ceratomyxa labracis* (Figure 1C, Table 2). *Ceratomyxa labracis* initially described by Sitja-Bobadilla & Alvarez-Pellitero (1993a) from the bile and gall-bladder of wild and cultivated *D. labrax* in Spain. This particular myxozoan species has only been documented in *Dicentrarchus labrax*, so far. Furthermore, it exhibits a restricted geographical range, through the Eastern Mediterranean region, spanning from Italy to Sardinia, Corsica, and Spain, as well as along the Atlantic coasts of Portugal. (Merella et al., 2006; Fioravanti et al, 2006; Antonelli et al., 2016; Rocha et al., 2016; Castro et al., 2018). Not surprisingly, this species is not one of the five documented *Ceratomyxa* species (mentioned earlier) in Turkish coasts, thus, this study presents the first record of *C. labracis* from Türkiye and also from the Eastern Mediterranean.

Similar to *C. diplodae*, the annual infection prevalence of *C. labracis* in this study was higher in Muğla (4.2%) fish samples compared to İzmir (0.8%) samples (Figure 4, Supplementary Table 3). This disparity may also attributed to the high density of aquaculture activities in Muğla district, much like in the case of *C. diplodae*. On the other hand, these annual prevalence values were quite low when compared to the other contries where *C. labracis* was documented. The annual prevalence values were especially high in the eastern Mediterranean (from Italy to Spain), ranking between 1.7% to 42% (Sitjà-Bobadilla & Álvarez-Pellitero, 1993c; Fioravanti *et al*., 2006; Merella *et al.*, 2006), and were between 6.2% and 12% in Portugal (Castro *et al.*, 2018). When considering the distribution and abundance, the origin of this species is possibly eastern Mediterranean, where it was initially identified, and it was transfered to Türkiye relatively recently. Thus the lower annual prevalence of the parasite may be due to the fact that the parasite is not fully adapted to the Aegean Sea. For instence, it may not have a convinient invertabrate (main) host to efficiently complete its life cycle.

Ceratomyxa species are coelozoic in the gall bladder of most marine fishes and some species were also determined in the kidneys, gonads and urinary bladders of host fishes (Dyková & Lom, 1988, 2007; Álvarez-Pellitero & Sitjà-Bobadilla, 1993; Gunter et al., 2009; Alama-Bermejo et al., 2011; Okamura et al., 2015). Concordant with this data, in this study specimens of *C. diplodae* and *C. labracis* were only detected in the bile (as scattered) of the European seabass.

Conclusion

Consequently, most important results obtained in this study can be summarised as follows; **a)** Three myxozoan species, *K. dicentrarchi*, *C. diplodae* and, *C. labracis* were determined from *D. labrax* grown in the sea cages located in the Aegean Sea coasts of Türkiye (İzmir and Muğla district); **b)** This study provides the first molecular data for *K. dicentrarchi* from *D. labrax* in Turkish coasts; **c)** This study also provides the first records for *C. diplodae* and *C. labracis* from the Turkish coasts.

Ethical Statement

All fish used in this study were caught by fishermen and euthanized. No live animals were used in the study thus there is no need for Ethical Approval.

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Author Contribution

All authors attended the laboratory studies and data analyses. Additionally, all of them were involved in writing the manuscript and approved the final version.

Conflict of Interest

The authors declare they have no conflict of interest that are directly or indirectly related to the work submitted for publication.

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Supplementary Table 1. Source information of *Kudoa* sp.-1 (*K. dicentrarchi*) genotypes obtained in this study in addition to SSU genotypes of different *Kudoa* species obtained from GenBank for phylogenetic analyses

Species	Host	Tissue Origin	Locality	GenBank Acc. No.	Source
DTIG_1	*Dicentrarchus labrax*	Gonad	İzmir/Türkiye	PP788709	**This study**
DEIS_3	*Dicentrarchus labrax*	Gallbladder	İzmir/Türkiye	PP788710	**This study**
DEIG_6	*Dicentrarchus labrax*	Gonad	İzmir/Türkiye	PP788711	**This study**
DEBG_3	*Dicentrarchus labrax*	Gonad	Muğla/Türkiye	PP788712	**This study**
DAIG_1	*Dicentrarchus labrax*	Gonad	İzmir/Türkiye	PP788713	**This study**
DTBG_5	*Dicentrarchus labrax*	Gonad	Muğla/Türkiye	PP788714	**This study**
Kudoa acentrogobia	*Acentrogobius chlorostigmatoides*	Trunk muscle	China	LC493824	Li et al. (2020a)
Kudoa amamiensis	*Pempheris ypsilychnus*	Musculature	Australia	AY152748	Whipps et al. (2003)
Kudoa anatolica	*Atherina hepsetus*	Musculature, Urinary bladder, Kidney	Türkiye	MH310913	Özer et al. (2018)
Kudoa bora	*Osteomugil perusii*	Trunk muscle	Pasific Ocean	LC493813	Li et al. (2020b)
Kudoa carcharhini	*Carcharhinus cautus*	Musculature	Australia	GU324968	Gleeson et al. (2010)
Kudoa chaetodoni	*Caesio cuning*	Brain	Australia	JQ026218	Miller and Adlard (2012)
Kudoa cheilodipteri	*Cheilodipterus quinquelineatus*	Musculature and Intestinal mucosa	Australia	JX090295	Heiniger et al. (2013)
Kudoa ciliatae	*Sillago ciliata*	Brain	Australia	DQ519390	Burger et al. (2006)
Kudoa cookii	*Ostorhinchus cookii*	Musculature and Intestinal mucosa	Australia	JX090294	Heiniger et al. (2013)
Kudoa dicentrarchi	*Dicentrarchus labrax*	Musculature	Portugal	KT970638	Rangel et al., (2016)
Kudoa eugerres	*Dicentrarchus labrax*	Musculature	Brazil	MH581487	Casal et al. (2019)
Kudoa hemiscylli	*Orectolobus ornatus*	Musculature	Australia	GU324962	Gleeson et al. (2010)
Kudoa hypoepicardinalis	*Nomeus gronovii*	Heart	U.S.A.	AY302722	Blaylock et al. (2004)
Kudoa iwatai	*Lateolabrax japonicus*	Musculature	Japan	AB553295	Matsukane et al. (2011)
Kudoa kenti	*Amphiprion akindynos*	Musculature	Australia	FJ792713	Burger and Adlard (2010)
Kudoa leptacanthae	*Zoramia leptacantha*	Pericardial cavity	Australia	JQ974029	Heiniger and Adlard (2012)
Kudoa lutjanus	*Acanthopagrus latus*	Trunk muscle	Pasific Ocean	LC493818	Li et al. (2020b)
Kudoa megacapsula	*Sphyraena pinguis*	Musculature	China	AB188529	Yokoyama and Itoh (2005)
Kudoa miniauriculata	*Sebastes paucispinis*	Musculature	Canada	AF034639	Hervio et al. (1997)
Kudoa musculoliquefaciens	*Istiophorus platypterus*	Musculature	Pasific Ocean	LC097084	Kasai et al. (2016)
Kudoa nilüferi	*Neogobius melanostomus*	Musculature	Türkiye	MH310915	Özer et al. (2018)
Kudoa nova	*Neogobius melanostomus*	Musculature	Ukraine	EF644198	Pascual et al. (2012)
Kudoa neothunni	Thunnus alvacares	Musculature	Japan	AB693049	Li et al. (2013)
Kudoa ogawai	*Paralichthys olivaceus*	Trunk muscle	Korea	MK850343	Shin et al. (2016)
Kudoa paraquadricornis	*Carangoides plagiotaenia*	Musculature	Australia	FJ792718	Burger and Adlard (2010)
Kudoa petala	*Sillago sihama*	Gallbladder wall	Pacific Ocean	LC493820	Li et al. (2020b)
Kudoa saudiensis	*Rastrelliger kanagurta*	Oocytes	Saudi Arabia	KF830719	Mansour et al. (2015)
Kudoa scomberi	*Scomber japonicus*	Trunk muscle	Japan	AB693044	Li et al. (2013)
Kudoa shiomitsui	*Thunnus orientalis*	Heart	Japan	GU124635	Zhang et al. (2010)
Kudoa surabayaensis	*Mugil cephalus*	Trunk muscle	Indonesia	LC543976	Yunus et al. (2021)
Kudoa thunni	*Thunnus albacares*	Trunk muscle	Japan	LC200502	Kasai et al. (2017)
Kudoa trachuri	*Trachurus japonicus*	Trunk muscle	Japan	AB553299	Matsukane et al. (2011)
Kudoa sp. (VMY02)	*Moolgarda cunnesius*	Gallbladder	Vietnam	OL339421	Yurakhno et al. (2022)
Unicapsula motomurai	*Pentanemus quinquarius*	Trunk muscle	Atlantic Ocean	LC474133	Li et al. (2020b)
Unicapsula galeata	*Unicapsula galeata*	Trunk muscle	Pacific Ocean	LC474137	Li et al. (2020b)

Supplementary Table 2. Source information of *Ceratomyxa* sp.-1 (*C. diplodae*) genotypes obtained in this study in addition to SSU genotypes of different *Ceratomyxa* species obtained from GenBank for phylogenetic analyses

Species	Host	Tissue Origin	Locality	GenBank Acc. No.	Source
DTIS_2	*Dicentrarchus labrax*	Bile	İzmir/Türkiye	PP788707	**This study**
DEBS_4	*Dicentrarchus labrax*	Bile	Muğla/Türkiye	PP788708	**This study**
Ceratomyxa atkinsoni	*Lethrinus atkinsoni*	Gallbladder	Australia	FJ204244	Gunter et al. (2009)
Ceratomyxa barnesi	*Siganus lineatus*	Gallbladder	Australia	FJ204245	Gunter et al. (2009)
Ceratomyxa bryanti	*Abudefduf whitleyi*	Gallbladder	Australia	EU440357	Gunter and Adlard (2008)
Ceratomyxa collarae	*Chaetodon decussatus*	Gallbladder	India	KU726595	Sanil et al. (2017)
Ceratomyxa diplodae	*Dicentrarchus labrax*	Gallbladder	Portugal	KX099691	Rocha et al. (2016)
Ceratomyxa kenti	*Abudefduf whitleyi*	Gallbladder	Australia	EU440357	Gunter and Adlard (2008)
Ceratomyxa labracis	*Dicentrarchus labrax*	Gallbladder	Spain	AF411472	Palenzuela et al. (2002)
Ceratomyxa nowakae	*Gymnocranius audleyi*	Gallbladder	Australia	FJ204252	Gunter et al. (2009)
Ceratomyxa puntazzi	*Diplodus puntazzo*	Gallbladder	Spain	JF820290	Alama-Bermejo et al. (2011)
Ceratomyxa reidi	*Chaetodon vagabundus*	Gallbladder	Australia	GU136394	Gunter et al. (2010)
Ceratomyxa scorpaeni	*Scorpaena porcus*	Gallbladder	Tunisia	KU240024	Garbouj et al. (2016)
Ceratomyxa seriolae	*Seriola quinqueradiata*	Bile	Japan	AB530265	Yokoyama et al. (2010)
Ceratomyxa sparusaurati	*Sparus aurata*	Gallbladder	Spain	AF411471	Palenzuela et al. (2002)
Ceratomyxa verudensis	*Scorpaena porcus*	Gallbladder	USA	KM273027	Fiala et al. (2015b)
Ceratomyxa sp. 1 (LFR-2017)	*Trachinus draco*	Gallbladder	Tunisia	MF540150	Azizi et al. (2020)
Ceratomyxa sp. 1 ex *Sparus aurata*	*Sparus aurata*	Gallbladder	Spain	JF820292	Alama-Bermejo et al. (2011)
Ceratomyxa sp. 2 ex *Sparus aurata*	*Sparus aurata*	Gallbladder	Spain	JF820293	Alama-Bermejo et al. (2011)
Ceratomyxa sp. ex *D. annularis*	*Diplodus annularis*	Gallbladder	Spain	JF820291	Alama-Bermejo et al. (2011)
Ceratomyxa sp.1 (NG-2010)	*Zebrasoma veliferum*	Gallbladder	Australia	GU136395	Gunter et al. (2010)
Ceratomyxa sp. (RM)	*Siganus rivulatus*	Gallbladder	Israel	DQ333429	Diamant and Lipshitz (Unpublished)
Ceratomyxa sp. (SRR)	*Siganus rivulatus*	Gallbladder	Israel	DQ333431	Diamant and Lipshitz (Unpublished)

Supplementary Table 3. The table showing the monthly variations in infection prevalences of *D. labrax* with three myxozoan species observed in this study.

	***Kudoa* sp.-1 (*K. dicentrarchi*)**			***Ceratomyxa* sp.-1 (*C. diplodae*)**			***Ceratomyxa* sp.-2 (*C. labracis*)**		
	İzmir	**Muğla**	**Total**	**İzmir**	**Muğla**	**Total**	**İzmir**	**Muğla**	**Total**
January	0% (0/10)	0% (0/10)	0% (0/20)	70% (7/10)	20% (2/10)	45% (9/20)	0% (0/10)	0% (0/10)	0% (0/20)
February	10% (1/10)	50% (5/10)	30% (6/20)	10% (1/10)	30% (3/10)	20% (4/20)	0% (0/10)	20% (2/10)	10% (2/20)
March	10% (1/10)	0% (0/10)	5% (1/20)	50% (5/10)	40% (4/10)	45% (9/20)	0% (0/10)	0% (0/10)	0% (0/20)
April	20% (2/10)	0% (0/10)	10% (2/20)	60% (6/10)	60% (6/10)	60% (12/20)	10% (1/10)	0% (0/10)	5% (1/20)
May	20% (2/10)	40% (4/10)	30% (6/20)	10% (1/10)	30% (3/10)	20% (4/20)	0% (0/10)	20% (2/10)	10% (2/20)
June	0% (0/10)	80% (8/10)	40% (8/20)	0% (0/10)	50% (5/10)	25% (5/20)	0% (0/10)	10% (1/10)	5% (1/20)
July	90% (9/10)	40% (4/10)	65% (13/20)	40% (4/10)	0% (0/10)	20% (4/20)	0% (0/10)	0% (0/10)	0% (0/20)
August	70% (7/10)	90% (9/10)	80% (16/20)	70% (7/10)	70% (7/10)	70% (14/20)	0% (0/10)	0% (0/10)	0% (0/20)
September	100% (10/10)	60% (6/10)	80% (16/20)	0% (0/10)	90% (9/10)	45% (9/20)	0% (0/10)	0% (0/10)	0% (0/20)
October	90% (9/10)	40% (4/10)	65% (13/20)	0% (0/10)	90% (9/10)	45% (9/20)	0% (0/10)	0% (0/10)	0% (0/20)
November	70% (7/10)	50% (5/10)	60% (12/20)	0% (0/10)	60% (6/10)	30% (6/20)	0% (0/10)	0% (0/10)	0% (0/20)
December	0% (0/10)	0% (0/10)	0% (0/10)	30% (3/10)	30% (3/10)	30% (6/20)	0% (0/10)	0% (0/10)	0% (0/20)
Annual	**40.00%**	**37.50%**	**38.75%**	**28.3%**	**47.5%**	**37.92%**	**0.8%**	**4.2%**	**2.5%**