

Article

Preliminary Evidence about the Colonisation Process of *Kyphosus* Species (Perciformes: Kyphosidae) in the Subtropical–Temperate Northeast Atlantic Ocean and Mediterranean Sea

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Abstract: A review of the non-native *Kyphosus* species historically recorded in Galician waters (north-western Spain) based on morphological and molecular characteristics is carried out. The list is composed of 15 specimens recorded from 2002 to 2022, showing a clearly unbalanced ratio in favour of *K. vaigiensis* with respect to *K. sectatrix* (6.5:1). A similar analysis was performed by consulting ichthyological literature on the *Kyphosus* species reported in the subtropical–temperate Northeast Atlantic Ocean and Mediterranean Sea. The results seem to reflect a more recent and conspicuous appearance of *K. vaigiensis* in the Northeast Atlantic–Mediterranean area, suggesting a higher invasive capacity than that of its congener *K. sectatrix*, perhaps related to its greater mobility. DNA barcoding supports the morphological identification of *K. vaigiensis* from Galicia and confirms the Atlantic–Mediterranean and Indo–Pacific distribution of the species. In addition, the main distinctive morphological characters found in the ichthyological literature have been revised and the taxonomic status of one published record has been changed. The results indicate the need to monitor non-indigenous marine species in the current global warming scenario of the Anthropocene era.

Keywords: *Kyphosus vaigiensis*; *Kyphosus sectatrix*; DNA barcoding; Galician waters; chronology; non-native species



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1. Introduction

There is good evidence that climate change has affected the distribution and composition of marine fish communities. The rise in the sea temperature might be at the basis of the geographical spread and shifts in abundance and distribution of fishes of southern origin to more temperate waters, a process often termed “tropicalization” [1].

The family Kyphosidae contains 12 species classified in two genera, inhabiting the Atlantic, Indian and Pacific Oceans. The genus *Kyphosus* Lacepède 1801 consists of approximately 11 species worldwide distributed in warm waters [2]. The sea chubs *Kyphosus* species typically inhabit shallow waters over sandy, rocky or grassy bottoms around coral reefs, and juveniles are commonly found among floating algae or below flotsam [3].

The taxonomy of the genus *Kyphosus* is problematic. Two taxonomic revisions with different Atlantic–Mediterranean species proposals have been published in the last decade [2,4]. The subsequent results strongly support the species arrangement proposed by Knudsen and Clements [5], which is the one most followed in subsequent works, including the present research.

In this context, two species of *Kyphosus* have been reported so far in the north-eastern Atlantic and the Mediterranean: The Bermuda sea chub *Kyphosus sectatrix* (Linnaeus 1758),

reported also as *Kyphosus saltatrix* (Linnaeus, 1758) or *Kyphosus sectator* (Linnaeus, 1758), and the brassy chub *Kyphosus vaigiensis* (Quoy & Gaimard 1825), reported in many cases as *Kyphosus incisor* (Cuvier 1831). A third species, *Kyphosus bigibbus* Lacepède, 1801, is also noted as probable by Knudsen and Clements [2], although no records are available.

Delimiting the different species of *Kyphosus* is difficult and currently based on the examination of a combination of morphological traits, such as the number of anal and dorsal soft fin rays, the scale row and gill rakers counts, colour patterns, relative body proportions and relative size and placement of fins [2]. Molecular taxonomy has been successfully implemented with the traditional morphological analysis in the systematic study of *Kyphosus* species in the context of an integrative taxonomy. A variety of mitochondrial markers such as *COI* and *16S* [6], *Cyt b*, *12S* and *16S* [7], *COI*, *Cyt b*, *12S-16S* [8] or *COI* [1,9–11] have been employed in the identification of the Atlantic–Mediterranean *Kyphosus* species.

In recent decades, the number of observations of *Kyphosus* species has increased in both the Mediterranean Sea and the north-eastern Atlantic Ocean, probably denoting a natural expansion of their range and an increased abundance related to climate change and warming of waters [9].

The aim of this research was to establish the identity of the specimens of the genus *Kyphosus* that most frequently arrive on the north-western coasts of the Iberian Peninsula. To this end, an integrative approach to taxonomy has been used, complementing morphological and molecular identifications. With the same purpose, a review of published records from the northeast Atlantic and Mediterranean areas has been carried out.

2. Materials and Methods

2.1. Sampling and DNA Extraction

The area studied covers the northern range of the distribution of *Kyphosus* species in the NE Atlantic, from Morocco to France, including the Mediterranean Sea, and with special attention to Galician waters (NW Spain). The Macaronesia region is excluded from this analysis because, although these species are presumably more frequent on these islands than on the mainland, little information is available.

Fish sampling was opportunistic, based on the report of non-directed catches made by artisanal fisheries or spear fishermen at different locations along the Galician coasts. The only criterion for the sampling method is that samples are available and willing to be donated to researchers. In the laboratory, specimens were identified at the species level following Knudsen and Clements [2]. An extensive literature search for records of the species occurring in the remaining study area was also carried out, including the main morphological distinctive characters. In this aspect, the number of dorsal and anal fin rays reported by Ligas et al. [12] is dubious (see the Discussion section) and was not considered.

Voucher specimens were deposited in the Museo de Historia Natural da Universidade de Santiago de Compostela (MHN USC, Santiago de Compostela, Spain) under reference codes MHN USC-25201-1 to MHN USC-25201-5. DNA was extracted from 30 mg of muscular tissue, using the E.Z.N.A. Tissue DNA Kit (Omega Bio-Tek) according to the manufacturer's instructions, employing 100 µL of elution buffer in the final recovery step.

Abbreviations as follow: total length (TL), standard length (SL), dorsal fin rays (D), anal fin rays (A), gill rakers (GR).

2.2. Mitochondrial Sequence Data

The mitochondrial cytochrome c oxidase subunit I (*COI*) gene was amplified using the primer set C_FishF1t1-C_FishR1t1 [13], combined with the Phire Green Hot Start II PCR Master Mix (Thermo Scientific) and 2 µL of template DNA, in a final reaction volume of 20 µL. PCR products were purified by treatment with ExoSAP-IT (Thermo Fisher Scientific, Waltham, MA, USA), and subjected to sequencing reactions using the BigDye 3.1 cycle sequencing kit and primers M13F (-21) and M13R (-27) [14], whose products were resolved in a SeqStudio Genetic Analyzer. All information regarding these specimens including

DNA barcodes, images, coordinates of capture and other complementary data are available at the Barcoding of Life Database (BOLD, www.boldsystem.org, accessed on 29 June 2022) as Process IDs FIGAL045-22 to FIGAL049-22. The COI sequences were also deposited in the GenBank repository with accession numbers ON774729 to ON774733.

The COI sequences were used, on the one hand, to validate the morphological identification of self-sampled specimens by DNA barcoding and, on the other hand, to test the possible genetic structure across individuals from different sampling sites, taking advantage of the sequences deposited in the BOLD and GenBank databases. For this purpose, a haplotype network was created by a median-joining network analysis [15] with relationships among haplotypes visualised in PopART 1.7 [16], with $\epsilon = 0$, to examine genetic distances between haplotypes and their prevalence in different geographic areas. The sequences were collapsed into haplotypes using the online version of FaBox [17]. The figure was edited using the free software Inkscape (www.inkscape.org, accessed on 29 June 2022).

3. Results

The historical records of *Kyphosus* specimens caught in the Galician waters are shown in Table 1. A total of 15 specimens was recorded from 2002 to 2022, of which 10 are reported for the first time. Among them, only two specimens were identified as *K. sectatrix*, of 271 and 450 mm TL, while 13 specimens were recognised as *K. vaigiensis* (Figure 1), the latter ranging from 285 to 580 mm TL, and recorded from 2007 onwards. The distinctive meristic counts were D: XI + 11–12, A: III + 12 and GR: 24 and 26 for *K. sectatrix* and D: XI + 13–14, A: III + 12–13 and GR: 25–32 for *K. vaigiensis*.

Table 1. Historical records of *Kyphosus* specimens in Galician waters (NW Spain) with its morphological and molecular characterization. TL in mm, *K.s.* = *Kyphosus sectatrix*, *K.v.* = *Kyphosus vaigiensis*.

Year	Source	TL	D	A	GR	GenBank	Species
2002	[18]	271	XI + 12	III + 12	26	—	<i>K.s.</i>
2007	This manuscript	285	XI + 13	III + 13	28	—	<i>K.v.</i>
2007	This manuscript	314	XI + 14	III + 13	28	—	<i>K.v.</i>
2010	This manuscript	311	XI + 13	III + 13	28	—	<i>K.v.</i>
2011	This manuscript	320	XI + 13	III + 12	31	—	<i>K.v.</i>
2013	[9]	450	XI + 11	III + 12	24	KT780867	<i>K.s.</i>
2014	[9]	482	XI + 14	III + 13	32	KP116934	<i>K.v.</i>
2014	[9]	280	XI + 14	III + 13	32	KP116935	<i>K.v.</i>
2018	[1]	450	XI + 14	III + 13	28	MH980022	<i>K.v.</i>
2019	This manuscript	519	XI + 13	III + 12	29	—	<i>K.v.</i>
2021	This manuscript	518	XI + 14	III + 12	25	ON774733	<i>K.v.</i>
2021	This manuscript	485	XI + 13	III + 12	28	ON774731	<i>K.v.</i>
2021	This manuscript	505	XI + 13	III + 13	30	ON774730	<i>K.v.</i>
2022	This manuscript	580	XI + 14	III + 13	29	ON774732	<i>K.v.</i>
2022	This manuscript	486	XI + 14	III + 13	26	ON774729	<i>K.v.</i>



Figure 1. *Kyphosus vaigiensis* MHN USC-25201-4, 580 mm TL caught in Galician waters.

Nine *COI* sequences from *K. vaigiensis* individuals caught in waters off Galicia (NW of Spain) were aligned with others retrieved from BOLD and GenBank to generate a set of 42 sequences, which were represented by 10 haplotypes. The median-joining network based on 616 nucleotide fragments does not suggest separation between the sampling sites (Figure 2). The most frequent haplotype ($N = 27$ sequences) is common to all geographical locations, including the north-western waters of the Iberian Peninsula, with the exception of Haiti and Malta, whose two sequences are associated with the second most common haplotype ($N = 6$ sequences).

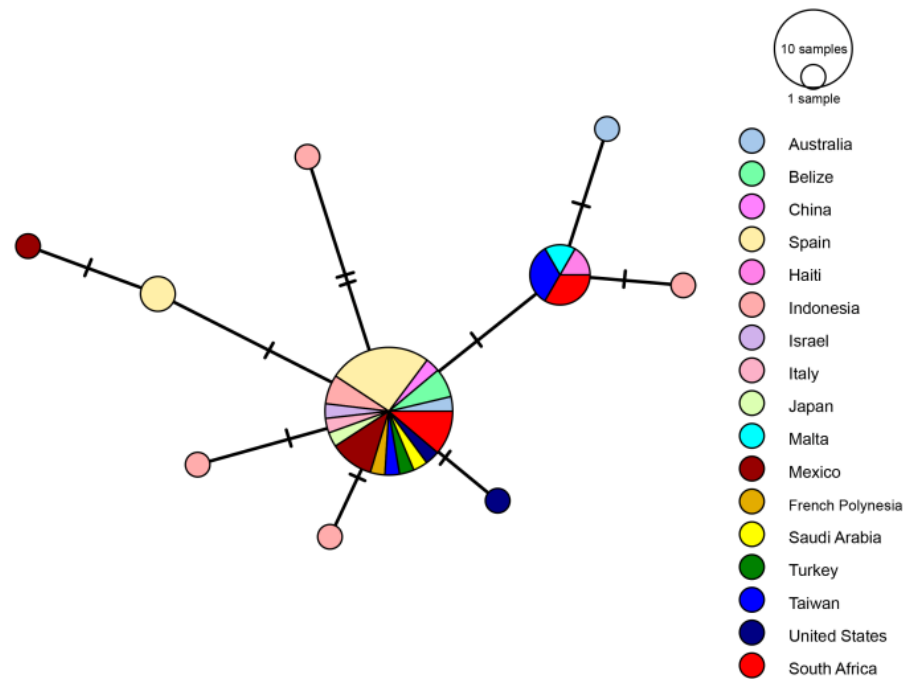


Figure 2. Haplotype network of *COI* sequences of *Kyphosus vaigiensis* ($N = 42$). Median-joining network ($\epsilon = 0$) created in PopART v1.7. Each circle represents a haplotype; the size of circles corresponds to the number of individuals with the haplotype. Colours indicate sampling sites. Bars indicate the number of mutations between two haplotypes. The samples from Spain are of Atlantic origin (Galicia), and those from the United States come from Hawaii.

The remaining historical records for the area of study are compiled in Table 2 according to the ichthyological literature. This dataset includes 26 records, of which 21 are from the Mediterranean. By species, 11 specimens of *K. sectatrix* and 10 of *K. vaigiensis* were reported in the Mediterranean area by only four and one, respectively, in the Atlantic. Sizes ranged from 195 to 610 mm TL for *K. sectatrix* and from 157 to 531 mm TL for *K. vaigiensis*. The distinctive meristic counts were D: X–XI + 11–13, A: III + 10–12 and GR: 23–27 for *K. sectatrix* and D: XI + 13–14, A: III + 12–13 and GR: 21–30 for *K. vaigiensis*.

Based on the distinctive characters reported by Knudsen and Clements [2], the record of *K. sectatrix* from Moroccan waters [19], with counts of D: XI + 14 and A: III + 13, should be reassigned to *K. vaigiensis*.

Figure 3 represents the chronology of *K. vaigiensis* detection in the northern Atlantic–Mediterranean range (see also Tables 1 and 2 for details).

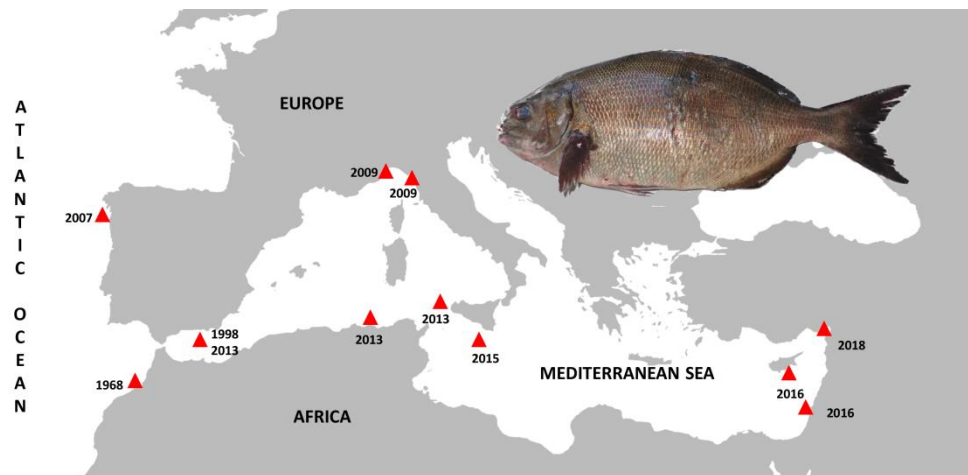


Figure 3. Distribution map of *Kyphosus vaigiensis* showing the chronology of detection from subtropical to temperate Atlantic and Mediterranean Sea.

Table 2. Historical records of *Kyphosus* specimens in NE Atlantic–Mediterranean area, excluding Galician records, with its morphological characterization. TL in mm, Atl. = Atlantic Ocean, Medit. = Mediterranean Sea, *K.s.* = *Kyphosus sectatrix*, *K.v.* = *Kyphosus vaigiensis*. (*) Originally misidentifications.

Area	Year	Source	TL	D	A	GR	Species
Medit.	1846	[20]	195	XI + 12	III + 11	+ 17	<i>K.s.</i>
Medit.	1883	[21]	—	—	—	—	<i>K.s.</i>
Medit.	1903	[22]	—	—	—	—	<i>K.s.</i>
Atl.	2004	[23]	523	XI + 12	III + 11	27	<i>K.s.</i>
Atl.	1968	[19]	290	XI + 14	III + 13	—	<i>K.v.</i> *
Atl.	1993	[24]	610	—	—	—	<i>K.s.</i>
Medit.	1996	[25]	216	XI + 12	III + 11	24	<i>K.s.</i>
Medit.	1998	[26]	310	XI + 14	III + 12	29	<i>K.v.</i>
Medit.	2003	[27]	485	XI + 12	III + 12	—	<i>K.s.</i>
Medit.	2005	[28]	415	XI + 11	III + 11	—	<i>K.s.</i>
Medit.	2006	[29]	489	XI + 13	III + 11	25	<i>K.s.</i>
Atl.	2006	[24]	275	—	—	—	<i>K.s.</i>
Atl.	2008	[24]	480 (SL)	—	—	—	<i>K.s.</i>
Medit.	2009	[30]	480	XI + 13	III + 13	29	<i>K.v.</i>
Medit.	2009	[12]	495	XI + 12?	III + 11?	28	<i>K.v.</i> *
Medit.	2010	[31]	200–250	—	—	—	<i>K.s.</i>
Medit.	2010	[32]	475	XI + 12	III + 11	24	<i>K.s.</i>
Medit.	2011	[7]	265	XI + 11	III + 10	25	<i>K.s.</i>
Medit.	2013	[33]	460	—	—	—	<i>K.v.</i>
Medit.	2013	[6]	475	XI + 13	III + 11	30	<i>K.v.</i>
Medit.	2013	[34]	415	XI + 13	III + 12	29	<i>K.v.</i>
Medit.	2015	[8]	157	XI + 13	III + 12	—	<i>K.v.</i>
Medit.	2016	[10]	505	XI + 13	III + 12	21	<i>K.v.</i>
Medit.	2016	[35]	272	XI + 14	III + 13	29	<i>K.v.</i>
Medit.	2018	[11]	531	XI + 13	III + 13	27	<i>K.v.</i>
Medit.	2021	[36]	485	X + 13	III + 11	23	<i>K.s.</i>

4. Discussion

The colonisation of new fish species is a slow process that can take several decades; during this period, their presence in the area of arrival is scarce and sampling is opportunistic, making it difficult to obtain a large number of specimens for study. In spite of this, the observation of new species in a new area represents the first, and sometimes

the only opportunity to follow and study the dynamics of colonisation; monitoring the spread is crucial to understanding how a new species arrives, tracking its movements and developments and recognising the impact that it may have [37].

The morphology of *K. vaigiensis* and *K. sectatrix* is similar, so that they are indistinguishable in the field, but can be easily identified by the dorsal and anal soft ray counts, and the number of gill rakers [38]. Following Knudsen and Clements [2], *K. vaigiensis* has D: X–XI + 13–15, A: III + 12–14 and GR: 21–33, while *K. sectatrix* has D: X–XI + 11–12, A: III + 10–12 and GR: 19–26. The counts reported in this study agree in general terms with these ranges with some exception. The 13 soft rays in the dorsal [29] and 27 gill rakers [23] for *K. sectatrix*, and the 11 soft rays in the anal for *K. vaigiensis* [6] are slightly out of range.

Misidentifications or dubious identifications are also not uncommon. The *K. sectatrix* specimen reported by Ligas et al. [12] should be re-identified as *K. vaigiensis*, based on the molecular sequences, the gill rakers re-count and the photo image obtained from this specimen [2]. However, the number of dorsal and anal fin rays of this specimen has not been re-counted, as the counts given in the original manuscript by Ligas et al. [12] correspond to a *K. sectatrix* species. Doubts also exist in the identification of a *K. sectatrix* specimen by Canas et al. [23], which resembles a *K. bigibbus* one [2]. The specimen of *K. sectatrix* (reported as *K. saltatrix*) off Benghazi (Libya) reported by Elbaraasi et al. [32] looks rather like *K. vaigiensis* [10], but morphological data do not support this change, since the reported counts (D: XI + 12; A: II + 11; GR: 24) are well in range established for *K. sectatrix* by Knudsen and Clements [2].

The chronology of the findings of the two species of *Kyphosus* in the Mediterranean Sea shows that the oldest species that inhabited it is *K. sectatrix*, recorded for the first time in 1846 [20], more than a century ago, while the presence of *K. vaigiensis* seems to be a recent and perhaps invasive phenomenon [39]. In this sense, the first record of *K. vaigiensis* in the Mediterranean Sea occurred in 1998 [26], and since then and until 2016, four more records of *K. vaigiensis* were reported from across the Mediterranean [10], increasing up to 10 specimens if records are extended to the present, according to our revision.

Due to the scarcity of individual *Kyphosus* records, the chronology in the Atlantic area is unclear. Dessouter [40] reported *K. sectatrix* from the south of Morocco to the Gulf of Guinea, whereas *K. vaigiensis* was only recorded in Angola and Sao Tiago Island. More recently, Sakai and Nakabo [41] reported a similar distribution range for both species, although with different taxonomic names, from Morocco, throughout Madeira, the Canary Islands and Cape Verde Islands, including Ascension and southwards of Angola, adding also the Ascension and St Helena Islands for *K. sectatrix*. However, contrary to this range, *K. vaigiensis*, for example, is not recorded in the Canary Islands [42].

The haplotype network compiled from COI sequences of *K. vaigiensis* specimens captured in the Atlantic waters of the Iberian Peninsula, and publicly available sequences in databases, confirm the cosmopolitan character previously established for this species [2], with two haplotypes common to almost 80% of the individuals sampled worldwide, including specimens from the Atlantic Ocean and the Mediterranean Sea.

The molecular results support and validate the distinctive morphological characters reported by Knudsen and Clements [2] for *K. vaigiensis*. Therefore, the misidentified Moroccan record of this species in 1968 [15] would be its earliest record at the northernmost range, probably signalling the initial colonisation process, in chronological agreement with the first subsequent occurrences in Mediterranean in 1998 [26] and in Atlantic European waters in 2007.

Considering the chronology of occurrence of the species and the fact that the *K. vaigiensis* records have outnumbered the ones from *K. sectatrix* in the last decades, a more recent and rapid colonisation of *K. vaigiensis* in its northern range seems plausible.

The fact that tropically derived taxa such as *K. sectatrix* and *K. vaigiensis* can be found in temperate macroalgal-dominated habitats supports arguments that tropical species have maintained a capacity for geographically extensive dispersal and an ability to colonize highly variable environments [43]. Regarding this, differences in mobility behaviour

between the two species could be behind the ability to colonise new habitats. Mobility of fishes defines the distribution and abundance of their populations and occurs on a range of spatial and temporal scales [44]. *Kyphosus sectatrix* is a sedentary species, with a minimal activity space largely restricted to reef habitats [45]. In contrast, *K. vaigiensis* shows expansive movements along inshore habitats that do not seem to be influenced by habitat contiguity or limited by habitat breaks [46].

One of the predicted effects of global warming has to do with increased variability in the abundance and distribution of living beings, although for the observation of these patterns, information at the temporal and geographical scales is often not available [46]. The design of future natural scenarios will depend to a large extent on the ability to identify the species involved in these redistribution processes and the speed at which they are occurring [37]. This information is also essential for the development of new biogeographical patterns to replace the current ones [47].

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