1 **Signals of changes in the ichthyofauna composition of Galician waters**

2 **(NW Iberian Peninsula)**

3 Rafael Bañón^{a,b,*}, Marta Caballero-Huertas^c, Alexandre Alonso-Fernández^{d,e}, David
4 Barros-García^f, Jesús Otero^g, Alejandro de Carlos^h

5
6 ^a*Servizo de Planificación, Consellería do Mar, Xunta de Galicia, Rua dos Irmandiños*
7 *s/n, 15701 Santiago de Compostela, Spain*

8 ^b*Grupo de Estudos do Medio Mariño (GEMM), Edif. Club Náutico baixo, 15960 Ribeira,*
9 *Spain*

10 ^c*International MSc in Marine Biological Resources, Ghent University, Krijgslaan*
11 *281/S8, 9000 Ghent, Belgium.*

12 ^d*Instituto de Investigaciones Marinas, Consejo Superior de Investigaciones Científicas,*
13 *IIM-CSIC, Eduardo Cabello 6, 36208 Vigo, Pontevedra, Spain*

14 ^e*Asociación Ecoloxía Azul – Blue Ecology. Pontevedra, Spain*

15 ^f*Centro Interdisciplinar de Investigación Marinha e Ambiental (CIIMAR/CIMAR),*
16 *Terminal de Cruzeiros do Porto de Leixões, Avenida General Norton de Matos, S/N*
17 *4450-208 Matosinhos, Portugal*

18 ^g*Cofradía de Pescadores S. Martín de O Grove, Pza. de O Corgo nº 2, 36.980, O*
19 *Grove, Pontevedra, Spain*

20 ^h*Departamento de Bioquímica, Xenética e Inmunoloxía, Facultade de Bioloxía,*
21 *Universidade de Vigo, Rúa Fonte das Abelleiras s/n, 36310 Vigo, Spain.*

22
23 ^{*}*Corresponding author E-mail address: anoplogaster@yahoo.es (R. Bañón)*

24 **ABSTRACT**

Evidences of changes in the fish fauna of Galician waters is documented based on the occurrence of 24 specimens belonging to eight warm affinity fishes. Information about the morphology and new findings of *Desmodema polystictum* (Trachipteridae), *Halobatrachus didactylus* (Batrachoididae), *Dactylopterus volitans* (Dactylopteridae) *Anthias anthias* (Serranidae), *Callanthias ruber* (Callanthiidae), *Seriola rivoliana* (Carangidae), *Uranoscopus scaber* (Uranoscopidae) and *Sphyraena sphyraena* (Sphyraenidae), is reported from Galician waters, where they are unusual or rare. Morphometric and meristic parameters confirmed the identification to species level of each specimen, which was also supported by DNA barcoding. In addition, sex identification by histology and oocyte measurements of several specimens were carried out. The record of *D. polystictum* supposes the first occurrence for Atlantic European waters and a new northernmost record of the distribution in the Eastern Atlantic. A Neighbor-Joining comparison of *COI* mitochondrial DNA sequences of *D. volitans* suggests the possible occurrence of an undescribed cryptic species or the existence of a species that could be resurrected from one of its many catalogued synonyms. According to the rate, *S. rivoliana* is the species more commonly recorded. The gonad histological analysis proposes *A. anthias* and *C. ruber* as protogynous hermaphrodite species.

Keywords: Ichthyofauna; Distribution shifts; Global warming; Barcoding; Protogynous; Reproduction

1. Introduction

Increasing temperature is the most pervasive of present-day impacts on marine systems related with the global warming (Brierley and Kingsford, 2009). The Iberian

Atlantic coast, where Galicia is located, is one of the most affected areas by this major aspect of climate change. The net sea surface temperature (SST) in the Iberian Atlantic coast has increased in 0.68 °C between 1982 and 2006, making this region included in the “rapid warming” cluster (net SST > 0.6 °C) together with the North Sea, Baltic Sea, Black Sea, Mediterranean Sea and Celtic-Biscay Shelf (Belkin, 2009). This increase is even greater, of 0.90 °C, when a wider period of time, between 1957 and 2012, is considered (Belkin, 2016). Studies from Galician waters, off the north western Iberian coast, show similar results, with a rise of 0.24 °C per decade since 1974 (Gómez-Gesteira et al., 2011). Depending on the latitude, changes in sea surface temperature range in the Iberian upwelling margin are predicted to vary between 1.4 and 2.4 °C in the range from 1960-1990 to 2070-2100 (Philippart et al., 2011).

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. One of the most evident effects correlated with global warming in marine species is the geographical poleward spread of species of warm water affinity, favouring their occurrence and establishment, whether exotic or native (Booth et al., 2011). For the Atlantic European waters, Quéro (1998) have noted a northward extension of “rare” tropical fishes along the continental slope since 1963 related to the water warming. There is much evidence of fish species moving north along European Atlantic coasts, from the south of the Iberian Peninsula to the North Sea from then on (e.g. Bañón et al., 2002).

The northward spread and increase in the abundance of the native warm water biota has been termed as “meridionalization”, whereas the arrival, establishment and range extension of tropical and subtropical non-native species is known as “tropicalisation” (Boero et al., 2008). Bianchi (2007), however, defines tropicalisation

as the occurrence and establishment of warm-water species, whether exotic or native and with this meaning is mostly used in the ichthyological literature.

Not all marine fishes are responding to climate change at the same time and with the same intensity. When an exotic species is found in a new area, timely information is needed to understand “what’s going on” and to assess the stage or status of the range expansion (Azzurro, 2010). Identifying how many and which species are involved in this process and knowing the speed at which it is happening is very important for designing future scenarios. The purpose of this research is to describe and analyse the abundance of some fish species of new apparition or already present as indicators of the tropicalisation phenomenon in Galician waters and to provide information on the reproductive status of these individuals.

2. Materials and Methods

2.1. Morphological data

A total of 24 specimens belonging to eight species have been recorded between 2009 and 2019 in Galician waters. The specimens were firstly preserved fresh or frozen and afterwards, specimens were identified in the laboratory to species level, mainly following Lloris (2015). The main morphometric and meristic characters were recorded according to the literature as follows: Total length (TL), Standard length (SL), Head length (HL); Pre-orbital length (PO); Eye diameter (ED); Post orbital Length (POL); Inter-orbital length (IO); Predorsal length (PD); Pre-first dorsal length (PD1); Pre-second dorsal length (PD2); Pre-anal length (PA); First dorsal fin base length (DB1); Second dorsal fin base length (DB2); Anal fin base length (AB); Pre-pectoral length

(PP); Pre-pelvic length (PV); Pectoral fin length (PL); Pelvic fin length (VL); Maximum body depth (BH); Caudal peduncle depth (CP); Number of rays in first dorsal fin (D1); Number of rays in second dorsal fin (D2); Number of rays in pectoral fin (P); Number of rays in anal fin (A); Branchiostegal rays (BR); Gill-rakers (GR). With the exception of TL and SL, measurements are distances perpendicular to the length of the fish measured with a digital calliper to the nearest mm. All measurements are expressed as the percentage of standard length (%SL). Descriptive data are reported individually for species represented by one or two specimens and ranges are reported when there are more than two.

2.2. Molecular data

Muscle samples were collected from 23 specimens and DNA was purified with the E.Z.N.A. Tissue DNA kit (Omega Bio-tek). The standard 5' barcoding region of the mitochondrial *COI* gene was PCR-amplified and sequenced following procedures described elsewhere (Bañón et al., 2016). The identities of most barcodes were confirmed by comparison with those deposited in the Barcode of Life Database (BOLD; www.boldsystems.org) by means of the Batch ID Engine tool, which returns species-level identification when one is possible. In the case of the Flying gurnard *Dactylopterus volitans*, a Neighbor-Joining (NJ) tree (Saitou and Nei, 1987) with *p*-distances (Nei and Kumar, 2000) and using a bootstrap resampling procedure (Felsenstein, 1985) was constructed. Voucher specimens were deposited in the Museo de Historia Natural da Universidade de Santiago de Compostela (MHNUSC, Santiago de Compostela, Spain). All information regarding these specimens as well as their barcodes, images, places of capture and other complementary data are available in the

project “Marine Fishes from Galicia” (code FIGAL) at www.boldsystems.org. The *COI* sequences were also deposited in GenBank, with accession numbers MN134643 to MN134665.

2.2. Reproductive data

Fourteen gonads corresponding to all species except one, *Desmodema polystictum*, were processed histologically to classify them according to sex and maturity phase (Nagahama, 1983; Brown-Peterson et al., 2011). Gonads were removed and fixed immediately in 4% formaldehyde buffered with $Na_2HPO_4 \cdot 2H_2O$ (0.046 M) and $NaH_2PO_4 \cdot H_2O$ (0.029 M). A central section of the gonad of each individual was extracted, dehydrated and embedded in paraffin in order to be sectioned at 3 μ m and stained with haematoxylin-eosin for its examination under microscope. Then, their maturity phase was determined based on the most advanced oocyte development stage present, indications of previous spawning or other structural details (Brown-Peterson et al., 2011). The quality of histological slides and the proper sex and/or maturity phase classification were affected in some cases when fish were frozen before the biological sampling was done. In order to explore the size range for each oocyte developmental stage in *Callanthias ruber*, *D. volitans* and *Sphyrna sphyraena*, the mean diameter for each oocyte stage (n = 10 oocytes per stage) was calculated as the average between the major and minor axes in the histological sections. Using R software version 3.5.1. (R Development Core Team, 2018), one-way analysis of variance (ANOVA) test was performed to explore the differences in diameter among the oocyte stages within each of the species studied. Conversely, when homoscedasticity assumption was violated, data were analysed with Generalized Least Squares (GLS) statistical technique. Then, post-

hoc Tukey's range test was applied to each species to find out which specific oocyte stages means were significantly different from each other. Statistically significant differences were considered if $P < 0.05$.

3. Results

3.1. Morphological and reproductive analysis

A total of 24 specimens belonging to eight tropical or subtropical species were found in Galician waters. Data of the first occurrence, number of specimens and period when these species were then recorded and a ratio calculated from this period are shown in the Table 1. For each of the specimens listed below, only confirmed reproductive information based on histological analysis is provided. Mean oocyte diameter resulted significantly different among development stage in the three species analysed (*C. ruber*, *D. volitans* and *S. sphyraena*).

Polka-dot ribbonfish *Desmodema polystictum* (Ogilby, 1898) (Fig. 1A)

Material examined: MHNUSC 25165-1, 1242 mm SL; 30th January 2019, Ría de Arousa, 42.4466 °N, -8.9716 °W, 60 m depth. Morphology: HL: 9.7; PO: 3.1; POL: 2.7; ED: 3.9; IO: 2.2; PD: 8.9; DB: 91.1; PL: 3.4; BH: 11.3; D: 145; P: 10; BR: 6; GR: 3+10.

Lusitanian toadfish *Halobatrachus didactylus* (Bloch & Schneider, 1801) (Fig. 1B)

Material examined: MHNUSC 25166-1, male, 258 mm TL, 215 mm SL; 24th December 2018, Galician waters, 42.2582 °N, -8.8557 °W, 15 m depth. Morphology:

176 HL: 39.1; PO: 8.8; POL: 25.1; ED: 5.1; IO: 13.0; PD1: 33.5; PD2: 45.1; DB1: 7.0;
 177 DB2: 47.0; PA: 59.5; AB: 34.0; PV: 27.0; PP: 36.3; VL: 20.0; PL: 23.3; CP: 9.3; BH:
 178 20.5; D1: III; D2: 20; A: 16; P: 24; V: I+2; BR: 6. Reproduction: The specimen was a
 179 spawning capable male, as it showed a large number of spermatozoa in the lumen of
 180 lobules of its testicular tissue, and all the spermatogenic stages were clearly observed.

181

182 Swallowtail seaperch *Anthias anthias* (Linnaeus, 1758) (Fig. 1C)

183 Material examined: MHNUSC 25168-1, male, 258 mm TL, 175 mm SL, 25th
 184 June 2008, 43.4058 °N, -8.8812 °W, 72 m depth; MHNUSC 25168-2, male, 273 mm
 185 TL, 185 mm SL, 20th December 2016, 42.8718 °N, -9.2720 °W, 40 m depth; MHNUSC
 186 25168-3, male, 267 mm TL, 189 mm SL, 9th October 2017, 44.0462 °N, -7.1989 °W,
 187 250 m depth. MHNUSC 25168-4, male, 290 mm TL, 188 mm SL, 12th June 2018,
 188 42.2977 °N, -9.0200 °W, 146 m depth. MHNUSC 25168-5, 280 mm TL, 185 mm SL,
 189 28th April 2019, 42.5573 °N, -9.1961 °W, 50 m depth. Morphology: HL: 30.3-32.8; PO:
 190 5.1-9.0; POL: 14.3-16.6; ED: 7.6-10.3; IO: 8.1-10.3; PD: 22.2-28.2; DB: 54.5-61.7; PA:
 191 60.0-64.3; AB: 17.0-18.5; PP: 32.4-32.8; PV: 29.7-34.3; PL: 24.6-27.6; VL: 52.6-71.8;
 192 BH: 37.0-40.0; D: X+15-16; A: III+7-8; P: 18-19; V: I+5; BR: 7; GR: 13-14+29-31.
 193 Reproduction: All specimens histologically assessed were males. Two of them (267 mm
 194 and 290 mm TL) presented spermatocysts but lacked spermatozoa, being classified as
 195 developing males. A potentially reproductively male (258 mm TL), which showed
 196 spermatozoa in sperm ducts was also identified. Melanomacrophage centers were
 197 present in this individual (Fig. 2A). The maturity phase of one of the histologically
 198 assessed specimens could not be established due to the status of preservation and
 199 fixation of the reproductive tissue.

200

201 Flying gurnard *Dactylopterus volitans* (Linnaeus, 1758) (Fig. 1D)

202 Material examined: MHNUSC 25167-1, female, 538 g, 392 mm TL, 331 mm
 203 SL; 4th January 2019, Malpica, 43.3186 °N, -8.7638 °W, 46 m depth. Morphology: HL:
 204 22.1; PO: 6.3; POL: 10.6; ED: 5.1; IO: 13; PD1: 36.3; DB1: 9.4; PD2: 53.8; DB2: 20.2;
 205 PA: 60.4; AB: 13; PP: 25.1; PV: 28.7; PL: 70.4; VL: 25.7; BH: 16. D1: IV; D2: 8; A: 6;
 206 P: 6+29; V: I+4. Reproduction: The female specimen of *D. volitans* was likely at a
 207 developing phase without clear evidence of reproductive activity, although this
 208 observation was difficult to confirm due to the poor stage of preservation of the sample.
 209 Primary growth ($30.60 \pm 4.86 \mu\text{m}$) and cortical alveoli ($73.40 \pm 12.40 \mu\text{m}$) stages were
 210 identified.

212 Parrot seaperch *Callanthias ruber* (Rafinesque, 1810) (Fig. 1E)

213 Material examined: MHNUSC 25169-1, 245 mm TL, 148 mm SL, 16th January
 214 2019, 44.0462 °N, -7.1989 °W, 250 m depth; MHNUSC 25169-2, female, 182 mm TL,
 215 135 mm SL, 16th January 2019, 44.0462 °N, -7.1989 °W, 250 m depth; MHNUSC
 216 25169-3, male, 295 mm TL, 175 mm SL, 16th January 2019, 44.0462 °N, -7.1989 °W,
 217 250 m depth. Morphology: HL: 25.7-29.6; PO: 4.4-5.4; POL: 10.9-12.6; ED: 10.3-12.6;
 218 IO: 8.6-9.6; PD: 24-27.7; DB: 54.1-54.9; PA: 51.4-54.8; AB: 27-28.1; PP: 28-29.7; PV:
 219 29.6-30.4; PL: 20.6-23; VL: 22.9-24.3; BH: 26.7-30.4; D: XI+10-11; A: III+10-11; P:
 220 20-21; V: I+5; BR: 6; GR: 11+23-25. Reproduction: Regarding the 295 mm TL male, it
 221 seemed to be at a developing phase, as although the presence of spermatocysts was
 222 detected, no spermatozoa were identified. Also, melanomacrophage centers were
 223 observed (Fig. 2B). All the following oocytes stages and structures were determined in
 224 the female 182 mm TL: Primary growth ($57.50 \pm 12 \mu\text{m}$), cortical alveoli (186 ± 30.30
 225 μm), early vitellogenesis ($292 \pm 9.96 \mu\text{m}$), advanced vitellogenesis ($382 \pm 35.90 \mu\text{m}$),

migratory nuclei, hydrated oocytes, post ovulatory follicles and atresia, allowing its consideration as a spawning capable individual (Fig. 2C).

Longfin yellowtail *Seriola rivoliana* Valenciennes, 1833 (Fig. 1F)

Material examined: MHNUSC 25170-1, 415 mm TL, 341 mm SL, 24th September 2014, 42.5617 °N, -9.0757 °W, 13 m depth; MHNUSC 25170-2, 330 mm TL, 287 mm SL, 26th August 2015, 42.1889 °N, -8.8894 °W, 8 m depth; MHNUSC 25170-3, 480 mm TL, 400 mm SL, 13th June 2017, 43.7562 °N, -7.6162 °W, 12 m depth. MHNUSC 25170-4, 451 mm TL, 364 mm SL, 15th January 2019, 42.4460 °N, -8.9575 °W, 35 m depth. Morphology: HL: 25.8-28; PO: 7.9-10.3; POL: 11.8-12.7; ED: 3.9-5; IO: 5.2-5.5; PD1: 31.1-33.8; PD2: 43.1-47.5; DB1: 11.8-12.5; DB2: 38.8-43.4; PA: 55.5-60.1; AB: 26.4-30.3; PL: 15.2-15.8; VL: 16.7-18.7; D1: VI-VII; D2: I+28-30; A: II+I+19-20; P: 20-22; V: I+5; BR: 7; SLL: 136-145; BR: 7; GR: 7-8+1+16-17. Reproduction: Due to the conservation status of the gonads, neither the sex nor the maturation stage of the 451 mm TL specimen could be identified.

Stargazer *Uranoscopus scaber* Linnaeus, 1758 (Fig. 1G)

Material examined: MHNUSC 25170-1, female, 330 mm TL, 258 mm SL; 12th January 2012, Galician waters, 42.8390 °N, -9.2810 °W, 60 m depth; MHNUSC 25170-2, female, 242 mm TL, 184 mm SL; 19th January 2017, Galician waters, 42.8814 °N, -9.2582 °W, 15 m depth; MHNUSC 25170-3, female, 302 mm TL, 228 mm SL; 23th June 2016, Galician waters, 43.7268 °N, -7.4486 °W, 25 m depth; MHNUSC 25170-4, female, 273 mm TL, 207 mm SL; 4th July 2018, Galician waters, 42.4285 °N, -9.0035 °W, 50 m depth; MHNUSC 25170-5, female, 279 mm TL, 212 mm SL; 13th March 2019, Galician waters, 43.3276 °N -8.7456 °W, 53 m depth. Morphology: HL: 33-38.2;

PO: 7.6-9.7; POL: 20.3-26.6; ED: 3.3-3.9; IO: 6.1-7.8; PD1:38.8-45.2; PD2:50.4-57;
 DB1: 8.7-11; DB2: 31-38.7; PA: 50-54.3; AB: 33.7-39.6; PV: 9.4-13; PP: 25-29.9; VL:
 19.8-22.8; PL: 30.7-36; CP: 10.1-11.1; BH: 25.5; D1: IV; D2: 14-15; A: I+13; P: 16-18;
 V: 5; BR: 5. Reproduction: All the analysed specimens were females and two of them,
 273 mm and 279 mm TL individuals, seemed to be close to spawning capable stage
 because of the appearance of advanced vitellogenic oocytes. However, the maturation
 stage of the other three specimens could not be established.

European barracuda *Sphyræna sphyræna* (Linnaeus, 1758) (Fig. 1H)

Material examined: MHNUSC 25172-1, 351 mm TL, 302 mm SL, 17th June
 2009, 42.4230 °N, -8.7039 °W, 6 m depth; MHNUSC 25172-2, 330 mm TL, 287 mm
 SL, 17th June 2009, 42.3287 °N, -8.8521 °W, 15 m depth; MHNUSC 25172-3, 400 mm
 TL, 356 mm SL, 24th October 2014, 43.2846 °N, -9.0694 °W, 25 m depth. MHNUSC
 25172-4, female, 465 mm TL, 403 mm SL, 16th January 2018, 42.8950 °N, -9.2084 °W,
 45 m depth. Morphology: HL: 29.8-30.3; PO: 14-15; POL: 10.6-12.1; ED: 3.9-5; IO:
 4.6-5.7; PD1: 44.7-45.9; PD2: 70.2-74.4; DB1: 6.3-9.6; DB1: 8.3-9.1; PA: 70.2-74.9;
 AB: 7.9-8.9; PP: 29.2-31.4; PV: 44.1-46.7; PL: 9.4-10.7; VL: 7.7-8.9; BH: 11.5-12.4;
 D1: V; D2: I+9; A: II+9; P: 13; V: I+5; BR: 7; SLL: 136-145. Reproduction: The gonad
 of the only histologically processed individual for reproductive assessment presented
 primary growth ($67.80 \pm 10.60 \mu\text{m}$), cortical alveoli ($122 \pm 20.90 \mu\text{m}$) and few and
 dispersed early vitellogenic oocytes ($199 \pm 26.50 \mu\text{m}$), characteristic of developing
 phase initiating the annual sexual cycle.

273

274 3.2. Molecular Identification

275

As part of the Galician fish barcoding initiative, 23 sequences of *COI* from eight different species were obtained and employed as queries to track the BOLD database using its own identification tool. The return consists of every *COI* barcode record with a species level identification and a minimum sequence length of 500 bp. This includes many species represented by only one or two specimens as well as all species with interim taxonomy. Most of the *COI* sequences obtained a maximum identity value of 100% with voucher specimens of the same species present in the database, and was also coincident with the results of the morphological examinations. In the case of *C. ruber*, no match was obtained due to the fact that the barcoding database lacks records of this species. The *COI* sequence obtained from *D. volitans* was unambiguously identified by the search engine coinciding with the morphological assignation. Interestingly, the alignment of the available sequences of this species produced two robust groupings in a representation of Neighbor-Joining that also showed a coherent geographic division between the Atlantic Ocean and the Mediterranean Sea (Fig. 3). While the genetic distance within each group was kept at low values of 0.2%, the distance separating both groupings was 3.2%, 16 times higher.

4. Discussion

The presence of warm-water affinity fishes in the temperate waters of the Atlantic is occasional but recurrent over time. Integrative studies of newcomer individuals will provide important information of these species in a new area. In this case, morphological and genetic analysis will allow us to ensure the correct taxonomic identification and to find geographical divergences. Moreover, analysis of the reproductive condition provides information on the reproductive potential of the species

studied at a certain time of the year, useful for classifying them as seasonal migrant visitors or established local spawners.

All recorded species are at or near the northern limit of their range of distribution in the eastern Atlantic, and only some of them were occasionally reported further north (Quigley et al., 2004; Quigley, 2007; Anderson, 2016; Russell, 2016). The records reported here add new biological and biogeographical information for the eastern Atlantic in the present climate change scenario. Several species, previously scarce or rare, such as *U. scaber* and *S. sphyraena*, have become more frequent, while others, such as *D. polystictum* and *D. volitans* are new records to the zone. For instance, the record of *D. polystictum* supposes a large latitudinal jump in its distribution range of about 3000 km northwards (Smith-Vaniz, 2015; Deshmukh et al., 2017), and constitutes a new extended northern limit for its distribution in the eastern Atlantic. Moreover, the 1242 mm SL of *D. polystictum* establishes a new maximum size for the species, greater than 1100 mm reported until now (Vakily et al., 2002). The specimen of *D. volitans* constitutes the first record in Galician waters, although this species has been found occasionally further north, to Ireland (Quigley et al., 2004). The diagnostic characters of *D. volitans* include a first dorsal fin with two free anterior dorsal-fin spines, with their bases closely adjacent to each other, interconnected by only a basal membrane and separated from the rest of the dorsal fin (Roux, 1986; Smith-Vaniz, 2016). However, the first two spines are missing in our individual, where only four spines, all well interconnected by a complete membrane, can be observed, without any evidence of rupture, or amputation. The records of *A. anthias* in Galicia constitute the present northern boundary of its distribution in the eastern Atlantic (Smith-Vaniz and Iwamoto, 2015). This species was originally known in Galicia for three individuals caught between 1979 and 1981 (Devesa and Solórzano, 1983), but only seven individuals have

been recorded afterwards. The catch of *H. didactylus* supposes the second record in a short period, which confirms its presence in Galician waters (Bañón et al., 2019).

The identification of these species by the similarity of their barcodes with those existing in the BOLD database was successful in all cases where there were representatives in the latter. The deposit for the first time of *C. ruber* barcodes in the BOLD database is a remarkable fact of the present investigation. As serendipity, the identification of the barcode of the individual *D. volitans* caught in Galician waters allowed the observation of a certain degree of geographical differentiation between the Atlantic and the Mediterranean individuals. While intraspecific values in both geographic groups are typically low, the distance value separating them rises to congeneric ranges. This result, together with the presence of morphological differences found in the specimen examined, suggests the possible occurrence of crypticism. The existence of numerous catalogued synonyms for *D. volitans* (Fricke et al., 2020) suggests that this could be a case of erroneous synonymizing of another sister species that would require taxonomic resurrection. Another explanation would be the possibility of heteroplasmy (the presence of more than one type of mitochondrial genome in the same individual) in this species. These hypotheses deserve to be investigated through the morphological examination of new individuals and the alignment of their *COI* sequences and, if possible, the comparison of nuclear markers (to avoid bias induced by the maternal transmission of mitochondrial genomes).

Taken into account the year of the first record, species already reported in the past (*S. sphyraena*, *H. didactylus*, *U. scaber*) but which have recently reappeared, can be distinguished from the group of only recently found species (*D. volitans*, *D. polystictum*, *S. rivoliana*, *A. anthias*, *C. ruber*). Despite the great time difference in the presence of these two groups of species, there is not enough information to relate these

two groups to native and non-native species. Time lags can be found throughout the range expansion process, including in the arrival, establishment, and impacts of colonizers (Crooks, 2005). Moreover, there is often a temporal detection lag between the real arrival time and the first published record of a new migrant species (Costello and Solow, 2003). These latency periods can range from few years to several centuries and could be the cause of the long period elapsed until these old species are found again. However, a lesser historical sampling effort than contemporary effort should not be ruled out as possible cause of this lag. Among the reported species in the past, *U. scaber* with a ratio of 1.3 individuals/year and *S. sphyraena* with 0.6 individuals/year are the most recorded species. With regard to newly-emerging species, *S. rivoliana* with a ratio of 2.2 individuals/year is the most represented species, by only 0.2 individuals/year in *A. anthias* and *C. ruber*.

Although our sampling is opportunistic, not standardized, the ratio of individuals by year can be used as a rough quantitative index for the new colonizer species, probably related to the warming of the waters and the tropicalisation phenomenon, and the monitoring of this process over time.

Changes in species distribution should be particularly obvious in those transitional areas that are close to biogeographic boundaries, i.e., at the limits of regions inhabited by a different biota (Bianchi, 2007). Galicia, which is located in the northwest corner of the Iberian Peninsula, is a transitional zone between the warm-temperate north-eastern Atlantic and the cold-temperate regions (Kaimuddin et al., 2016) and an obligatory way of southern species of the continental shelf displacing northwards. This seems to be confirmed by the numerous records of tropical fishes reported for the first time in this area such as the red cornetfish *Fistularia petimba* Lacépède 1803 (Bañón and Sande, 2008), the redbanded seabream *Pagrus auriga* Valenciennes 1843, bastard

grunt *Pomadasys incisus* (Bañón et al., 2014) and the prickly puffer *Ephippion guttifer* (Bañón et al., 2018) among others.

In spite of that continuous occurrence of new tropical fishes, there are very few studies regarding the impact of these species on the native ecosystems. Warming seems to be implicated in the increase of strict herbivorous fishes such as the newcomers *Kyphosus sectatrix* and *K. vaigiensis*, which could have affected negatively some native algae populations, already declining by the warming itself (Bañón et al., 2017). A recent investigation has showed the introduction of new parasitic fauna into European Atlantic waters by the arrival of the two non-native tropical fishes *E. guttifer* and *Parapristipoma octolineatum* (Rodríguez et al., 2019). These foreign parasites could be more damaging to local hosts because there has not been evolutionary time to reach an equilibrium relationship (Azzurro, 2010).

This study shows evidence of normal gonadal development and spawning activity for the species analysed. The reproductive aspects of the fishes are important cues that can provide information regarding settlement and constitution of new populations (Bañón et al., 2008), since colonizers that reach the maturation and become active spawners are key in such a process (Azzurro, 2010). It has been documented that the spawning period of *S. sphyraena* takes place during spring-summer in Egyptian Mediterranean waters off Alexandria (Allam et al., 2004), what could fit with the fact that the individual caught on January presented signs of ovarian developing phase. *Halobatrachus didactylus* male caught in December presented signs of spawning capability, as in Bañón et al. (2019), which male specimen captured in July, 2018 also seemed to be in spawning capable condition. This could be key to determine if this species could be generating stable populations in the study area. Regarding size at maturation of *H. didactylus*, i.e. size at which half of the population reaches maturity, was

302 mm TL in the south of Spain (Palazón-Fernández et al., 2001), slightly higher than the 258 mm TL of the spawning capable male processed. Çoker et al. (2008) documented the reproductive period of *U. scaber* in Aegean Sea ranging from March to September, with a peak in May, encompassing females between 170-291 mm TL, so in accordance with our results, since two specimens captured in this season (in March, 279 mm TL and July, 273 mm TL) were the ones that showed signs of an upcoming spawning activity.

From the two specimens of *C. ruber*, the female of 182 mm TL showed evidence of asynchronous oocyte development (Wallace and Selman, 1981; Murua and Saborido-Rey, 2003), and the presence of hydrated and post ovulatory follicles indicates recent spawning activity of a batch spawner fish species (Brown-Peterson et al. 2011). It is relevant to indicate that both *C. ruber* and *A. anthias* have been suggested to be protogynous hermaphrodites (Tortonese, 1972; Micarelli et al., 2005). However, as far as we known, this reproductive strategy has not been previously confirmed by histological procedures in any of these species. This study provides more clues about this type of sequential hermaphroditism, as we observed melanomacrophage centres in *C. ruber* (295 mm TL) and *A. anthias* (258 mm TL) testes. These structures are frequent after sex transition in hermaphroditic fish species because of female tissue degeneration through phagocytosis during sex reversal period (Lo Nostro and Guerrero, 1996; Costa et al., 2016). That may be an indicator that the individuals once were mature females able to spawn that ended up becoming functional males at the moment of the capture. Nevertheless, more research effort is required to confirm this.

Oocyte size is a commonly reported life-history parameter that can be used as criteria for oocyte stage and maturity phase classification. Cortical alveoli oocytes, of the most developed stage observed in *D. volitans*, did not exceed 91 µm. Cortical

alveoli oocytes were reported in *S. sphyraena* ranging from about 100 μm to 162 μm , in line with Villegas-Hernández et al. (2014), which described sizes from 100 μm to 250 μm for this stage. Early vitellogenic oocytes of *S. sphyraena* were between 169 and 256 μm , smaller than the 300-400 μm described as immature by Allam et al. (2004) but similar to 200-350 μm reported by Villegas-Hernández et al. (2014), both in the Mediterranean Sea.

Summarizing, histological examination of reproductive tissue provides evidence of spawning activity for some species, i.e. *A. anthias*, *H. didactylus* and *C. ruber*. However, no spawning capable females of *A. anthias* or *H. didactylus* were detected, so their settlement cannot be verified based on local spawning activity. Regarding *C. ruber*, the female specimen analysed presented oocyte structures, hydrated oocytes and recent post ovulatory follicles, indicating very recent spawning (Lowerre-Barbieri et al., 2009). Thus, we consider *C. ruber* as a potential settled local spawner. For the rest of the species, we do not have clear evidence of local spawning activity, so, with current information we could classify them as vagrant species.

One of the expected effects of global warming will be an increase in the variation of the abundance and distribution of marine organisms, which can already be detected, but information at the appropriate temporal and geographical scales is often lacking to observe these patterns (Azzurro et al., 2011). Documenting the arrival of a fish species to a new region is crucial since it is the only measure in time and space available to scientists (Shakman et al., 2017). Moreover, monitoring the spread of these species and its potential for reproduction and settlement is crucial to understand its dynamics of colonization, how a new species arrives, what its movements and developments are and the impact that it may have (Azzurro, 2010). The data obtained of long-term fish monitoring has increased the knowledge about the occurrence of warm

water affinity fishes in temperate latitudes like the Galician waters. Many of the findings reported here constitute the current northern distribution boundary in the eastern Atlantic, highlighting the important role that the Galician waters play in the study of this phenomenon in the Atlantic European waters.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Rafael Bañón: Conceptualization, Methodology, Resources, Writing- Original draft preparation, Writing- Reviewing and Editing. **Marta Caballero-Huertas:** Resources, Writing- Original draft preparation, Writing- Reviewing and Editing. **Alexandre Alonso-Fernández:** Formal analysis, Writing- Original draft preparation, Writing- Reviewing and Editing. **David Barros-García:** Resources, Writing- Original draft preparation, Writing- Reviewing and Editing. **Jesús Otero:** Resources. **Alejandro de Carlos:** Resources, Writing- Original draft preparation, Writing- Reviewing and Editing.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Acknowledgments

The authors would like to thank to all Confrarías staff of Galician, technical assistances, spear fishermen and artisanal fishers who kindly donating the individuals and associated data. Special thanks to Berta Ríos (Confraría de Cangas) and José María (Confraría de Fisterra) for their continuous collaboration and the supply of numerous individuals. Also thanks to Lucia Sánchez-Ruiloba (IIM-CSIC) for the help with the fish photographic composition.

References

- Allam, S.M., Faltas, S.N., Ragheb, E., 2004. Reproductive biology of *Sphyræna* species in the Egyptian Mediterranean waters off Alexandria. Egypt J. Aquat. Res. 30, 255–270.
- Anderson, W.D., 2016. Callanthiidae. In: Carpenter, K.E., De Angelis, N. (Eds.), The living marine resources of the Eastern Central Atlantic, Vol. 4: Bony fishes part 2 (Perciformes to Tetradontiformes) and Sea turtles. FAO, Rome, pp. 2414–2415.
- Azzurro, E., 2010. Unusual occurrences of fish in the Mediterranean Sea: an insight into early detection. In: Golani, D., Appelbaum-Golani, B. (Eds.), Fish Invasions of the Mediterranean Sea: Change and Renewal. Pensoft Publishers, Sofia-Moscow, pp. 99–126.
- Azzurro, E., Moschella, P., Maynou, F., 2011. Tracking signals of change in Mediterranean fish diversity based on local ecological knowledge. PLoS ONE, 6, e24885. <https://doi.org/10.1371/journal.pone.0024885>

- 500 Bañón, R., del Río, J.L., Piñeiro, C., Casas, M., 2002. Occurrence of tropical affinity
 501 fishes in Galician waters NW Spain. J. Mar. Biol. Assoc. UK 82 (5), 877–880.
 502 <https://doi.org/10.1017/S0025315402006288>
- 503 Bañón, R., Garazo, A., 2006. Presencia de Medregal negro *Seriola rivoliana*
 504 Valenciennes, 1833 y barracuda *Sphyraena sphyraena* (Linnaeus, 1758)
 505 (Perciformes) en la costa de Galicia. NACC Biología 15, 95–97.
- 506 Bañón, R., Sande, C., 2008. First record of the cornetfish *Fistularia petimba*
 507 (Syngnathiformes: Fistularidae) from Galician waters. A northernmost
 508 occurrence in the eastern Atlantic. J. Appl. Ichthyol. 24 (1), 106–107.
 509 <http://dx.doi.org/10.1111/j.1439-0426.2007.00918.x>
- 510 Bañón, R., Garazo, A., Fernández, A., 2008. Note about the presence of the lumpsucker
 511 *Cyclopterus lumpus* (Teleostei, Cyclopteridae) in Galician waters (NW Spain). J.
 512 Appl. Ichthyol. 24 (1), 108–109. [http://dx.doi.org/10.1111/j.1439-](http://dx.doi.org/10.1111/j.1439-0426.2007.00839.x)
 513 [0426.2007.00839.x](http://dx.doi.org/10.1111/j.1439-0426.2007.00839.x)
- 514 Bañón, R., Barros-García, D., Mucientes, G., de Carlos, A., 2014. Northernmost records
 515 of *Pagrus auriga* (Actinopterygii: Perciformes: Sparidae) and *Pomadasys*
 516 *incisus* (Actinopterygii: Perciformes: Haemulidae) in the eastern Atlantic. Acta
 517 Ichthyol. Piscat. 44 (4), 323–327. <http://dx.doi.org/10.3750/AIP2014.44.4.07>
- 518 Bañón, R., Arronte, J.C., Armesto, A., Barros-García, D., de Carlos, A., 2016. Halosaur
 519 fishes (Notacanthiformes: Halosauridae) from Atlantic Spanish waters according
 520 to integrative taxonomy. Zootaxa 4184 (3), 471–490.
 521 <http://dx.doi.org/10.11646/zootaxa.4184.3.3>
- 522 Bañón, R., Barros-García, D., de Carlos, A., 2017. Integrative taxonomy supports the
 523 presence of two species of *Kyphosus* (Perciformes: Kyphosidae) in Atlantic

- European waters. Sci. Mar. 81 (4), 467–475.
<http://dx.doi.org/10.3989/scimar.04601.08A>
- Bañón, R., Alonso-Fernández, A., Barros-García, D., Rios, M., de Carlos, A., 2018. Geographic range expansion of *Ephippion guttifer* (Tetraodontidae) in the north-eastern Atlantic. J. Fish Biol. 93 (4), 733–737. <https://doi.org/10.1111/jfb.13761>
- Bañón, R., Tejerina, R., Morales, X., Alonso-Fernández, A., Barros-García, D., de Carlos, A., 2019. Unusual occurrences of fishes along the Northeast Atlantic: new biological and distributional data. Mediterr. Mar. Sci. 20 (1), 189–196. <http://dx.doi.org/10.12681/mms.19307>
- Bianchi, C.N., 2007. Biodiversity issues for the forthcoming tropical Mediterranean Sea. Hydrobiologia 580, 7–21. <https://doi.org/10.1007/s10750-006-0469-5>
- Belkin, I.M., 2009. Rapid warming of Large Marine Ecosystems. Prog. Oceanogr. 81 (1-4), 207–213. <https://doi.org/10.1016/j.pocean.2009.04.011>
- Belkin, I.M., 2016. Sea surface temperature trends in large marine ecosystems. In: IOC, UNESCO, UNEP (Eds.), Chapter 5.2, Large Marine Ecosystems: Status and Trends. United Nations Environment Programme, Nairobi, pp. 101–109.
- Boero, F., Féral, J.P., Azzurro, E., Cardin, V., Riedel, B., Despalatović, M., Munda, I., Moschella, P., Zaouali, J., Fonda-Umani, S., Theocharis, A., Wiltshire, K., Briand, F., 2008. Climate warming and related changes in Mediterranean marine biota. CIESM Workshop Monographs, 35, 5–21.
- Booth, D.J., Bond, N., Macreadie, P., 2011. Detecting range shifts among Australian fishes in response to climate change. Mar. Freshw. Res. 62 (9), 1027–1042. <https://doi.org/10.1071/MF10270>

- 547 Brierley, A.S., Kingsford, M.J., 2009. Impacts of climate change on marine organisms
 548 and ecosystems. *Curr. Biol.* 19 (14), R602–R614.
 549 <https://doi.org/10.1016/j.cub.2009.05.046>
- 550 Brown-Peterson, N.J., Wyanski, D.M., Saborido-Rey, F., Macewicz, B.J., Lowerre-
 551 Barbieri, S.K., 2011. A standardized terminology for describing reproductive
 552 development in fishes. *Mar. Coast. Fish.* 3, 52–70.
 553 <https://doi.org/10.1080/19425120.2011.555724>
- 554 Çoker, T., Akyol, O., Özaydın, O., Leblebici, S., Tosunoğlu, Z., 2008. Determination of
 555 batch fecundity in *Uranoscopus scaber* Linnaeus, 1758 from the Aegean Sea,
 556 Turkey. *J. Appl. Ichthyol.* 24 (1), 85–87. [https://doi.org/10.1111/j.1439-](https://doi.org/10.1111/j.1439-0426.2007.01035.x)
 557 [0426.2007.01035.x](https://doi.org/10.1111/j.1439-0426.2007.01035.x)
- 558 Costa, M.P.V., Sampaio, L.A., Robaldo, R.B., Cousin, J.C.B., 2016. Seasonal changes
 559 in sex ratio and size-related sex reversal of the protogynous hermaphroditic
 560 bluespotted seabass *Cephalopholis taeniops* (Valenciennes, 1828). *J. Appl.*
 561 *Ichthyol.* 32 (5), 943–947. <https://doi.org/10.1111/jai.13094>
- 562 Costello, C.J., Solow, A.R., 2003. On the pattern of discovery of introduced species.
 563 *PNAS* 100 (6), 3321–3323. <https://doi.org/10.1073/pnas.0636536100>
- 564 Crooks, J.A., 2005. Lag times and exotic species: The ecology and management of
 565 biological invasions in slow-motion. *Écoscience* 12 (3), 316–329.
 566 <https://doi.org/10.2980/i1195-6860-12-3-316.1>
- 567 Deshmukh, A., Dragičević, B., Kumar-Paidi, C., Muniraj, K., 2017. New record of
 568 *Desmodema polystictum* from northwestern Indian Ocean. *Cybium* 41 (4), 379–
 569 380. <https://doi.org/10.26028/cybium/2017-414-009>
- 570 Devesa, S., Solórzano, M.R., 1983. Aportaciones para un mejor conocimiento de la
 571 ictiofauna del litoral gallego. *Cuad. INICE* 6, 37–45.

- 572 Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the
 573 bootstrap. *Evolution* 39 (4), 783–791. <https://doi.org/10.1111/j.1558-5646.1985.tb00420.x>
 574
- 575 Fricke, R., Eschmeyer, W.N., Van der Laan, R., 2020. Eschmeyer's catalog of fishes:
 576 genera, species, references.
 577 [http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.](http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp/)
 578 [asp/](http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp/) (accessed 03 April 2020).
- 579 Gómez-Gesteira, M., Gimeno, L., de Castro, M., Lorenzo, M.N., Álvarez, I., Nieto, R.,
 580 Taboada, J.J., Crespo, A.J.C., Ramos, A.M., Iglesias, I., Gómez-Gesteira, J.L.,
 581 Santo, F.E., Barriopedro, D., Trigo, I.F., 2011. The state of climate in NW
 582 Iberia. *Clim. Res.* 48, 109–144. <http://dx.doi.org/10.3354/cr00967>
- 583 Kaimuddin, A.H., Laë, R., Tito de Morais, L., 2016. Fish species in a changing world:
 584 the route and timing of species migration between tropical and temperate
 585 ecosystems in eastern Atlantic. *Front. Mar. Sci.* 3 (162), 1–20.
 586 <https://doi.org/10.3389/fmars.2016.00162>
- 587 Quigley, D.T.G., Flannery, K., O'Shea, J., Blake, G., Smith, T., 2004. First records of
 588 flying gurnard *Dactylopterus volitans* (L.) from Irish waters and a review of NW
 589 European records. *Ir. Nat. J.* 27 (12), 458–460.
- 590 Quigley, D.T.G., 2007. Carangidae in Irish & Northern European Waters. *Sherkin*
 591 *Comment* 43, 14.
- 592 Lo Nostro, F.L., Guerrero, G.A., 1996. Presence of primary and secondary males in a
 593 population of the protogynous *Synbranchus marmoratus*. *J. Fish Biol.* 49 (5),
 594 788–800. <https://doi.org/10.1111/j.1095-8649.1996.tb00079.x>
- 595 Lloris, D., 2015. *Ictiofauna marina*. Omega, Barcelona.

- 596 López-Seoane, V., 1866. Reseña de la historia natural de Galicia. Sada, A Coruña.
- 597 Edición do Castro, O Castro-Sada, A Coruña.
- 598 Lowerre-Barbieri, S.K., Henderson, N., Llopiz, J., Walters, S., Bickford, J., Muller, R.,
- 599 2009. Defining a spawning population (spot-ted seatrout *Cynoscion nebulosus*)
- 600 over temporal, spatial, and demographic scales. Mar. Ecol. Prog. Ser. 394, 231–
- 601 245. <https://doi.org/10.3354/meps08262>
- 602 Micarelli, P., Barlettani, M., dell'Argentario, A.M., dei Navigatori, L., 2005. Husbandry
- 603 of *Anthias anthias* under natural conditions. Bull. Inst. Océanogr. (Monaco), 77
- 604 (1477), 127–129.
- 605 Murua, H., Saborido-Rey, F., 2003. Female reproductive strategies of marine fish
- 606 species of the North Atlantic. J. Northwest Atl. Fish. Sci. 33, 23–31.
- 607 Nagahama, Y., 1983. The functional morphology of teleost gonads. In: Hoar, W.S.,
- 608 Randall, D.J., Donaldson, E.M. (Eds.). Fish physiology, Vol. 9. Academic Press,
- 609 New York, pp. 223–275.
- 610 Nei, M., Kumar, S., 2000. Molecular evolution and phylogenetics. Oxford University
- 611 Press, Oxford.
- 612 Palazón-Fernández, J.L., Arias, A.M., Sarasquete, C., 2001. Aspects of the reproductive
- 613 biology of the toadfish, *Halobatrachus didactylus* (Schneider, 1801) (Pisces:
- 614 Batrachoididae). Sci. Mar. 65 (2), 131–138.
- 615 <https://doi.org/10.3989/scimar.2001.65n2131>
- 616 Philippart, C.J.M., Anadón, R., Danovaro, R., Dippner, J.W., Drinkwater, K.F.,
- 617 Hawkins, S.J., Oguz, T., O'Sullivan, G., Reid, P.C., 2011. Impacts of climate
- 618 change on European marine ecosystems: observations, expectations and
- 619 indicators. J. Exp. Mar. Biol. Ecol. 400 (1-2), 52–69.
- 620 <https://doi.org/10.1016/j.jembe.2011.02.023>

- Quéro, J.C., 1998. Changes in the Euro-Atlantic fish species composition resulting from fishing and ocean warming. *Ital J Zool* 65 (1), 493–499.
<https://doi.org/10.1080/11250009809386873>
- Quigley, D.T.G., Flannery, K., O'Shea, J., Blake, G., Smith, T., 2004. First records of flying gurnard *Dactylopterus volitans* (L.) from Irish waters and a review of NW European records. *Ir. Nat.' J.* 27 (12), 458–460.
- Quigley, D.T.G. (2007) Carangidae in Irish & Northern European Waters. *Sherkin Comment* 43: 14.
- R Development Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
<https://www.R-project.org/>.
- Rodríguez, H., Bañón, R., Ramilo, A., 2019. The hidden companion of non-native fishes in Northeast Atlantic waters. *J. Fish Dis.* 42 (7), 1013–1021.
<https://doi.org/10.1111/jfd.13005>
- Roux, C., 1986. Dactylopteridae. In: Whitehead, P.J.P., Bauchot, M.L., Hureau, J.C., Nielsen, J., Tortonese, E. (Eds.), *Fishes of North-eastern Atlantic and Mediterranean*, Vol. 3. UNESCO, Paris. pp. 1284–1285.
- Russell, B.C., 2016. Sphyraenidae. In: Carpenter, K.E., De Angelis, N. (Eds.), *The living marine resources of the Eastern Central Atlantic*, Vol. 4: Bony fishes part 2 (Perciformes to Tetradontiformes) and Sea turtles. FAO, Rome, pp. 2865–2872.
- Saitou, N., Nei, M., 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* 4 (4), 406–425.
<https://doi.org/10.1093/oxfordjournals.molbev.a040454>

- Shakman, E.A., Ben-Abdalha, A., Talha, F., Al-Faturi, A., Bariche, M., 2017. First records of seven marine organisms of different origins from Libya (Mediterranean Sea). *Bioinvasions Rec.* 6 (4), 377–382. <https://doi.org/10.3391/bir.2017.6.4.13>
- Solórzano, M.R., Roddríguez, J.L., Iglesias, J., Pereiro, F.X., Álvarez, F., 1988. Inventario dos Peixes do Litoral Galego (Pisces: Cyclostomata, Chondrichthyes, Osteichthyes). *Cadernos da área de Ciencias Biológicas, (Inventarios), Seminario de Estudos Galegos, Vol IV. Edición do Castro, O Castro-Sada, A Coruña.*
- Smith-Vaniz, W.F., 2015. *Desmodema polystictum*. The IUCN Red List of Threatened Species 2015: e.T190073A21909640. <http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T190073A21909640.en>
- Smith-Vaniz, W.F., Iwamoto, T., 2015. *Anthias anthias*. The IUCN Red List of Threatened Species 2015: e.T198711A42691624. <http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T198711A42691624.en>
- Smith-Vaniz, W.F., 2016. Dactylopteridae. In: Carpenter, K.E., De Angelis, N. (Eds.), *The living marine resources of the Eastern Central Atlantic, Vol. 4: Bony fishes part 2 (Perciformes to Tetradontiformes) and Sea turtles, FAO Species Identification Guide for Fishery Purposes. FAO, Rome, pp. 2249–2250.*
- Tortonese, E., 1972. On the affinities and systematic position of the genus *Callanthias* after a study of its type species *C. ruber* (Raf.) (Pisces Percoidei). *Ital. J. Zool.* 39 (1), 71–82. <https://doi.org/10.1080/11250007209429177>
- Vakily, J.M., Camara, S.B., Mendy, A.N., Marques, V., Samb, B., Dos Santos, A.J., Sheriff, M.F., Ould-Taleb-Sidi, M., Pauly, D., 2002. *Poissons Marins de la Sous-*

- 669 Région Nord-Ouest Africaine. EUR 20379 FR, Commission Européenne,
670 Bruxelles, Italy.
- 671 Villegas-Hernández, H., Muñoz, M., Lloret, J., 2014. Life-history traits of temperate and
672 thermophilic barracudas (Teleostei: Sphyraenidae) in the context of sea warming
673 in the Mediterranean Sea. J. Fish Biol. 84 (6), 1940–1957.
674 <https://doi.org/10.1111/jfb.12411>
- 675 Wallace, R., Selman, K., 1981. Cellular and dynamic aspects of oocyte growth in
676 teleosts. Am. Zool. 21 (2), 325–343. <https://doi.org/10.1093/icb/21.2.325>
677

Fig. 1 Warm affinity fishes collected in Galician waters: A: *Desmodema polystictum*, MHNUSC 25165-1, 1242 mm TL; B: *Halobatrachus didactylus*, MHNUSC 25166-1, 258 mm TL; C: *Anthias anthias*, MHNUSC 25168-5, 280 mm TL; D: *Dactylopterus volitans*, MHNUSC 25167-1, 392 mm TL; E: *Callanthias ruber*, MHNUSC 25169-1, 245 mm TL; F: *Seriola rivoliana*, MHNUSC 25170-1, 415 mm TL; G: *Uranoscopus scaber*, MHNUSC 25170-1, 330 mm TL; H: *Sphyræna sphyræna*, MHNUSC 25172-4, 465 mm TL.

Fig. 2 Histological slides of the gonads of A: *Anthias anthias* male 258 mm TL (developing), B: *Callanthias ruber* male 295 mm TL (developing), C: *Callanthias ruber* female 182 mm TL (spawning capable). MC = melanomacrophage center; POF = post ovulatory follicle; PG = primary growth oocyte; CA = cortical alveoli; EVT = early vitellogenesis; VTA = advanced vitellogenesis; MN = migratory nuclei.

Fig. 3 Neighbor-Joining tree of *Dactylopterus volitans* COI barcode sequences. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (2000 replicates) is shown next to the nodes. Only values higher than 70% are shown. The tree is drawn to scale; with branch lengths computed using the *p*-distance method and are in units of the number of base differences per site. The analysis involved 17 nucleotide sequences and 655 nucleotide positions.

CRedit authorship contribution statement

Rafael Bañón: Conceptualization, Methodology, Resources, Writing- Original draft preparation, Writing- Reviewing and Editing. **Marta Caballero-Huertas:** Resources, Writing- Original draft preparation, Writing- Reviewing and Editing. **Alexandre Alonso-Fernández:** Formal analysis, Writing- Original draft preparation, Writing- Reviewing and Editing. **David Barros-García:** Resources, Writing- Original draft preparation, Writing- Reviewing and Editing. **Jesús Otero:** Resources. **Alejandro de Carlos:** Resources, Writing- Original draft preparation, Writing- Reviewing and Editing.