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Ongoing tropicalization of marine fishes: is range expansion and establishment occurring in the Gulf of Cadiz (southernmost Europe)?

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Abstract

'Tropicalization', the phenomenon of species shifting their ranges, has become increasingly prevalent as a response to environmental modifications induced by global change. This study points to an accelerated tropicalization process of marine fish species in the Gulf of Cadiz, a bioinvasion hotspot adjacent to the Strait of Gibraltar. We report accelerated, unusual, and rare occurrences of 15 fish species expanding and potentially establishing their ranges in the Gulf of Cadiz, driven by ocean warming over the past decade. These new insights are the combined consequence of a range expansion of some species, likely facilitated by temperature increases, an intensification of maritime traffic (with a consequent rise in propagule pressure), and a possible increase in sampling efforts and citizen science.

Introduction

The effects of global warming are driving the poleward expansion of marine species' distribution ranges (Bates *et al.*, 2014; Zarzyczny *et al.*, 2024). The changes in marine fishes can be exceptionally rapid, with numerous species markedly responding to recent sea temperature increases (Azzurro, 2008). This process has been coined as 'tropicalization', and it has the potential to change community assemblages over decadal periods (Bianchi and Morri, 2003; Verges *et al.*, 2014) and induce long-term ecological and evolutionary consequences, such as ecosystem phase shifts, phenotypic interactions, and economic effects on fisheries and tourism (Zarzyczny *et al.*, 2024).

The most well-known instances occurred in temperate seas, where the biota has adapted to the large seasonal temperature variability characteristic of mid-latitudes (Schuster *et al.*, 2022). Since 1950, evidence of tropicalization in North-East Atlantic marine regions has been noted in several areas, initially described in Portuguese waters (Quéro, 1998; Quéro *et al.*, 1996), and subsequently in the North Sea (Beare *et al.*, 2004), British waters (Stebbing *et al.*, 2002), the northwest of Spain (Bañón *et al.*, 2002), Macaronesia (Afonso *et al.*, 2013; Brito *et al.*, 2005; Castro *et al.*, 2021), and the Mediterranean Sea (Bianchi and Morri, 2003), with the Gulf of Cadiz (GoC) being no exception.

The GoC, located on the Atlantic side adjacent to the Strait of Gibraltar, has been recognized as a bioinvasion hotspot due to the accelerated arrival of non-native species in recent years (Cuesta *et al.*, 2024; de Carvalho-Souza *et al.*, 2024a; González-Ortegón *et al.*, 2020b, 2020a). This process involves two primary components: the arrival of novel non-native species in south-western Europe and a creeping spread from the Mediterranean and African coasts, the latter known as the 'African Creep' – the northward expansion of Atlantic native species with thermal affinities (Canning-Clode and Carlton, 2017). The occurrence and spread of thermophilic species from the African continent in the GoC are influenced by four main factors: human-mediated introductions, the influx of Mediterranean waters, Lessepsian migration, and ongoing sea warming. The first three processes provide the presence of these species outside their natural range, while the fourth also supplies the favourable conditions for their northward expansion to Europe from Africa.

Here, we present accelerated, unusual, and rare occurrences of 15 fish species that are expanding and potentially establishing their distribution range in the GoC due to ocean warming. We include additional data on the number of records, sizes, and distributions, as well as the possible pathways of their introduction. These findings improve our understanding of the tropicalization process in the region and highlight the critical need for ongoing monitoring and conservation efforts.

Material and methods

Data on unusual fish species reported in the GoC for the period 2008–2024 have been compiled. Since 2013, the Agencia de Gestión Agraria y Pesquera de Andalucía has carried out fishing monitoring of species that occur in areas of the GoC. Also, in the last decade, the Instituto de Ciencias Marinas de Andalucía has built a database of terminological and identification data for commercial fish species on the Andalusian coasts, called 'ICTIOTERM' (http://www.ictioterm.es). During these monitoring and projects, we also maintained close relationships with several stakeholders, such as fishers, staff of fish markets, and technicians from fishermen's associations. Additional information was obtained from spearfishers, as citizen science has become a valuable tool for detecting and monitoring non-native species. Thus, reports of non-directed catches were also obtained opportunistically from professional and recreational fishermen and other users at several localities throughout the GoC. To ensure accuracy, records were included only if they contained specimen data and photographs, and each species was verified by ichthyologists with extensive expertise in fish research. The species classification is organized in taxonomic order, in accordance with 'Catalog of Fishes' (Van der Laan *et al.*, 2024). Species names are alphabetized within each family.

To review the non-native occurrence records of fish species, we conducted comprehensive bibliographic research, compiling and updating records. The search encompassed literature published from 1970 to September 2024, sourced from the Web of Science database and Google Scholar. The search employed a variety of keywords for each species, including actual and previous scientific names, common English names, and others such as 'tropicalisation/tropicalization', 'first record', 'occurrence', 'range expansion', 'non-native', 'exotic', 'alien'. Additional bibliographic sources were obtained by reviewing the reference lists of the localized publications. Furthermore, the information was cross-verified with the updated national checklist of marine fish in Spanish and Portuguese waters (Báez *et al.*, 2019; Carneiro *et al.*, 2014), data obtained from the GBIF database (https://www.gbif.es), and citizen science platforms (e.g. iNaturalist.com and Observadoresdelmar.es).

Results

We present findings on 15 fish species across 12 families that are expanding and/or potentially establishing their distribution range in the GoC (Supplementary Table S1).

Carlarius parkii Günther, 1864, family: Ariidae, order: Siluriformes

In 2021, an individual of *Carlarius parkii* Günther, 1864 was captured in the GoC and subsequently commercialized in markets near the mouth of the Guadalquivir (Figure 1a). The individual was estimated to be ∼70 cm in total length. Typically found in the East Atlantic region from Cape Blanc (Mauritania) to Angola, *C. parkii* has been documented outside its native range only once in Israel (Golani and Ben-Tuvia, 1986). Notably, this marks the first recorded instance of this species in European waters (Supplementary Figure S1). This species primarily inhabits coastal waters on muddy bottoms, with recurrent forays into the brackish waters of estuaries and coastal lagoons (Conand *et al.*, 1995). This species is a benthic predator that feeds mainly on fish and shrimp, displaying opportunistic feeding behaviour (Diouf, 1996). Males exhibit buccal incubation, carrying fertilized eggs in their mouths until hatching (Golani *et al.*, 2002), a reproductive strategy that may enhance offspring survival during dispersal.

Grammicolepis brachiusculus Poey, 1873, family: Grammicolepididae, order: Zeiformes

In 2022, a specimen of *Grammicolepis brachiusculus* Poey, 1873 was captured in the GoC and later sold in a local market (Figure 1b); in 2023, two additional specimens were captured in the same area and were also commercialized. The specimen was estimated to be ∼50 cm in total length. The Thorny tinselfish, *G. brachiusculus* is a rare deep ocean species distributed across the Pacific Ocean, Indian Ocean, and the western Atlantic (Froese and Pauly, 2024). In the northeastern Atlantic, this species has only previously been observed in rare reports (Quigley and Ní Churraidhin, 2021): off Sisargas Island, NW Spain (Quéro, 1998); off El Hierro, Canarias Island (González *et al.*, 2000); off Brittany, NW France (Quéro *et al.*, 2001); off the Algarve coast, southern Portugal (Vasconcelos *et al.*, 2003); on Pico Island and Terceira Island, Azores (Barreiros *et al.*, 2011); in Grindavikurdjup, SW Iceland (Valdimarsson *et al.*, 2012); off Halinn, NW Iceland (Valdimarsson *et al.*, 2012); West of Hebridies, Scotland (Iglésias, 2014); and on the Porcupine Bank, West Ireland (Quigley and Ní Churraidhin, 2021). Previously, in the GoC, two specimens were documented in technical reports (Sobrino and Burgos, 2012) during a long-term bottom trawl survey program. Alongside the specimens described here, these constitute the first five records of the species in this locality (Supplementary Figure S2). Currently, the available information on the biology and ecology of this species is sparse.

Diretmichthys parini Post & Quéro, 1981, family: Diretmidae, order: Trachichthyiformes

Two specimens of *Diretmichthys parini* Post & Quéro, 1981 were captured in 2022 and 2023 at the GoC and sold in fish markets (El Puerto de Santa Maria and Sanlúcar de Barrameda, respectively) (Figure 1c). The total length of the individual was estimated to be approximately 35–40 cm. The Parin's spinyfish, *D. parini* is a deep-water species found in the Pacific Ocean, Indian Ocean, and the Atlantic Ocean (Smith-Vaniz, 1986) (Supplementary Figure S3). Within the northeastern Atlantic, this species has previously been recorded off northwestern Morocco and the Madeira Archipelago (Post, 1986), off the Canary Islands (López-Abellán *et al.*, 1994), off the southern coast of Portugal (Sanches and Pinto, 1991), in the Bay of Biscay and Galician waters (Arronte and Heredia, 2006; Bañon *et al.*, 2016), off the northwest coast of Scotland and off the Faroe Islands, Northern Ireland (Quéro *et al.*, 1994, 1998), and off Iceland (Jónsson and Pálsson, 2003), and more recently, various records have been compiled for the North Sea and Nordic Sea (Cresson *et al.*, 2017, 2021; Lynghammar *et al.*, 2020). This is the first record of *D. parini* in the GoC. Limited data exist on the biology and ecology of this uncommon fish, but a 33-year-old specimen from the North Sea provided some insights (Cresson *et al.*, 2017). These authors analysing stable isotopes revealed their vertical feeding migrations between deep, cold habitats and shallower, warmer epipelagic zones to eat zooplankton. The species produces pelagic eggs, which may increase larval dispersal potential (Post, 1986).

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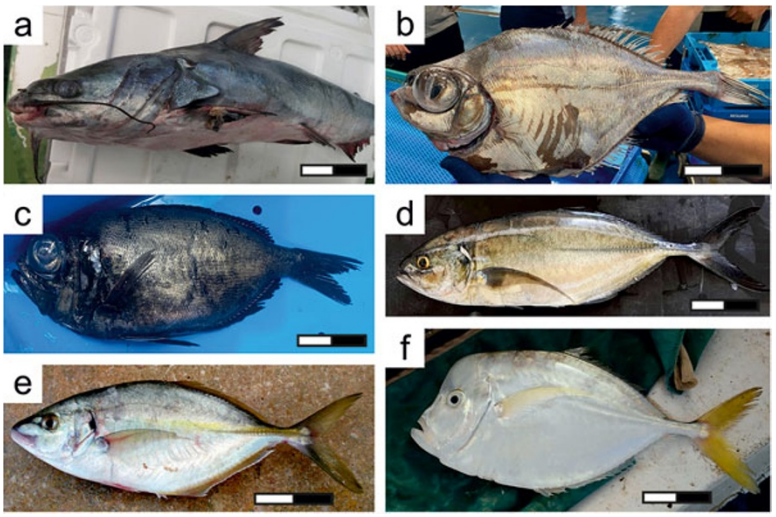

Figure 1. Newly observed species in the Gulf of Cadiz, ordered taxonomically: (a) *Carlarius parkii*; (b) *Grammicolepis brachiusculus*; (c) *Diretmichthys parini*; (d) *Caranx crysos*; (e) *Pseudocaranx dentex*; and (f) *Selene dorsalis*. Scale: 10 cm.

Caranx crysos Mitchill, 1815, family: Carangidae, order: Carangiformes

Between 2017 and 2024, several specimens ($n = 7$) of *Caranx crysos* Mitchill, 1815 were captured and sold in fish markets located in the GoC (Figure 1d). The total length of these specimens varied approximately between 30 and 35 cm. The blue runner, *C. crysos* is widely reported across the Atlantic Ocean, ranging from Brazil to Nova Scotia (Canada) in the western Atlantic and from Senegal to Angola in the east Atlantic, including the Mediterranean (Di Blasi *et al.*, 2024; Psomadakis *et al.*, 2011; Smith-Vaniz, 2002). It is established in the Canary Islands (Brito *et al.*, 2005). Recent expansions in its distribution range have been documented in several regions, including the Adriatic Sea (Dulčić *et al.*, 2009), the Bay of Biscay (Iglésias *et al.*, 2021; Quéro *et al.*, 1994), Galician waters (Bañon and Casas-Sánchez, 1997), the west coast of Ireland (Quigley, 2022), British and Newfoundland waters (Canada), and Argentine waters (Delpiani *et al.*, 2011; Devine and Fisher, 2014; Swaby *et al.*, 1996; Wheeler *et al.*, 2004), as well as in the present records. Although there have been several records, this species has not yet been documented in the Spanish Suratlantic waters (Supplementary Figure S4). The blue runner generally forms schools and is found inshore at depths of <100 m. Juveniles of *C. crysos* are frequently associated with jellyfish and floating debris (de Carvalho-Souza, 2015), while adults associate with rocky reefs (Smith-Vaniz, 2002). The blue runner is an opportunistic predator that primarily preys on small fish and crustaceans. Its length at sexual maturity ranges from approximately 210 to 250 mm, typically reached at 2.4–2.8 years of age (Sley *et al.*, 2012). This species is oviparous, exhibiting high fecundity and producing pelagic eggs that disperse with ocean currents (Sley *et al.*, 2012).

Pseudocaranx dentex Bloch & Schneider, 1801, family: Carangidae, order: Carangiformes

A single specimen of *Pseudocaranx dentex* Bloch & Schneider, 1801 was captured in May 2010 and sold at the Rota fish market (Figure 1e). Later occurrences included one individual in October 2013, another in November 2016, two in October 2018, one in June 2023, and at least five more individuals in 2024, with their total lengths varying approximately from 40 to 60 cm. The white trevally, *P. dentex* is a tropical reef species widely distributed on continental and island shelves across the Atlantic, the Mediterranean, and the Indo-Pacific (Smith-Vaniz, 2002) (Supplementary Figure S5). Only a few records of *P. dentex* are known from the Andalusian coast (ICTIOTERM, 2024; Rivas and Pasquier, 2003). In Galician waters, the species was recorded for the first time in May 1997 (Fernández-Cordero and Bañon, 1997). More recently, a northernmost occurrence was documented in the Istanbul Strait, which serves as the passage between the Sea of Marmara and the Black Sea (Keskin, 2023). The white trevally juveniles typically inhabit inshore waters, with young fish often seen in shoals following mullets, striped seabream, and other demersal fish on sandy bottoms, while adults live solitarily (Froese and Pauly, 2024). They commonly seek refuge from predators under floating structures (Keskin, 2023).

Selene dorsalis Gill, 1863, family: Carangidae, order: Carangiformes

In 2017, a specimen of *Selene dorsalis* Gill, 1863 was captured and sold in a local market in the GoC (Figure 1f). The estimated total length of the individual was approximately 30 cm. The African moonfish, *S. dorsalis* is a demersal species found in tropical and subtropical waters of the East Atlantic, from the Cape Verde Islands and Senegal to South Africa (Smith-Vaniz, 1986) (Supplementary Figure S6). Previously, it was recorded in Madeira (Wirtz *et al.*, 2008) and Canary Islands (Castro-Hernández, 2001), Moroccan waters (Baddyr and Guénette, 2001), Mediterranean Sea (Vella and Deidun, 2009), and GoC (Juarez *et al.*, 2006), this being the second record for this fish species in the GoC (Supplementary Figure S6). The African moonfish is a schooling species primarily found within a depth range of 20–100 m (Smith-Vaniz, 1986). It primarily feeds on small fish and planktonic crustaceans (Smith-Vaniz, 1986).

Seriola rivoliana Valenciennes, 1833, family: Carangidae, order: Carangiformes

Since 2016, several specimens ($n = 170$) of *Seriola rivoliana* Valenciennes, 1833 were captured and sold in fish markets in the GoC (Figure 2a). The total sizes of these individuals spanned approximately from 40 to 60 cm. The longfin yellowtail, *S. rivoliana* is frequently found in the Pacific Ocean, Indian Ocean, and the western Atlantic (Fischer, 1978), spanning at least 114

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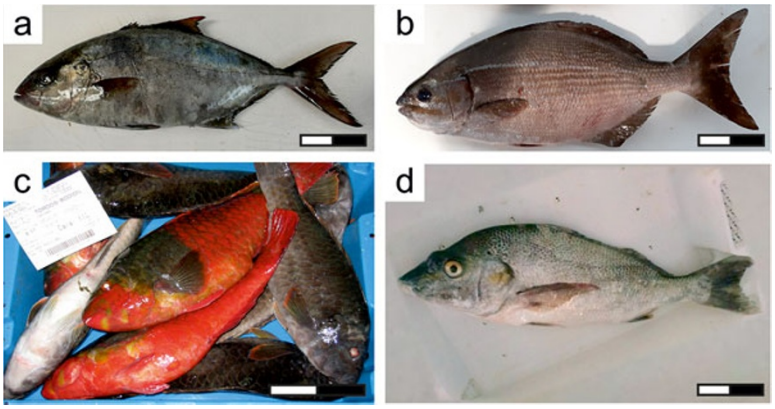

Figure 2. Newly observed species in the Gulf of Cadiz, ordered taxonomically: (a) *Seriola rivoliana*; (b) *Kyphosus vaigiensis*; (c) *Sparisoma cretense*; and (d) *Pomadasys rogerii.* Scale: 10 cm.

countries/territories (Froese and Pauly, 2024; Quigley, 2021) (Supplementary Figure S7). This species is also recorded in the Mediterranean Sea (Castriota *et al.*, 2002, 2004). Within the Iberian biogeographic regions, it has been recorded in Portugal (Fischer *et al.*, 1981), as well as observed in the Balearic Islands (Valls *et al.*, 2011), Port of Cadiz in 1995 (ICTIOTERM, 2024), and in the Bay of Biscay and Galician waters (Bañon and Garazo, 2006; Quéro, 1998). Adults of *S. rivoliana* are pelagic and epibenthic, while juveniles are typically found offshore, utilizing floating objects as shelter (Fischer, 1978).

Kyphosus vaigiensis Quoy & Gaimard, 1825, family: Kyphosidae, order: Centrarchiformes

Two individuals of *Kyphosus vaigiensis* Quoy & Gaimard, 1825 were captured in July 2015 and landed at the Rota and Chipiona fish markets (Figure 2b). Afterward, one individual was reported in 2020, two in 2021, and several specimens in 2022 (Supplementary Figure S8). These individuals ranged from around 45 to 55 cm in total length, a common size relative to the maximum of 70 cm (Froese and Pauly, 2024). This circumtropical species has a wide distribution across the Pacific, Indian, and Atlantic Oceans, as well as the Red Sea and Mediterranean Sea (Azurro et al. 2013; Groud *et al.*, 2021; Knudsen and Clements, 2013; Mannino *et al.*, 2015). It was first recorded in the waters of Galicia in 2014 with two specimens, marking the northernmost record in the eastern Atlantic (Bañon *et al.*, 2017). Typically, this species is found as adults over hard bottoms near the shore and coastline, while juveniles are often associated with floating objects (Knudsen and Clements, 2016).

Sparisoma cretense Linnaeus, 1758, family: Labridae, order: Labriformes

Since 2008, several individuals of *Sparisoma cretense* ($n = 100$) were captured and sold in fish markets along the Cadiz coast (Barbate, Algeciras, and Chipiona) (Figure 2c). These individuals ranged from around 20 to 30 cm in total length. The Mediterranean parrotfish, *S. cretense*, is distributed along the southern and eastern coasts of the Mediterranean, the northwest coast of Africa, and the Macaronesian archipelagos (Azores, Madeira, Canary Islands, and Cape Verde) (Froese and Pauly, 2024). Esposito et al. (2001) documented the northward expansion of this species in the Mediterranean Sea and its colonization process. Within the southwestern Iberian Peninsula, it has been recorded in the Ria Formosa lagoon, southern Portugal (Abecasis *et al.*, 2008), and in Bolonia and Tarifa, southern coast of Spain (ICTIOTERM, 2024; Otero and Galeote, 1996) (Supplementary Figure S9). The Mediterranean parrotfish is a reef-associated species that generally occurs in shallow water to about 50 m (Pollard *et al.*, 2012). The species feeds on algae and small invertebrates by utilizing its fused beak-like jaws to excavate or scrape the surfaces of rocks and carbonate substrates (Hoey and Bonaldo, 2018). The breeding season generally spans from July to September, and juveniles are recruited in late summer (Guidetti and Boero, 2001).

Pomadasys rogerii Cuvier, 1830, family: Haemulidae, order: Acanthuriformes

A single *Pomadasys rogerii* was observed at GoC in 2014 (Figure 2d). The specimen's total length was approximately 50 cm. The Pigsnout grunt, *P. rogerii*, is found in the Eastern Atlantic, from southern Mauritania to Angola (Froese and Pauly, 2024; Ly *et al.*, 1996). This is the first record of *P. rogerii* in European waters (Supplementary Figure S10). This coastal pelagic is often found on the seabed up to 60 m, but it is also found in estuaries (Ly *et al.*, 1996). The Pigsnout grunt is benthophagous, being one of the dominant species in the estuarine zones, especially during early life stages (Costa *et al.*, 2002).

Lobotes surinamensis Bloch, 1790, family: Lobotidae, order: Acanthuriformes

More than 30 individuals of *Lobotes surinamensis* Bloch, 1790 were sold in fish markets in the GoC between 2015 and 2023 (Figure 3a). An individual was first reported in Chipiona (GoC, SW Spain) in 2015, followed by increasing reports in several other localities in subsequent years (Supplementary Figure S11 and Table S1). Previously, a unique specimen was reported in the locality of Rota in 1998 (ICTIOTERM, 2024). These individuals had a total size ranging approximately from 26.5 to 51 cm. The tripletail, *L. surinamensis* is a pelagic species found in the tropical and subtropical waters of all oceans (Fisher, 1978; Iglésias *et al.*, 2020). Earlier, this species was considered exceptional or rare in the zone, as well as in the Azores (Afonso *et al.*, 2013; Santos *et al.*, 1997), Madeira (Wirtz *et al.*, 2008), and Canary Islands (Brito *et al.*, 2002; Espino *et al.*, 2018). Tripletails often associated with channel markers, jetties, wrecks, flotsam, *Sargassum* algae, or other types of drift algae and anthropogenic floating debris (Baughman, 1941; Dooley, 1972).

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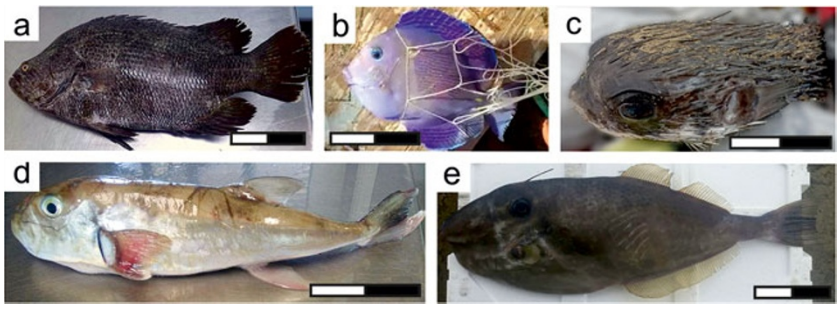

Figure 3. Newly observed species in the Gulf of Cadiz, ordered taxonomically: (a) *Lobotes surinamensis*; (b) *Acanthurus coeruleus*; (c) *Diodon holocanthus*; (d) *Lagocephalus laevigatus*; and (e) *Aluterus monoceros.* Scale: 10 cm.

Acanthurus coeruleus Bloch & Schneider, 1801, family: Acanthuridae, order: Acanthuriformes

In October 2021, an individual of *Acanthurus coeruleus* Bloch & Schneider, 1801 was captured in the GoC by an artisanal fisherman (Figure 3b). Known as the Blue Tang, this species is typically found in the Western Atlantic, ranging from New York and Bermuda to the Gulf of Mexico and Brazil, with additional records from Ascension Island in the Eastern Atlantic (Froese and Pauly, 2024). In the Mediterranean, *A. coeruleus* has been documented in Cyprus (Langeneck *et al.*, 2012), Israel (Golani *et al.*, 2015), Malta (Evans *et al.*, 2015), and the Canary Islands (Pajuelo *et al.*, 2016), marking this recent record in the Eastern Atlantic as the first for the Iberian Peninsula (Supplementary Figure S12). This surgeonfish reaches up to 39 cm in total length and inhabits coral reefs as well as inshore grassy or rocky areas, forming small groups and displaying primarily diurnal behaviour while feeding on algae (Böhlke and Chaplin, 1993).

Diodon holocanthus Linnaeus, 1758, family: Diodontidae, order: Tetraodontiformes

In November 2022, an individual of *Diodon holocanthus* Linnaeus, 1758 was found by a spearfisher in the coastal waters of the Cadiz Bay (Figure 3c). The total length of the individual was estimated to be approximately 30 cm. The long-spined porcupinefish, *D. holocanthus*, is a circumtropical species distributed along the Indian, Atlantic, and Pacific oceans (Froese and Pauly, 2024) (Supplementary Figure S13). In the eastern Atlantic, *D. holacanthus* has been known to inhabit southwestern Morocco and west-central Namibia (Duron and Queró, 1990), with records extending up to South Africa (Leis, 2001). This species has also been documented in the Canary Islands (Brito and Falcón, 2006) and the Azores Islands (Afonso *et al.*, 2013). Pelagic juveniles are often found under floating rafts, while demersal adults are found on all types of substrates, up to at least 100 m deep (Froese and Pauly, 2024). They feed on molluscs, urchins, and crustaceans at night (Leis, 2001).

Lagocephalus laevigatus Linnaeus, 1766, family: Tetraodontidae, order: Tetraodontiformes

An individual of *Lagocephalus laevigatus* Linnaeus, 1766 was collected in 2017 at the GoC (Figure 3d). The total length of the individual was estimated to be approximately 35 cm. The smooth puffer, *L. laevigatus* is an amphi-Atlantic species distributed in the western Atlantic Ocean from Bermuda and New England, USA, to Argentina, whereas in the eastern Atlantic Ocean, it is recorded from Mauritania to Namibia (Froese and Pauly, 2024). Previously, this species has had other records north of its distribution, in the Cies Islands in Galician waters (Bañon and Santas, 2011) and in the lower Guadiana estuary (Encarnação *et al.*, 2019), being the first report of this species for the GoC and the second for the Iberian Peninsula (Supplementary Figure S14). The smooth puffer typically inhabits shallow waters down to depths of 180 m, primarily on mud or silt substrates, where it is commonly encountered either solitary or in small groups (Shipp, 1981).

Aluterus monoceros Linnaeus, 1758, family: Monacanthidae, order: Tetraodontiformes

An individual of *Aluterus monoceros* Linnaeus, 1758 was captured in 2017 at the GoC (Figure 3e). The total length of the specimen was estimated to be approximately 50 cm. The Unicorn leatherjacket filefish, *A. monoceros*, is a circumtropical species distributed in the Western Atlantic Ocean from Massachusetts, USA, to Argentina; in the Eastern Atlantic Ocean along the west coast of tropical Africa; in the Eastern Pacific Ocean from Guatemala to Chile, and likely in Mexico; and in the Western Indian Ocean from Mozambique to South Africa (Froese and Pauly, 2024). This species has previously has been reported in the Azores (Santos *et al.*, 1997), Madeira (Freitas and Biscoito, 2002), and the Canary Islands (Brito, 2002), as well as in the Mediterranean Sea (Guallart and Vicent, 2009), off Arcachon, Bay of Biscay (Quéro and Laborde, 1996) and two specimens (1995 and 2008) in the coastal waters off Chipiona in the GoC (Galeote *et al.*, 1996; ICTIOTERM, 2024), making this the third specimen recorded occurrence in the studied area (Supplementary Figure S15). While *A. monoceros* adult are demersal, juveniles are pelagic and often associate with floating objects (Sommer *et al.*, 1996), a behaviour that may facilitate the dispersal of individuals from the main distribution area when conditions are favourable.

Discussion

This study reports new, unusual, and rare occurrences of 15 fish species in the GoC ecosystem, confirming a significant range expansion and the potential establishment of species previously observed only occasionally or regarded as uncertain within this region. Despite the uncertainty surrounding the introduction vector in many bioinvasion cases, the ecological interpretation of these occurrences can be divided into three main pathways.

First, two coastal fishes with similar habitats and distribution, *P. rogerii* and *C. parkii*, are reported for the first time in European waters, possibly as a result of the climate-induced range expansion of West African biota northwards into European waters ('African Creep'; Canning-Clode and Carlton, 2017), although accidental introduction via ballast waters cannot be completely ruled out. This process has been documented in recent years for species such as *Lysmata uncicornis* Holthuis & Maurin, 1952, and *Penaeus notialis* Pérez Farfante, 1967 (González-Ortegón *et al.*, 2024, 2020a). The

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movement of fish species during their pelagic phase (eggs, larvae, and juveniles) can occur via oceanic currents from the northwest African coast to the southwestern Iberian Peninsula. The near-surface circulation in the GoC is characterized by upper-thermocline North Atlantic Central Waters (Machín *et al.*, 2006). Intense mixing with South Atlantic Central Water occurs in the coastal waters of Northwest Africa, where the northward advection along the inshore side is largely driven by the poleward undercurrent associated with coastal upwelling (Arístegui *et al.*, 2006). On the other hand, the past four decades have seen a general increase in sea surface temperatures and a weakening of upwelling intensity in the Iberian/Canary and Northwest African regions (Pardo *et al.*, 2011). Notably, sea temperatures in the Northeast Atlantic have risen by at least 0.4°C per decade since the late 1980s (Brander *et al.*, 2003) and continue to rise (Supplementary Figure S16). As these trends persist, the warming waters of the GoC create increasingly suitable conditions for these species.

Additionally, species such as *A. coeruleus, A. monoceros, D. holocanthus, P. dentex*, and *S. dorsalis*, previously observed in the Macaronesia zone (Azores, Canary Islands, and Madeira Islands), could potentially expand their range across these islands, which might serve as a stepping-stone for further expansion, together with the favourable oceanographic conditions mentioned earlier. The Macaronesia islands likely served as a stepping-stone for other tropicalization cases of fishes and decapod crustaceans (Castro *et al.*, 2021; Schäfer *et al.*, 2019). This expansion pattern seems similar to what is happening in the Mediterranean, where several Lessepsian migrants, such as the lionfish, *Pterois miles* Bennett 1828 and the blue swimming crab, *Portunus segnis* Forskål 1775, start in the Levantine Sea and gradually spread into the western Mediterranean, with the latter arriving at the GoC (Bernardi *et al.*, 2024; de Carvalho-Souza *et al.*, 2023).

Some of the records appear to be well established in the GoC ecosystem: *S. rivoliana, L. surinamensis*, and *S. cretense*. In these cases, due to the ecological traits of these species, there are multiple dispersal mechanisms, both natural and anthropogenic. For the first two species, currents and ballast water in its pelagic phase (eggs, larvae, and juveniles) or by rafting underneath floating debris or *Sargassum* spp. may facilitate, under suitable conditions, the dispersal and settlement of individuals from the main occurrence area (Baughman, 1941; Dooley, 1972; Keskin, 2023). For *S. cretense*, considering its Mediterranean origin and expansion patterns (Esposito *et al.*, 2001), we can also hypothesize its arrival in the GoC through the Strait of Gibraltar.

The records of *D. parini* and *G. brachiusculus* demand a more thorough approach, considering their broad distribution in tropical and temperate waters of the Atlantic, Pacific, and Indian Oceans. Various studies have indicated that the apparent increase in the occurrence of these species in Northern European Atlantic waters might be associated with ocean warming (Barreiros *et al.*, 2011; Cresson *et al.*, 2017; Quéro *et al.*, 1994, 1998; Valdimarsson *et al.*, 2012). On the other hand, a review of Icelandic fishery records shows that several unpublished observations for *D. parini* were overlooked (Cresson *et al.*, 2021), as they were mainly collected by fishery observers and occasionally by the fishermen themselves. Consequently, the frequency of these records is significantly affected by individual motivations driven by the discovery of a rare species or a personal interest in biodiversity. Furthermore, the complexity increases for deep-water species, since these habitats are poorly monitored, and their fish fauna is not as well documented as that of coastal regions (de Carvalho-Souza *et al.*, 2024b). Thus, the occurrence of new fish species alone cannot definitively indicate whether recent faunal shifts are a result of ocean warming or the outcome of intensified fishing, sampling efforts, or citizen science activities.

Therefore, these findings emphasize the necessity for ongoing monitoring studies, alongside early detection and rapid response strategies in the GoC (due to its strategic location), using fish species as indicators to predict the effects of climate change. Initiatives of this nature are essential given the significant alterations observed in the ichthyofauna of the southwestern Iberian Peninsula and their habitats in recent decades. These alterations are driven by well-documented factors that go beyond warming: overfishing and regime shifts; human activities in essential fish habitats; the introduction of species for aquaculture and aquarium trade; intensification of maritime traffic, which consequently increases propagule pressure; and the transportation of larvae and juveniles via ballast water (de Carvalho-Souza *et al.*, 2019, 2021; González-Ortegón *et al.*, 2024; González-Ortegón and Moreno-Andrés, 2021; Torres *et al.*, 2013).

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