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Tropicalization of fish fauna of Galician coastal waters, in the NW Iberian upwelling system

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A R T I C L E I N F O

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A B S T R A C T

The Galician coast, with 1498 km of shoreline, is located in the northwest corner of the Iberian Peninsula. This area is the northern boundary of the Canary upwelling system, at the transition between the subtropical and subpolar regimes of the North Atlantic, which makes it of particular interest for the detection of marine ecosystem changes. Relationships between the occurrence of non-native marine fishes in this coastal area and sea surface temperature fluctuations are investigated. Information about fish species were collected from published and unpublished material recorded since 1945, and with regular monitoring data since 1983. A total of 50 new additions to the Galician marine ichthyofauna were recorded over the period 1945–2022. One of these species, *Cynoscion regalis* (Sciaenidae), is considered an introduced species. Most of the remaining 49 species are the result of latitudinal range expansions, including 15 species that have reached the northern limit of their distribution in the north-east Atlantic. This evidence points towards the tropicalization of the Galician fish fauna. Satellite sea-surface temperatures over the period 1982–2020 showed that Galician oceanic and coastal waters are, respectively, 0.78 ± 0.01 °C and 0.32 ± 0.01 °C warmer than 40 years ago. This ocean warming, added to the high productivity of the area and the oceanographic features, support the different ranges of expansion found in marine fishes, reinforcing the process of tropicalization. The increasing presence of new marine fishes in Galician waters could lead to relevant impacts on this ecosystem, like the emergence of new fish parasites and the increase of top predators and herbivorous fish among others.

1. Introduction

An emerging threat to biodiversity is the drastic redistribution of species through their movement from one place to another due to anthropogenic activities on a global scale, with associated economic and environmental damage (Pecl et al., 2017). Biological invasions (the arrival, establishment and diffusion of species) threaten biodiversity in terrestrial, freshwater and marine ecosystems, requiring substantial conservation and management efforts (Macic et al., 2018). Biological invasions in marine ecosystems occur through two processes: introductions and range expansions (Castro et al., 2022). These processes occur as a sequence of (1) arrival, with the presence of one or more individuals in a new geographic region; (2) population increase, via migration/introduction and/or self-recruitment and (3) persistence, when range-extending populations remain demographically stable (Bates et al., 2014). Although distinction between human-mediated introductions and natural colonisations is valid for management and policy making, both are subject to the same barriers of survival, reproduction, dispersal and further range expansion, and therefore are identical from a scientific perspective (Hoffmann and Courchamp, 2016).

The term introduction is defined when an organism is directly or indirectly moved by human activities beyond the limits of its native geographical range (Falk-Petersen et al., 2006). Globally, there are 406 introduced marine fish species (Costello et al., 2021). Fish introductions

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have been linked to ballast water transport, marine aquaculture, aquarium trade, oil platforms and movements through artificial channels (Pajuelo et al., 2016). However, in many cases, the exact introduction pathway is unknown.

Range expansions consist of dispersal by natural mechanisms into a new region. The term neonative has been recently introduced to define species which have expanded geographically beyond their native range whose presence is due to human-induced changes of the biophysical environment (Essl et al., 2019). A common perception in the climate change debate is that species distributions generally shift polewards due to global warming (Booth et al., 2011). Rates of climate-driven redistributions suggest that marine species are shifting toward high latitudes between 6 and 10 times faster than terrestrial taxa (Lenoir et al., 2020). Regarding fishes, ocean warming has resulted in many fishes shifting their distributions poleward (Potts et al., 2014; Baudron et al., 2020). Pelagic species that rely on planktonic food throughout their lifespan (e.g. *Sardina pilchardus*, *Engraulis encrasicolus*) or highly mobile migratory species (e.g. *Scomber scombrus*) are most likely to exhibit rapid responses to climate change, although changes among migratory demersal fish have also been documented (Heath et al., 2012).

Documenting the process of bioinvasion is complex, especially in its early stages, when occurrences are scarce, but records of new "rare" or "unusual" fishes may testify to substantial extensions of species' geographical ranges (Azzurro, 2010; Bañón et al., 2019). Observation may differ among species due to the low population numbers, the magnitude and spatial-temporal distribution of the sampling effort, occupancy patterns, morphological and biological traits or cryptic characteristics (Bates et al., 2015). Unequal sampling effort and unreliable historical data may lead not only to inaccurate estimates of range shifts, but also to differences in the detection of extending and contracting edges of species distribution, that will depend upon where the temporal focus of sampling effort lies, and on the underlying error structure of the data (Shoo et al., 2006). Moreover, a lapse in time will always exist between the first entrance of a new arrived species and its subsequent discovery (Crooks, 2011). Local Ecological Knowledge (LEK) arises as an alternative information source on species presence, providing reliable information about some emerging changes in fish diversity (Azzurro et al., 2011).

A total of 874 non-indigenous species were identified across European seas by December 2020 including 22 species of parasites and pathogens, and 50 species of microalgae (Zenetos et al., 2022). In the North-East Atlantic, global warming has led to a change in the abundance and distribution of marine fishes and a tropicalization of coastal fish communities (Rijnsdorp et al., 2009; Afonso et al., 2013). Pioneering works recorded many tropical and subtropical fishes North of Portuguese waters (about 4 l°50' N) since 1950 (Quéro et al., 1996; Quéro, 1998). Subsequently, this phenomenon has also been observed northwards (Brander et al., 2003), in the northwest of Spain (Bañón et al., 2002), British waters (Stebbing et al., 2002), North Sea (Beare et al., 2004) and off Iceland (Valdimarsson et al., 2012).

The Galician coast is at the northern end of the Iberian Upwelling System, which brings this region great economic value in small-scale fisheries (Alonso-Fernández et al., 2021). Previous studies reported a net sea-surface temperature (SST) increase along the NW Iberian coast, which is predicted to continue (Relvas et al., 2009; Gómez-Gesteira et al., 2011; Varela et al., 2018). The SST increase together with the high productivity of the area, creates the right conditions for the arrival of species of tropical or subtropical origins into the area (Bañón et al., 2002).

This paper aims to list the fish biodiversity changes occurring in Galician waters from 1945 to 2022, while highlighting the importance of this area concerning the tropicalization of European Atlantic waters. The changes in fish biodiversity will be related to the long-term variability of SST, obtained from satellite data over the period 1982–2020, and the oceanographic peculiarities of the Galician coast. A brief discussion on potential consequences of the biological invasions in the study area is also included.

2. Materials and methods

2.1. Study region

Galicia is an Atlantic region of Spain with a 1498 km-long coast and characterised by the presence of the Rías, which are tectonic embayments penetrating the coast almost perpendicular to the shoreline, acting as extensions of the continental shelf (Fig. 1). The European Atlantic coast has a sharp north to south temperature gradient, which restricts the distribution of many species and leads to a biogeographic subdivision of the eastern Atlantic into two provinces: the boreal Atlantic and the subtropical Lusitanian. The Lusitania Province encompasses the warm temperate marine waters between the southern end of the English Channel, in the North, and the African Cape Juby or Cape Blanco, in the South, including the Mediterranean and the archipelagos of the Azores, Madeira and the Canary Islands (Briggs, 1995; Briggs and Bowen, 2012). This is a transition area between the adjacent north Boreal and the south Tropical Eastern Atlantic Provinces. Within the Lusitania Province, Galicia is situated in the Atlantic Iberia subdivision which ranges from the Strait of Gibraltar to the Bay of Biscay (Almada et al., 2013).

2.2. Hydrography and dynamics of the region

At Galician latitudes, the Iberian Upwelling System (Fig. 1a,b) constitutes the northern boundary of the Canary Upwelling System associated with the eastern boundary Canary Current (Barton, 1998). The Iberian Upwelling System is influenced by the North Atlantic Subtropical Gyre circulation, so the Eastern North Atlantic Central Water (ENACW) is the prevailing water mass and responsible for the fertilisation of the coast during upwelling events. Interannual variability of the subtropical gyre extension and intensity determines the presence of the two branches of ENACW, one of subpolar origin and the other of subtropical origin (Ríos et al., 1992).

The nutrient-rich subpolar ENACW is transported by the Portugal Current (PC), flowing southward year-round from 45º-50°N to 10º-20°W (Fig. 1a,b) (Mazé et al., 1997). During spring and summer, north-easterly winds predominate over Western Iberia (upwelling season) producing the southward flowing Portugal Coastal Current (PCC, Fig. 1a) at the surface (<100 m) (Peliz et al., 2005) and the northward flowing Iberian Poleward Current (IPC, Fig. 1a) at depth over the slope (Arístegui et al., 2006). At the same time, ENACW upwells over the shelf and enters the bottom layer of the Rías, which act as efficient nutrient traps (Fig. 1c,e) (Álvarez-Salgado et al., 2000). In contrast, during the rest of the year, south-westerly winds are predominant (downwelling season), generating a reversal of the surface circulation that causes the IPC to extend to the surface (Fig. 1b, Peliz et al., 2003). The IPC transports northwards the nutrient-poor subtropical ENACW that, by the action of the southerly winds, gets piled up along the Galician coast (Fig. 1d), generating downwelling events inside the Rías (Álvarez-Salgado et al., 2000). During this season, the enhanced river discharge gives rise to the Western Iberian Buoyant Plume (WIBP, Fig. 1b,f) (Peliz et al., 2005), a persistent feature characterised by salinity lower than 35.8, which transports nutrients of continental origin.

2.3. Marine non-native fish abundances in the Galician coast

The detection of marine non-native fishes (NNF) – i.e., both introductions and range expansions – is conditioned by the level of knowledge of the native fauna. Since the 16th century, Galicia has had a long tradition of studying fish fauna. The first ichthyological study of Galician marine fishes listed 65 species (Cornide, 1788). This number increased over time thanks to the efforts of numerous ichthyologists and

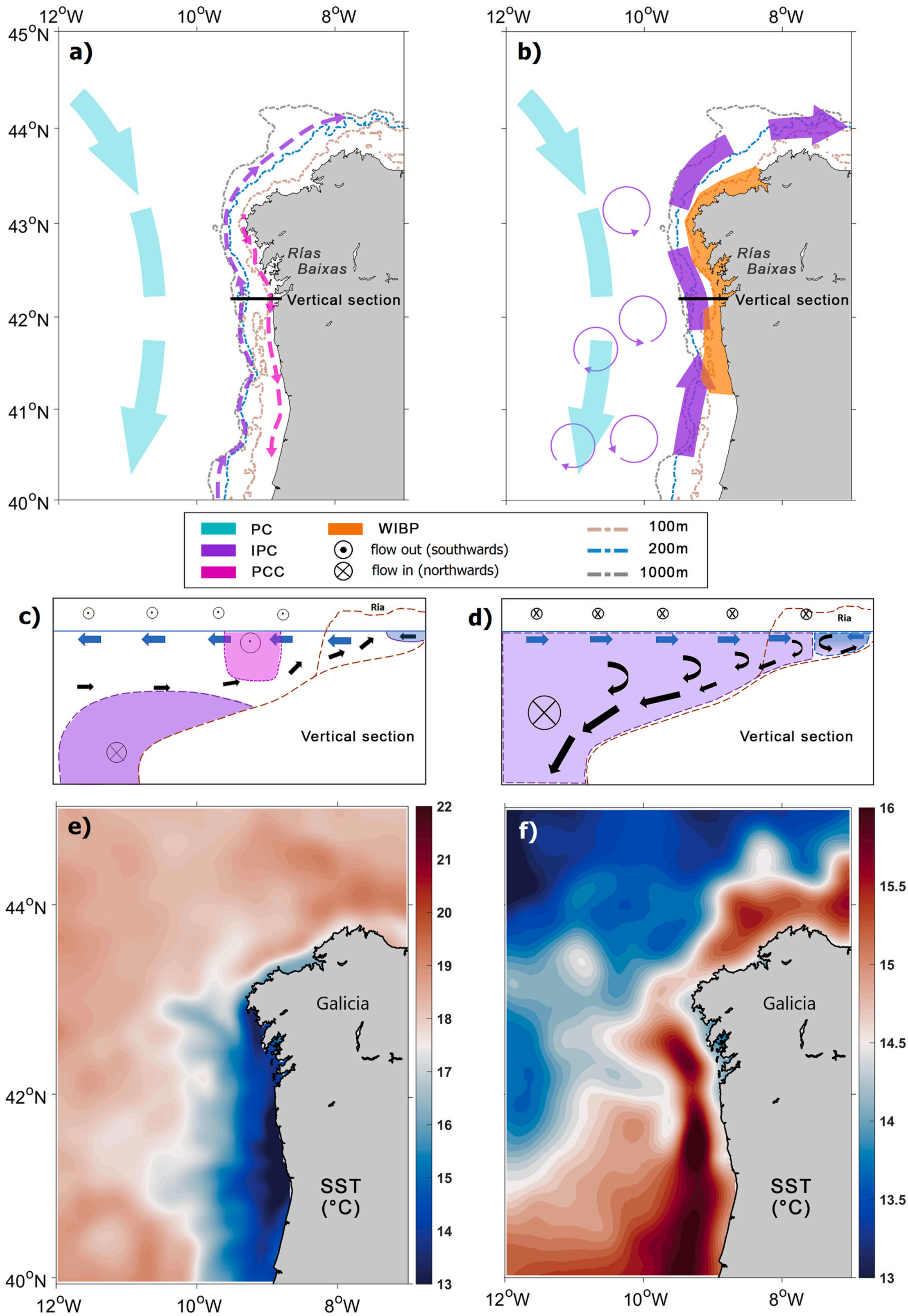

Fig. 1. Oceanographic features of the NW Iberian Peninsula. a) and c) corresponds to summer conditions and b), d) to winter conditions. Examples of the surface signature of Sea Surface Temperature (satellite images from the copernicus product: ESA SST CCI and C3S global, https://doi.org/10.48670/moi-00169) during e) intense upwelling during summer and f) intense Iberian Poleward Current during winter. PC: Portugal Current; IPC: Iberian Poleward Current; PCC: Portugal Coastal Current; WIBP: Western Iberian Buoyant Plume.
Schematics of the main currents along the area in a), b) horizontal views and c), d) vertical sections (adapted from Arístegui et al. (2009).

naturalists to reach the 462 fish species known today (Bañón and Maño, 2021a; b, 2022). The Galician marine fish diversity represents 34% of the 1349 species in European waters (Costello et al., 2001). This latest revision of Galician fishes also includes a precise chronology, providing historical knowledge and the date of the first record of each species. Therefore, for the purposes of this research, and considering the acceptable knowledge of the fish composition of the local ichthyofauna, it is assumed that new fish species found are most likely the result of changes in their areas of distribution.

Data on new fish species reported for the first time in Galicia for the period 1945–2022 have been compiled. The first year coincided with the first capture of *Balistes capriscus* (Balistidae) in Galicia. This species is one of the six thermophilic fishes that have contributed to the increase of fish abundance in the Mediterranean Sea, which is consistent with what would be expected under climate warming (Azzurro et al., 2011; Hattab et al., 2014). Deep-water species, which are primarily caught at depths greater than 400 m, have not been considered because these environments are less studied, and there are no historical data either. The exploration at these depths commenced in Galicia only in 1983 (Piñeiro et al., 1996). Similarly, cryptic species were not considered because, for most of them, their distribution is scarcely known.

Several sources of information were used in this study. A comprehensive literature search was conducted for marine NNF in its initial phase (1945–1982). Since 1983, monitoring actions have been developed, including citizen science and regular and opportunistic sampling. Citizen science has become a precious tool to detect and monitor non-native species. So, we implemented a citizen science program consisting of distributing informative posters with photos of the species of interest in tandem with a dissemination campaign through traditional media (press, radio and television) social media (Facebook, Twitter, blogs) and a website app called "Network of Marine Environment Observers of Galicia" (Red de Observadores del Medio Marino de Galicia) (https://redogal.xunta.gal/es/redogal) both launched in 2020. We also kept a tight relationship with fishers and technical assistances of fishermen's associations to whom we give lectures.

Regular sampling has its origin in two historical series. One is the annual demersal bottom trawl survey "Demersales", which has been carried out since 1983 by the Instituto Español de Oceanografía (IEO) along the north coasts of Spain during September. The other is the monitoring program of artisanal fisheries, which is carried out by the regional government (Xunta de Galicia) through its Technical Unit of Artisanal Fisheries (Unidade Técnica de Pesca de Baixura, UTPB, in Galician) with observers enrolled in fishing vessels since 1999 during the entire year. Opportunistic sampling is based on the report of non-directed catches made by professional and recreational fishermen, staff of fish markets, and other users at different locations along the Galician coast. The only criterion for this sampling method is that samples are available and willing to be donated to researchers.

A total of 30,317 specimens of 50 different species were recorded. The species were assigned to two ecotype classifications, according to biogeography and vertical habitat preference following Ellis et al. (2008) (now unavailable), later published by Engelhard et al. (2011) but including a lower number of species of southern origin. A qualitative ranking of abundances over time was carried out based on occurrences from 1983 to the present, in the combined databases, to evaluate the frequency of occurrence of each species. The occurrences were classified as follows: 1) exceptional, one to three records; 2) occasional, four to 10 records; 3) rare, 11 to 30 records; 4) frequent, more than 30 records; 5) common, regularly in captures and abundant.

2.4. Sea-surface temperature

SST data for the Galician coast from 1982 to 2020 were obtained from the reprocessed products ESA SST CCI and C3S global sea surface temperature that were downloaded from the Copernicus Marine Service (https://resources.marine.copernicus.eu/products, downloaded 20/10/2021). These satellite products (https://doi.org/10.48670/moi-00169) provide gap-free maps of daily average SST at 20 cm depth at 0.05°× 0.05° horizontal grid resolution. Satellite SST was retrieved and averaged over the period 1982–2020 for the Galician coast from 41.8°N to 44.8°N and from 7°W to 12°W (Fig. 1). We used bathymetric and latitudinal ranges to distinguish between coastal and open ocean areas. Surface areas north and south of 43°N with depths lower than 200 m were considered as coastal areas, while those deeper than 2000 m were considered as open ocean areas. Trends in SST were estimated for the Galician coastal region (41.8–44.8°N and 7–11°W) and for four different areas: Northern coastal area (NC, north of 43°N), Southern coastal area (SC, south of 43ºN), Northern adjacent ocean (NO) and Southern adjacent ocean (SO). SST was also used to assess the impact of the buffering effect of upwelling over ocean warming on the patterns of fish expansions.

2.5. Relationship between fish abundances/landings and SST

Multiple linear regression fits were performed using MATLAB (function fitlm) in order to find out the relationship between times series of fishes´ abundances and landings, and SST changes off Galicia. The logarithms abundance of three species (*Antigonia capros*, *Lepidotrigla dieuzeidei*, and *Trachurus picturatus*) and the landings of *B. capriscus* from 2004 onwards were fitted to a multiple linear regression with coastal SST and the SST difference between oceanic and coastal areas (ΔSST) as predictors. Logarithms of the abundances and landings were used to normalize both variables. Coastal SST is the average SST of the coastal areas and oceanic SST the average SST of the oceanic areas, with ΔSST = oceanic SST – coastal SSTs. For the correlation with *B. capriscus*' landings, we considered the average SST and ΔSST during the landing year and the three previous years (named as SST_{BC} and ΔSST_{BC}). For the fit with the abundance of the three species, we considered the average SST and ΔSST during the year when the abundance was reported and the two previous years (named as SST_{3sp} and ΔSST_{3sp}). The reason behind considering these averages of the coastal SST and ΔSST is to dampen the interannual variability and capture the average temperature. Coastal SST shows SST warming in coastal areas, where the studied fish species were captured, while ΔSST could be considered an index of upwelling intensity. The null hypothesis for each fit was that there is no relationship between the predictors and the fish abundances/landings (H0: $\beta1 = 0$, $\beta2 = 0$, considering $Y = \beta0 + \beta1 \times 1 + \beta2 \times 2$, where Y = landings/abundances and X1 = coastal SST and X2 = ΔSST).

3. Results

3.1. Case study: Chronology of the bioinvasion of Balistes capriscus

Balistes capriscus is considered the emblematic species off Galicia with respect to tropicalization of native fauna (Bañón et al., 2002). It was first reported on the 15th October 1945 in the port of Vigo (Navaz y Sanz, 1946). In the mid-1970 s this species was only frequent in southern Galicia during summer, extending northwards during the following decades. Fish landings statistics show a steady increase since 2004 (https://www.pescadegalicia.gal/estadisticas/), from 86 kg in 2004 to a maximum of 9304 kg in 2022 (Fig. 2a). Considering this chronology, we can establish a period of about 30 years (1945–1975) for the colonisation process and of 59 years (1945–2004) in order to be relevant in the fishery.

3.2. Marine non-native fishes off Galicia

A total of 50 marine Non-Native Fishes (NNF) recorded in Galician waters between 1945 and 2022 are listed in Table 1, eleven of which are pictured in Fig. 3. LEK was the only source of information for 22 NNF species and 17 from fishery monitoring surveys. Only *C. regalis*, native to the Atlantic coast of North America, was considered an introduced

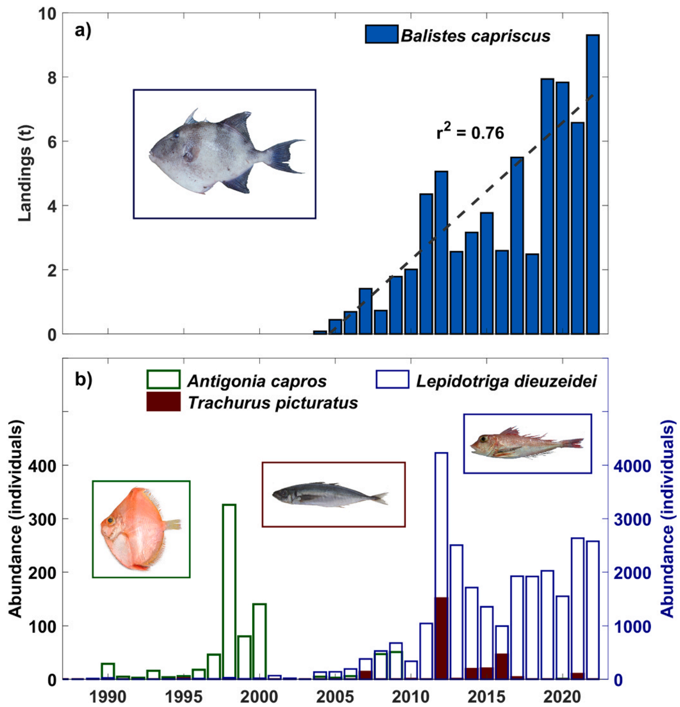

Fig. 2. a) Historical landings (in tons) of *Balistes capriscus* reported in Galician waters (https://www.pescadegalicia.gal/) showing the ascending trend line. b) Abundances (number of individuals) of *Antigonia capros*, *Lepidotriga dieuzeidei*, and *Trachurus picturatus* from the records of the "Demersales" sampling surveys. The right vertical axis shows abundances of *L. dieuzeidei* and the left vertical axis shows the abundances of the other 2 species.

species, while the remaining 49 species arrived through the process of range expansion and natural colonisation. Most of these 49 records pertained to tropical or subtropical species moving polewards, while 15 had Galician waters as their new northern distribution limit in the NE Atlantic.

The most speciose family is Carangidae, with eight species, while 24 are represented by one species. Most species are common to the Lusitanian province (46%), others are typical of the Atlantic (26%), and to a lesser extent, others have African (22%) or boreal (6%) affinities. In relation to the vertical habitat, 60% of species were demersal and 40% pelagic. Regarding the abundance categories, 54% are exceptional, 16% occasional, 8% rare, 12% frequent and 10% common (Table 1).

Three NNF species, *Antigonia capros*, *Lepidotrigla dieuzeidei* and *Trachurrs picturatus* were selected since they were the three most frequently captured species in the "Demersales" surveys (Fig. 2b). Considering the limitations of the sampling strategy, a single source of data, records show that *A. capros* was most frequently found between 1990 and 2009 (797 specimens), with no more catches after this period except for one specimen found in 2020. *Trachurus picturatus* was first found in 1995 but it has become more frequent since 2007 (775 specimens). *Lepidotrigla dieuzeidei* is the most abundant and frequent of the three species presented here, appearing in 1985 for the first time and increasing non-linearly through time but with abundances of ~ 2000 specimens in average since 2010.

3.3. Sea-surface temperature and its relationship with non-native fishes

The analysis of SST off Galicia shows that it increased 0.17 ± 0.04 °C per decade, but the increase was not homogeneous (Fig. 4). The long-term SST increase was significant in all areas except for the Southern coastal area (SC, Fig. 4), being higher in the Northern ocean area (0.21 ± 0.04 °C per decade) than in the Northern coastal area (0.11 ± 0.04 °C per decade). Respect to the relationships between fish abundance/landings and the SST, the linear fits between the logarithms abundance of *A. capros*, *L. diauzeidei*, and *T. picturatus*, and the landings of *B. capriscus* with the coastal SST (Figs. 5a, 5b) and ΔSST (Fig. 5c) were significant ($p < 0.001$, $\alpha = 0.05$), i.e., the null hypothesis is rejected. The coefficients of determination (r^2) were of 0.54 for *B. capriscus* and 0.68 for the 3 species (Fig. 5d,e), with a positive relationship between the abundances/landings and both SST and ΔSST.

4. Discussion

Despite the difficulties in detecting NNF, the use of regular and opportunistic samplings, the filters used in the selection of species and the fact that many of the species have shown a gradual northwards displacement (Bañón et al., 2002), with 15 of them representing a new northern limit of distribution in Galician waters, lend credibility to the compiled species list. LEK was the only source of information for 22 NNF species, 44% of the total. This shows that, in a habitat as vast as the sea, scientific or fishing surveys are clearly insufficient to detect the arrival of new species and the collaboration of fishermen is essential in monitoring this process.

The mid-location of Galician waters between the subtropical and subpolar regimes of the North Atlantic (Kaimuddin et al., 2016), and the fact that many species have their southern or northern distribution limits in the inter-regime area (Teixeira et al., 2014), makes this region an area of great sensitivity for the detection of climate change and novel immigrant fishes. Community studies in regions with overlapping subpolar and subtropical species, as it is the case of Galicia, base their climate change attribution on differential responses of these two categories. Subpolar marine fish species have tended to be stable or decline in abundance, whereas temperate species at the same site have increased in abundance and/or expanded their distributions (Parmesan and Yohe, 2003). In this regard, it should be noticed the 41% increase of the African species category from 17 species in 2010 (Bañón et al., 2010) to 24 at present. Regarding the colonization process of NNF, it appears to be comparatively faster in the Mediterranean due to the higher SST increase rate in this sea (0.35 ºC per decade, Pastor et al., 2020) compared to the NW Iberian Peninsula (Fig. 4). For example, the bluespotted cornetfish *Fistularia commersonii* has been able to colonize almost the entire Mediterranean region in only seven years after its first sighting, reaching colonisation rates of spread of around 1000–1500 km per year (Azzurro et al., 2013).

During the study period, 50 new fish species have appeared in Galician waters. The NNF composition includes the first occurrence in the area of new taxonomic groups, such as Batrachoidiformes, Acanthuriformes and Centrarchiformes orders and Kyphosidae (two species), Haemulidae (two species), Batrachoididae (one species) or Fistulariidae (one species) families. Other families already present have greatly increased their numbers. For example, Carangidae species increased from four species at the beginning of the 20th century to eleven at present (Bañón and Mucientes, 2009). Also, Echeneidae and Epinephelidae increased from one to three; Tetraodontidae from one to four and Scorpaenidae and Sciaenidae from three to five species. This tendency has also been observed in nearby areas. In Atlantic French waters, the carangids increased from three known species at the beginning of the 19th century to ten (Quéro et al., 2007). Due to the highly dispersive nature of carangids, this group is quite capable of colonizing new suitable habitats and can therefore be a useful indicator of ecosystem change (Devine and Fisher, 2014). The increase in abundance and the distribution changes of tetraodontiform fishes in Atlantic French waters have also been related to global warming (Quéro et al., 2008).

In the case of the *Lepidotrigla* species, the only two known species were first recorded after 1945, first *Lepidotrigla cavillone* and later *Lepidotrigla dieuzeidei*. However, since the discovery of *L. dieuzeidei*, no specimens of *L. cavillone* have ever been recorded in the area. *Lepidotrigla dieuzeidei* is a well-established species, which has gone from showing very low abundances to being present in 40% of the sampling stations,

Table 1
List of marine non-native fishes recorded in Galician waters since 1945. NLD: northern limit of the distribution from the NE Atlantic when the species has been published. Frequency categories as described in material and methods. Frequency categories are: 1 = exceptional (1–3 records); 2 = occasional (4–10 records); 3 = rare (11–30 records); 4 = frequent (> 30 records); 5 = common.

Family	Species	Vertical habitat	Frequency	Biogeographic guild	NLD
Ophichthidae	*Pisodonophis semicinctus*	Demersal	1	African	
Clupeidae	*Clupea harengus*	Pelagic	1	Boreal	
Ateleopodidae	*Ijimaia loppei*	Demersal	1	Atlantic	
Moridae	*Gadella maraldi*	Pelagic	2	Lusitanian	✓
Batrachoididae	*Halobatrachus dydactilus*	Demersal	4	Lusitanian	
Exocoetidae	*Cheilopogon heterurus*	Pelagic	2	Atlantic	
Parazenidae	*Cyttopsis rosea*	Pelagic	2	Lusitanian	
Grammicolepidae	*Grammicolepis rachiusculus*	Pelagic	1	Atlantic	
Zeniontidae	*Zenion hololepis*	Demersal	1	Atlantic	✓
Zeidae	*Zenopsis conchifer*	Pelagic	1	Lusitanian	
Fistulariidae	*Fistularia petimba*	Demersal	1	Atlantic	✓
Dactylopteridae	*Dactylopterus volitans*	Pelagic	1	Atlantic	
Scorpaenidae	*Pontinus kuhlii*	Demersal	2	African	
	Scorpaena loppei	Demersal	2	Lusitanian	
Triglidae	*Lepidotrigla dieuzeidei*	Demersal	5	African	✓
Peristediidae	*Peristedion cataphractum*	Demersal	1	Lusitanian	
Cyclopteridae	*Cyclopterus lumpus*	Pelagic	4	Boreal	
Trachinidae	*Trachinus araneus*	Demersal	1	Lusitanian	✓
Antigoniidae	*Antigonia capros*	Demersal	4	Atlantic	
Dicentrarchidae	*Dicentrarchus punctatus*	Pelagic	4	Lusitanian	
Epinephelidae	*Epinephelus costae*	Demersal	1	African	✓
	Epinephelus aeneus	Demersal	1	Lusitanian	
Serranidae	*Anthias anthias*	Demersal	3	Lusitanian	
Echeneidae	*Remora brachyptera*	Pelagic	1	Atlantic	
	Remora osteochir	Pelagic	1	Atlantic	✓
Carangidae	*Caranx crysos*	Pelagic	2	Lusitanian	
	Pseudocaranx dentex	Demersal	1	Lusitanian	✓
	Naucrates ductor	Pelagic	2	Atlantic	
	Seriola rivoliana	Pelagic	4	Lusitanian	
	Seriola fasciata	Pelagic	1	African	✓
	Seriola dumerilli	Pelagic	1	Lusitanian	
	Trachurus picturatus	Pelagic	5	Lusitanian	
	Trachinotus ovatus	Pelagic	3	Lusitanian	
Sparidae	*Pagrus auriga*	Pelagic	2	African	✓
	Diplodus cervinus	Demersal	5	Lusitanian	
	Lithognathus mormyrus	Demersal	5	Lusitanian	
Lobotidae	*Lobotes surinamensis*	Demersal	1	Lusitanian	
Sciaenidae	*Umbrina canariensis*	Demersal	3	Lusitanian	
	Cynoscion regalis	Demersal	4	Atlantic	✓
Kyphosidae	*Kyphosus sectatrix*	Demersal	1	African	
	Kyphosus vaigiensis	Demersal	3	Atlantic	✓
Haemulidae	*Pomadasys incisus*	Demersal	1	African	✓
	Parapristipoma octolineatum	Demersal	1	African	
Balistidae	*Balistes capriscus*	Pelagic	5	Lusitanian	
Tetraodontidae	*Lagocephalus laevigatus*	Demersal	1	Atlantic	✓
	Ephippion guttifer	Demersal	1	African	✓
Citharidae	*Citharus linguatula*	Demersal	1	Lusitanian	
Cynoglossidae	*Symphurus nigrescens*	Demersal	1	Lusitanian	
Pleuronectidae	*Microstomus kitt*	Demersal	1	Boreal	
Soleidae	*Microchirus boscanion*	Demersal	1	African	

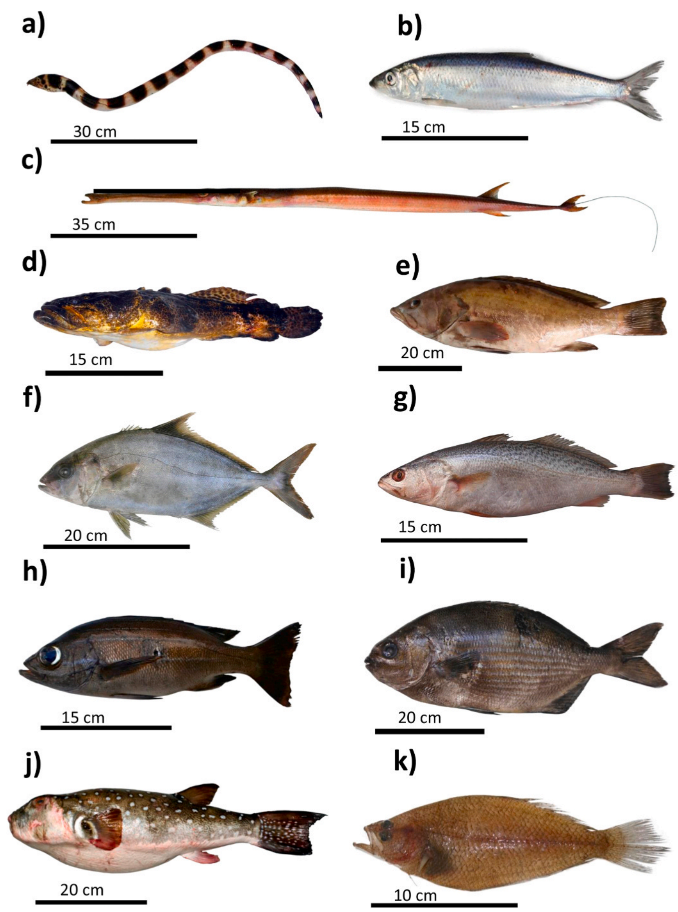

Fig. 3. A representative selection of marine NNF recorded in Galician waters. a) *Pisodonophis semicinctus*; b) *Clupea harengus*; c) *Fistularia petimba*; d) *Halobatrachus didactylus*; e) *Epinephelus costae*; f) *Seriola rivoliana*; g) *Cynoscion regalis*; h) *Parapristipoma octolineatum*; i) *Kyphosus vaigiensis*; j) *Ephippion guttifer*; k) *Citharus linguatula.*

indicating a clear progression in the north of Spain (Punzón et al., 2016), which seems to indicate a misidentification of *L. dieuzeidei* by previous authors.

The toadfish *Halobatrachus didactylus* is the last NNF incorporation to Galician waters, found for the first time in 2018 (Bañón et al., 2019). So far, a total of 81 specimens have been recorded in the southernmost part of the study area. This species shows low dispersal and colonisation abilities due to its ecological characteristics: low fecundity, presence of benthic eggs and larvae, parental care of the offspring and marked sedentary lifestyle of the adults (Costa et al., 2003). However, small oscillations in SST may cause local extinctions and subsequent recolonizations by a few migrants per generation, from Algarve or more southern locations expanded northwards (Robalo et al., 2013). The only introduced NNF found was *Cynoscion regalis*. This species is native to the western north Atlantic coasts of North America, and it has been caught since at least 2011 in the Gulf of Cádiz (south of Iberian Peninsula), where it is already established (Bañón et al., 2017). It can be found in Galician waters since 2016, probably due to a migratory route and/or expansion from the Gulf of Cadiz northwards (Bañón et al., 2018).

Results show high biodiversity of NNF but low abundance, as only 10% of the listed species are currently common. This fact points to a continuous arrival of southern species, but a failed or slow colonisation process in Galician waters. In the case of the pioneer *Balistes capriscus*, this was slow and took several decades. However, species of more recent arrival, like *Seriola rivoliana*, were faster. This species was first detected in 2005 and landings data have been available since 2019. The last species to arrive, *H. didactylus*, has also been the fastest to colonise Galician waters, which could indicate a more rapid colonisation process in recent times. Nevertheless, this species is also the one with the shallowest coastal habitat, favouring its detection and recording.

The tropicalization of coastal fish communities (Bianchi, 2007) in the Northeast Atlantic has been attributed mainly to ocean warming (Rijnsdorp et al., 2009; Afonso et al., 2013). Climate change and rising temperatures facilitate the establishment of many NNF of warmer areas origin in temperate regions (Rijnsdorp et al., 2009; Hattab et al., 2014). The increase in SST in Galician waters is not homogenous, and the SST increase rate weakens close to the coast (0.07 ± 0.03 °C per decade in average) with respect to the open ocean (up to 0.19 ± 0.03 °C per decade in average, Fig. 4) because of the buffering effect of the upwelling processes (Relvas et al., 2009). Most of the listed species are inhabitants of shelf and coastal areas, where a lower increase in SST is observed, and this could be the reason why the colonisation process is slow for the pioneer species *B. capriscus*. However, though at a lower rate in coastal areas, there has been a progressive warming in the region that could be enough to facilitate the expansion of species such as *H. didactylus*. The results from the multiple linear regressions (Fig. 5d,e) indicate positive relationships between the abundances of the three selected species and the landings of *B. capriscus* with coastal SST and the SST difference between oceanic and coastal areas (ΔSST). In fact, more than half of the variability in the landings of *B. capriscus* and almost 70% of the changes in abundances of the three selected species can be explained by changes in coastal SST and ΔSST.

The increase in ocean temperature is not the only factor for bioinvasions to occur, and the habitability of the new environment (availability of food, sheltering areas, etc) is of key relevance. Sousa et al. (2020) noted that the increase in SST could lead to stronger oceanic stratification, and Lønborg et al. (2020) stated that nutrient utilisation is more efficient under conditions of upwelling with stratification. Therefore, despite the increase in SST, the high productivity of the NW Iberian margin is likely to be maintained (Beca-Carretero et al., 2019), which could favour the arrival and sustainability of foreign marine fishes.

It is important to notice the role that the oceanographic features of the NW Iberian coast can have on the bioinvasion of tropical fishes. In this way, it has been shown that the mesoscale features associated with the dynamics of this coastal area (Fig. 1e,f) play a relevant role in the transport of larval stages to and from favourable nursery areas (e.g., Nolasco et al., 2013) as well as in the distribution of marine plankton communities (e.g., Santos et al., 2007), which could have a favourable impact on the range expansion of fishes. Another oceanographic feature to consider is the Iberian Poleward Current (IPC), which is responsible for the arrival of warm and salty waters to the NW Iberia region (Álvarez-Salgado et al., 2003), and that could also favour the northward transport of tropical fishes.

Apart from changes in SST and ocean dynamics, climate change has also relevant biological impacts on native marine species. The ecological impact of alien marine fishes can be categorized as (i) an alteration of habitat or food webs; (ii) competition with natives; (iii) predation on natives; (iv) vectoring parasites or pathogens; or (v) genetic impacts on native species (Arndt et al., 2018). Some of these impacts may already be occurring in Galician waters. Groupers (*Epinephelus* spp.) and Amberjacks (*Seriola* spp.) are top predator fishes that feed at higher trophic levels and are also among the biggest fishes in coastal marine waters. Therefore, changes in their distribution, abundance, and colonisation abilities would have a significant influence in the food chains on autochthonous communities due to direct predation or competition for food or space resources (Glamuzina, 1999).

The arrival of *Epinephelus guttifer* and *Parapristipoma octolineatum* showed a high new parasitic nematode load (Rodríguez et al., 2019). The introduction of parasite species into a new marine environment could negatively affect native fauna (Lymbery et al., 2014). These foreign parasites could be more damaging to local hosts because there has not been evolutionary time to reach an equilibrium relationship

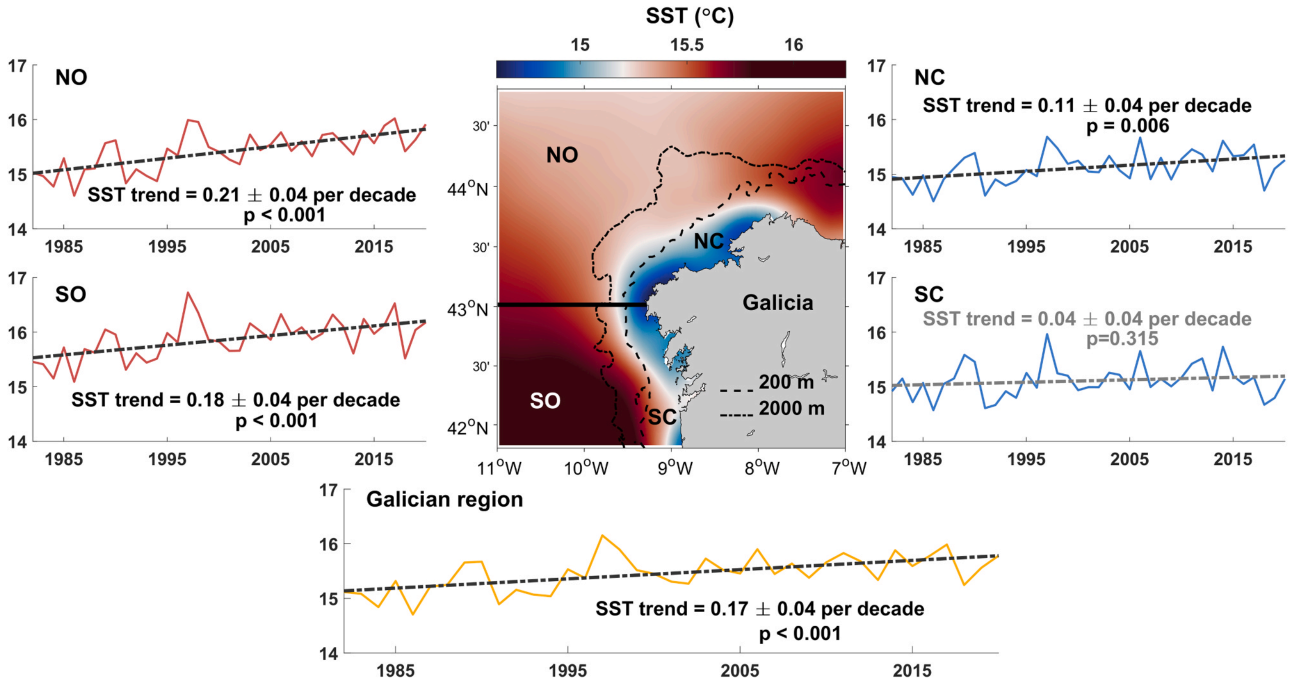

Fig. 4. Trends in SST (in °C per decade) for the Galician region and for four different areas in it: Northern (NO) and Southern (SO) oceanic areas and Northern (NC) and Southern (SC) coastal areas. For each area, the slope of the fit and its uncertainty are shown as well as the level of significance (p). Non-significant trends are shown in grey.

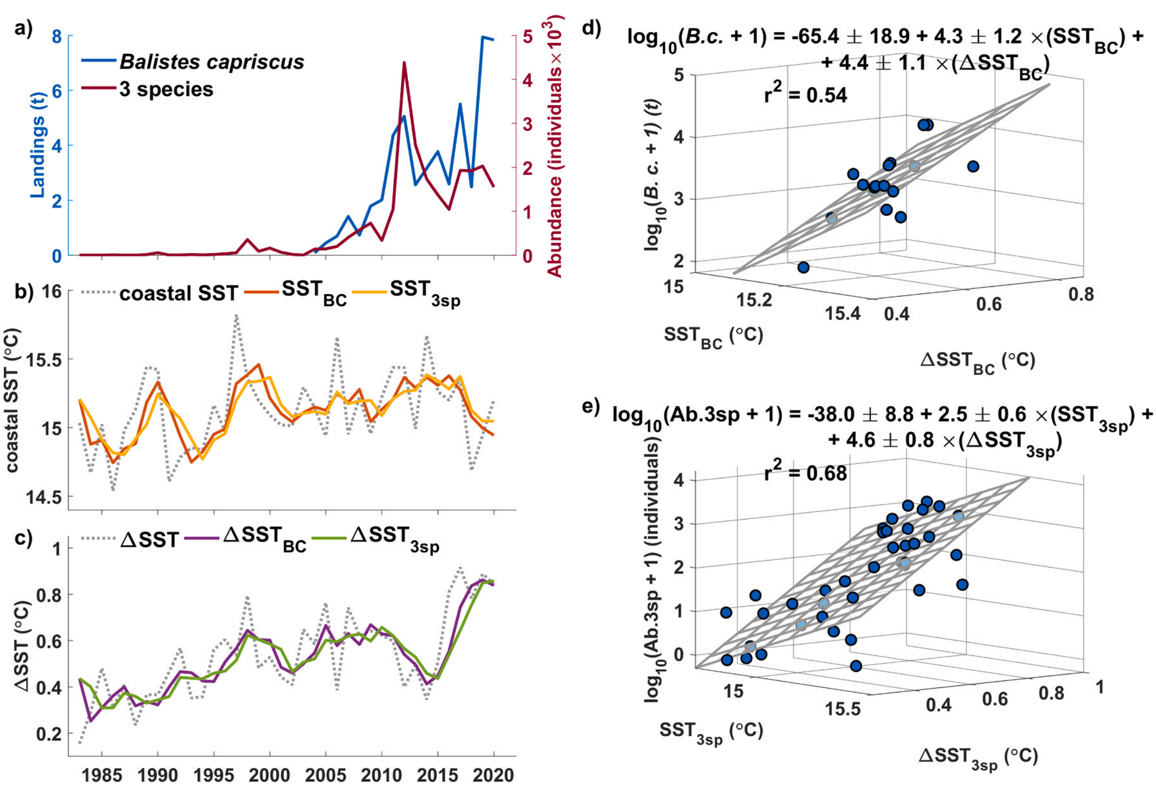

Fig. 5. a) Time series of the abundances (number of individuals) of *Antigonia capros*, *Lepidotriga dieuzeidei*, and *Trachurus picturatus* (3 species) and landings (in tons) of *Balistes capriscus*. b) Time series of coastal SST (mean of SST NC and SST SC, grey dotted line), SST_{3sp} (average of SST during the landing year and the two previous years, red line) and SST_{BC} (average of SST during the landing year and the three previous years, yellow line). c) Time series of ΔSST (difference of SST between oceanic and coastal areas, grey dotted line), ΔSST_{3sp} (average of ΔSST in the year of the captures and the two previous years, purple line) and ΔSST_{BC} (average of ΔSST in the year of the captures and the three previous years, green line). d) 3D plots of the multiple linear regressions for *B. capriscus* landings (B.c, in tons). e) 3D plots of the multiple linear regressions for the 3-species abundances (Ab. 3sp, number of individuals) selected (*Antigonia capros*, *Lepidotrigla dieuzeidei*, and *Trachurus picturatus*). Abundances/ landings were rescaled using $\log_{10}$ (x + 1) (x = abundances/landings).

(Azzurro, 2010).

Herbivorous fishes have a significant effect on macroalgal vegetation, not only in tropical but also in warm temperate waters (Franco et al., 2015). The expansion of tropical species increases the presence of herbivorous fishes and their grazing rates in temperate areas (Vergés et al., 2014). Species of the family Kyphosidae are strictly herbivorous and *Kyphosus* species are very important for understanding the feeding damage inflicted on seaweed beds by herbivorous fishes (Yamaguchi et al., 2010). In fact, a decline of the golden kelp *Laminaria ochroleuca* forests has recently been noted in some areas of Galicia due to excessive grazing of fishes, mainly by *Sarpa salpa*, the only native obligate herbivorous fish in the region (Barrientos et al., 2022). Although the impact of the two newly arrived kyphosid species, *Kyphosus sectatrix* and *Kyphosus vaigiensis*, on native algal populations has not yet been studied, the increase of one to three strict herbivore species in the area may presumably exert a negative synergistic effect on macroalgal populations.

5. Conclusions

Monitoring the presence of rare and non-indigenous fish species is a requirement for marine environmental management and sustainable development. Traditional fisheries monitoring surveys are clearly insufficient for this purpose, which needs to be reinforced or complemented by specific follow-up programmes and LEK.

A tropicalization of Galicia's marine ecosystem is confirmed by the new arrival of 49 NNF species of tropical and subtropical origin. This process is characterized by high biodiversity but low abundance.

The increase in SST found in Galician waters shows significant linear relationships with the arrival of NNF, corroborating the relevant role of global warming in the process of tropicalization. The differences found in this increase, of the order of 2.4 times higher in oceanic waters than in coastal waters, can be responsible for the different rate of expansion of some NNF species found in Galician waters. Also, the oceanographic features that characterize the NW Iberian coastal system could have a role in the expansion patterns of the new species arriving to Galician waters, and future studies on this matter are worth developing.

The impact of alien marine fish on the native ecosystem is still poorly studied and could have significant and possibly negative biological effects, as well as unpredictable economic consequences in a region with an important fisheries sector. The biological and oceanographic data gathered in this research could be useful, on the one hand, for the establishment of new EU policy actions and, on the other hand, to influence the need for new regulatory requirements and thus improve environmental management options.

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CRediT authorship contribution statement

Piedracoba Silvia: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **Arronte Juan Carlos:** Resources, Writing – review & editing. **Pardo Paula Conde:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Bañón Rafael:** Conceptualization, Data curation, Investigation, Visualization, Writing – original draft. **de Carlos Alejandro:** Resources, Writing – review & editing. **Álvarez-Salgado Xosé Antón:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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