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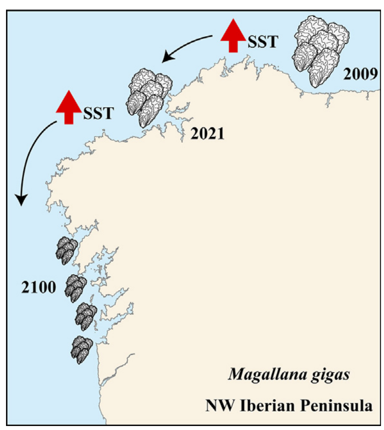
HIGHLIGHTS

- Analysis of historical expansion of *Magallana gigas* through *in situ* data
- Analysis of future expansion of *M. gigas* using numerical projections
- Rising water temperature will favor new settlements in the NW Iberian Peninsula
- *M. gigas* could naturalize in the Rías Baixas in the coming decades

GRAPHICAL ABSTRACT



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ABSTRACT

Magallana gigas is a naturalized species on the north coast of Galicia (Rías Altas, Northwest Iberian Peninsula), where it was unintentionally introduced. In recent decades, a greater abundance of *M. gigas* has been observed on the Galician coast, expanding towards the south, reaching the Artabro Gulf (Rías Centrales, NW Galician coast), probably due to ocean warming. Although this species has been cultivated in the Rías Baixas since the early 1990s and spawning has been reported, recruitment was never observed, which is likely due to the cold water upwelled during the spawning months. The future rise in seawater temperature may favor the naturalization of the non-indigenous species *M. gigas* southwards, in the Rías Baixas. Thermally, the Ría de Arousa seems to be the most favorable estuary for the future settlement of *M. gigas*, which may occur in the next decades. The extent of thermally favorable zones within estuaries is projected to increase rapidly by mid-century, and reaching 100 % of the estuarine area by the end of the century. As has already happened in other areas of the world, the expansion and naturalization of the Pacific oyster on the Galician coast will likely affect the native communities and economic activities, making it necessary to implement monitoring and management strategies to mitigate its effect.

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1. Introduction

Non-indigenous species (NIS) have been anthropogenically introduced into marine ecosystems for thousands of years. Several human activities such as aquaculture, ship traffic, aquarium escapes, floating litter, or canal constructions have been identified as introducing vectors for NIS (Geburzi and McCarthy, 2018; Raybaud et al., 2015). Aquaculture is a vector by intentionally introducing NIS as cultivated target species and involuntary transport of other associated organisms (Carlton, 1999; Geburzi and McCarthy, 2018; Mckindsey et al., 2007; Ruesink et al., 2005). Some of the introduced NIS have the potential to naturalize in the receiving ecosystem, that is, to successfully establish, be able to reproduce and grow, and even expand their natural range. The naturalization of NIS indicates that the environmental characteristics of the newly colonized area satisfy the survival, growth, and reproduction requirements of these organisms (Clarke Murray et al., 2014). The term "invasive species" has been generally used to refer to naturalized species that cause negative impacts on the receiving ecosystem.

The Pacific oyster *Magallana gigas* (Thunberg, 1793), formerly *Crassostrea gigas*, is a classic example of the introduction and subsequent naturalization of a NIS through aquaculture. Their establishment is characterized by the development of extensive and dense reef structures that produce significant changes in the receiving ecosystems, for which they are considered an ecosystem engineer (Dupuy et al., 1999; Jones et al., 1994; Troost, 2010). This species is invasive (Global Invasive Species Database, 2022) and its establishment and dispersal may threaten the conservation, goods, and benefits of marine ecosystems and conflict with commercial and recreational interests in the region (Dolmer et al., 2014). Native from East Asia, *M. gigas* has been introduced as an aquaculture animal to over 50 countries worldwide (Mann et al., 1991; Miossec et al., 2009; Ruesink et al., 2005; Shatkin et al., 1998). It was imported on a large scale from Japan and the Pacific coasts of Canada and the United States of America (USA) to several European locations in France, The Netherlands, the United Kingdom (UK) or Germany from the early 1960s to around 1980, as an alternative to the decline of the native flat oyster *Ostrea edulis* (Linnaeus, 1758) (Chew, 1990; Troost, 2010; Wolff and Reise, 2002). Although it was initially believed that the Pacific oyster would not reproduce due to the low water temperature of the North Sea (Geburzi and McCarthy, 2018), it eventually established and spread rapidly along the European coasts (Troost, 2010).

Plasticity in life-history strategies, behaviour, and physiology is a key feature of invasive species (Geburzi and McCarthy, 2018). Pacific oysters present many traits that confer this plasticity and contribute to their successful establishment and natural spread (Troost, 2010). Both adults and juveniles have been shown to tolerate a wide range of environmental conditions (Mann et al., 1991; Shatkin et al., 1998). In addition, it is characterized by an *r*-selected breeding strategy, which enables the development of high propagule pressure even from small founder populations (Geburzi and McCarthy, 2018). Thus, *M. gigas* mature for the first time at a shell length of about 50 mm (Kobayashi et al., 1997), which may already be reached in the summer, one year after settlement (Dolmer et al., 2014; Troost, 2010). *M. gigas* is also very fecund, with 80–150 mm length females producing between 50 and 200 million eggs per spawning (Quayle, 1988). It must be also noted that this species has a long-lasting planktonic larval stage (typically 2–4 weeks) that implies a large dispersal capacity and are more likely to settle far from the parent population (Guy et al., 2019). Simulation of larval transport of a non-native population under tidal behaviour on the west coast of the UK showed that dispersal generally covers radial distances of 35 km or more (Robins et al., 2017).

Although different environmental variables can influence oyster reproduction, seawater temperature is the most critical driver limiting recruitment and determining biogeographical limits at a regional scale (King et al., 2021). The optimum water temperature range for spawning and larval development is more restricted than for adult growth (Wiltshire, 2007), to the point that it seems paradoxical that a species that tolerates such a wide range of environmental conditions for its growth can be so strict in terms of the conditions necessary to achieve successful larval settlement (Castaños et al., 2009). Gonad development in *M. gigas* is also strongly influenced by water temperature (Mann, 1979). The initiation of gametogenesis requires a water temperature of at least 10 °C, with gonad development progressing faster at higher temperatures; even though ripening may occur at cooler temperatures, a temperature higher than 17 °C is required to promote spawning (Castaños et al., 2009; Wiltshire, 2007). Successful recruitment also requires successful larval development, as evidenced by the lack of spatfall after many observed spawning events (Wiltshire, 2007). The relationship between *M. gigas* larval survival and water temperature or salinity is not well known (Wood et al., 2021) and was normally established for oyster larvae reared in hatchery conditions. However, it has been stated that larval production is compromised when the water temperature is below 18 °C (Héral and Deslous-Paoli, 1991; Mann et al., 1991; Shatkin et al., 1998). Additionally, suitable temperature conditions ($T \geq 18$ °C) must be maintained for at least 2 weeks before pelagic larvae complete metamorphosis and become sessile animals (Shatkin et al., 1998).

A positive correlation between *M. gigas* expansion and the increase in seawater temperature has been reported elsewhere, resulting in faster gonad development, spawn and successful fertilization as well as larval development and recruitment rates (Diederich et al., 2005; Dutertre et al., 2010; Schmidt et al., 2008). Mainly since the mid-90s, the north European boundary of this species extended up to 60° N, which represents a 1400 km northward shift in approximately three decades (Wrange et al., 2010).

In Galicia (NW Spain), native flat oyster *O. edulis* have supported a traditional, profitable and intensive fishery for centuries, which led to the exhaustion of most oyster beds in the middle of the past century (Andreu, 1968). Then oyster farming was developed as an alternative, but the scarcity of local supply of flat oyster spat made it necessary to import large amounts of oysters from different countries. The first introductions of *M. gigas* in Galicia occurred during the 1980s and responded to unintentional immersions of Pacific oyster seed mixed with batches of *O. edulis* spat imported from France (Molares et al., 1986). Consequently, some local *M. gigas* populations were established in the Rías Altas (Fig. 1) >20 years ago. Initially, these naturalized oyster populations went unnoticed because they were erroneously identified as the Portuguese oyster *Magallana angulata*, but genetic analyses showed that they belong to *M. gigas*. An increase in their abundance and a range expansion towards the south has been evidenced nowadays as some Pacific oyster fisheries have been developed in the last five years (https://www.pescadegalicia.gal) over naturalized populations in estuaries from the Ártabro Gulf (Figs. 1 and 2). In the Rías Baixas (southern estuaries, Fig. 1), the experimental suspended culture of Pacific oysters in rafts was authorized by the Galician Government in 1991 to study the feasibility of this activity (Xunta de Galicia, 1992). Currently, >100 rafts have authorization, although <50 rafts continue to grow this species under experimental licences. Despite the spawning of *M. gigas* was reported (Ruiz et al., 1992), recruitment in the Rías Baixas has never been observed.

The geographical niche of the Pacific oyster could expand by the end of the century due to the increase in sea surface temperature (SST) projected under the different Representative Concentration Pathways (RCPs) (*e.g.* RCP8.5). This increase in SST could improve the environmental conditions necessary to reach optimal temperatures for larval settlement (King et al., 2021; Rinde et al., 2016; Robins et al., 2017; Thomas et al., 2016). The expansion of *M. gigas* populations, initially naturalized in the Rías Altas 20 years ago and reaching the Ártabro Gulf nowadays, suggests that their natural distribution limit is changing in Galicia and expanding towards the south due to ocean warming. Note that temperature along the Galician coast decreases southward due to coastal upwelling (Alvarez et al., 2011; Gómez-Gesteira et al., 2008). Future thermal conditions in the Rías Baixas may be suitable for the establishment of the NIS *M. gigas*, which would cause ecological and habitat changes that can affect fisheries, aquaculture, and other economic activities.

The present study aims to analyze the expansion of *M. gigas* along the Galician coast during the last decades and its relationship with the increase in water temperature associated with climate change. Additionally, an

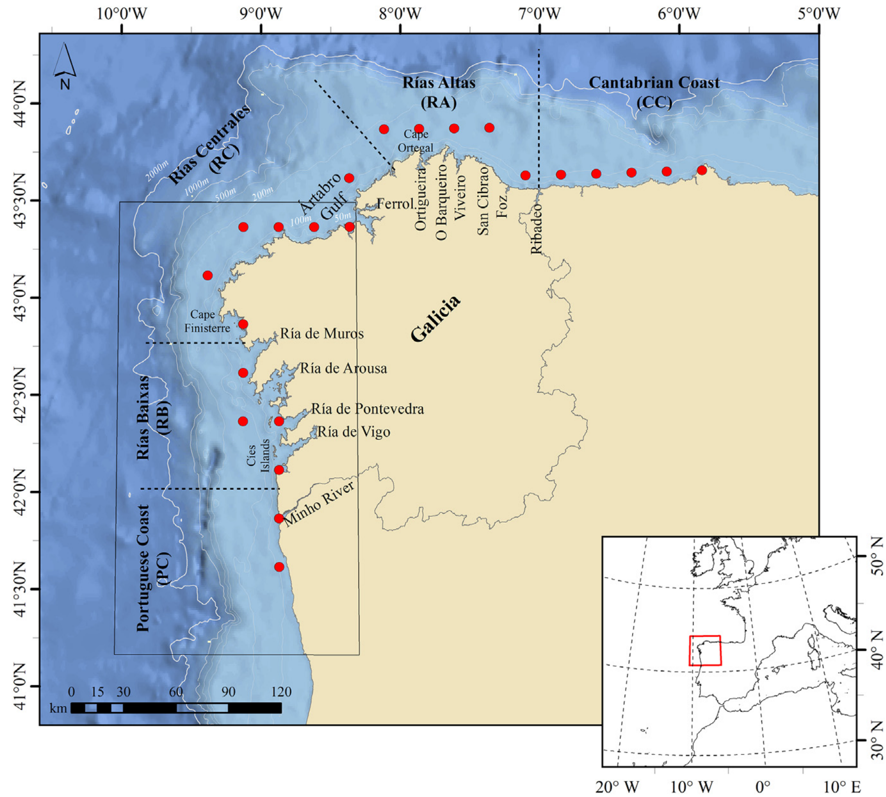

Fig. 1. Location of the study area showing the main geographical references. Red dots indicate locations where sea surface temperature data was retrieved from the Advanced Very High Resolution Radiometer Optimum Interpolation Sea Surface Temperature database. The red box indicates the modeled area using Delft3D-Flow. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

attempt is made to determine if the non-indigenous species *M. gigas* could undergo a naturalization process in the Rías Baixas in the incoming years or decades. To perform these tasks, the following main objectives were developed: i) to analyze the expansion of natural populations along the Galician coast, ii) to investigate the relationship between the appearance of new populations and the thermal suitability of the area using historical data of SST, and iii) to determine if future thermal conditions could favor the recruitment of *M. gigas* in the Rías Baixas. The last objective will be achieved by performing numerical simulations using the Delft3D-Flow hydrodynamic model for 1990–2099 under the RCP8.5 scenario.

2. Data and methods

2.1. Oceanography of the study area

Galicia is located in the extreme northwest of the Iberian Peninsula. This region has an extensive coastline that extends over 1720 km and is characterized by numerous inlets called rias, which are flooded incised valleys (Evans and Prego, 2003) with a river that flows into their innermost part. They are classified as partially mixed estuaries with a partially stratified estuarine circulation from a hydrographic point of view (Álvarez-Salgado et al., 2000; Gómez-Gesteira et al., 2003; Prego and Fraga, 1992; Taboada et al., 1998). Typically, the main river discharges into the head of the ria, promoting a positive estuarine circulation. Water exchange with the shelf is driven by the tidal range, continental runoff and coastal wind-driven upwelling/downwelling events (Alvarez et al., 2005; Alvarez-Salgado et al., 1993; Barton et al., 2015; deCastro et al., 2000; Gomez-Gesteira et al., 2006). The Galician rias are divided into Rías Baixas, Rías Centrales and Rías Altas (Fig. 1; Torre Enciso, 1958) by means of their geographic position, topographic features, and orientation.

The Rías Baixas are very productive systems that support extensive coastal fisheries, bivalve aquaculture and shellfish harvesting, mainly because of their privileged location at the northern boundary of the East Atlantic Upwelling System (Wooster et al., 1976). In the west coast, northerly coastal winds are favorable to the upwelling of the cold and nutrient-rich Eastern North Atlantic Central Water during the spring and summer, whereas southernly winds, prevailing during the autumn and winter, are favorable to the downwelling of surface coastal waters (Álvarez-Salgado et al., 2002; Wooster et al., 1976). On the other hand, on the north coast (Rías Altas), upwelling has been associated with northerly and northeasterly winds by Molina (1972), who set the eastern limit of the upwelling influence at the middle of the Cantabrian Sea (Piedracoba et al., 2005). For a comparison on the upwelling dependence on the coast orientation of Galicia the reader is referred to Alvarez et al. (2011). Despite the importance of winds (upwelling/downwelling events) that drive the residual circulation of the Galician rias, especially in the Rías Baixas, the tides and the input of freshwater from the rivers are the main hydrodynamic drivers in the Rías Altas and in the Rías Centrales (deCastro et al., 2004).

2.2. Assessment of the M. gigas presence

The viability of the Pacific oyster's culture on the Galician coast was assessed by an ambitious study funded by the regional Government of Galicia between 2004 and 2009. Experimental cultures were conducted in several locations, and the distribution of naturalized populations was surveyed to identify their location. Before the field survey, a poll was conducted among the Galician fishers guild's representatives to gather information about its presence in their coastal areas and delimitate the sites to be surveyed. Subsequently, the full extent and abundance of these populations were georeferenced in six estuaries in the Rías Altas during the fieldwork carried out in the framework of this study.

In addition, and at comparative effects, oyster spat collectors were placed in the Rías Altas in two consecutive summers, in intertidal areas where the naturalized population is abundant and in a southern ria where no recruitment was registered. In this last case, collectors were hung on ropes in Pacific oyster rafts and deployed onto iron tables where the experimental culture of this species took place in the framework of such study.

Some *M. gigas* naturalized populations began to be commercially exploited in 2007. This activity has to be authorized by the Consellería do Mar (Fisheries Ministry of the Galician Regional Government) after a stock assessment of the resource performed by technicians of the fisher guilds. The different exploitation plans authorized from 2007 to 2021 were analyzed, looking for the geographical coordinates of the exploited stocks and the effort and total allowed captures permitted. Information on sales corresponding to oyster catch in the different authorized guilds for the period 2007 to 2021 was obtained from the records of the Consellería do Mar, accessible through https://www.pescadegalicia.gal.

2.3. Historical data from the advanced very high resolution radiometer optimum interpolation SST database

Historical data of SST was used to investigate the relationship between the appearance of new populations and the thermal suitability of the area. July and August were chosen to perform this study because these are the months with the maximum atmospheric temperature and coincide with the spawning season of *M. gigas* (Ruiz et al., 1992). SST from the NOAA Optimum Interpolation 1/4° Daily Sea Surface Temperature (OISST) Analysis, Version 2 product (https://www.ncdc.noaa.gov/oisst) was downloaded for 1982 to 2020. This product combines satellite and *in situ* data covering a regular grid with a spatial resolution of 0.25° and daily temporal resolution. Data from the ocean cells close to the shore (a total of 23 points; Fig. 1) was used to detect and analyze shifts in the thermal-suitable areas for the settlement of the Pacific oyster by comparing two historical periods, 1982–2001 and 2002–2020.

2.4. Modeling historical and future water temperature with Delft3D

Modeled water temperature data were used to predict the favorable areas for *M. gigas* inside the Rías Baixas (NW Iberian Peninsula) in the future and to compare them with the historical ones to determine whether the oysters may undergo a naturalization process in the Rías Baixas.

The Flow module of the Delft3D hydrodynamic model was used to perform a downscaling of the GCMs' outputs in the Rías Baixas. Delft3D model was firstly implemented for the study area by Des et al. (2019) under realistic conditions. This parametrization was slightly modified by Des et al. (2020a) to adequately reproduce the hydrodynamics of the study area when the input data come from global and regional climatic models. It was previously used to downscale water temperature and salinity under different greenhouse gas emission scenarios for the study area (Des et al., 2020a, 2020b, 2021).

The main characteristics and inputs of the numerical model are summarized below:

The used grid covers from 8.33°W to 10.00°W and from 41.18°N to 43.50°N (Fig. 1). It is curvilinear and irregular. The horizontal resolution increases gradually from the west boundary (2200 m × 800 m) towards onshore (220 m × 140 m inside the Rías Baixas and 50 m × 77 m in the Minho River estuary). In the vertical, 16 sigma layers were considered, which are divided as follows, 1st and 2nd layers 1 %, 3th 3 %, 4th 4 %, 5th 5 %, 6th 6 % and from 7th to 16th 8 % of the depth.

The bathymetric dataset compiles data from different sources: nautical charts of the Spanish Navy Hydrographical Institute for the estuaries of Muros, Arousa and adjacent shelf; multibeam data with a spatial resolution of 5 m provided by the Spanish General Fishing Secretary for the estuaries of Pontevedra and Vigo; 100-m-resolution data from the Portuguese Navy Hydrographic Institute for the Minho estuary; and data from the General Bathymetric Chart of the oceans for filling gaps.

Water level, salinity and water temperature data were used to force the oceanic boundary. Flow conditions were forced as astronomic using the thirteen main harmonic constituents obtained from the TPXO 7.2 TOPEX/Poseidon Altimetry model (http://volkov.oce.orst.edu/tides/global.html). Salinity and water temperature data from MOHC-HadGEM2-Es GCM outputs (https://esgf-node.ipsl.upmc.fr/projects/esgf-ipsl/) were imposed per layer as transport conditions following the analysis performed by Sousa et al. (2020). Regarding atmospheric inputs, the heat flux model used was the "absolute flux, net solar radiation", and wind components and pressure data were imposed varying spatially. The required atmospheric data (air temperature, relative humidity, shortwave and longwave radiation, wind components and pressure) were downloaded from the MOHC-HadGEM2-Es-RCA4 RCM outputs (http://www.cordex.org/), also following Sousa et al. (2020). River discharges from the main tributaries in the modeled area were imposed as fluvial open boundaries. River discharge data were

Fig. 2. Settlements of *M. gigas* in the Ría de Ferrol, Ártabro Gulf (at the top); and in the Ría de O Barqueiro, Rías Altas (at the bottom).

downloaded from the Hype Web portal (https://hypeweb.smhi.se). A linear interpolation was performed to reduce river discharge following the HypeWeb portal predictions for the study area, a 10 % of river discharge reduction by 2050 and 25 % by 2080 (https://hypeweb.smhi.se/explore-water/climate-impacts/europe-climate-impacts/).

In the present study, the Delft3D model was run for July and August over the period 1990–2099 using a spin-up period of two weeks Des et al. (2020a, 2019) and obtaining outputs with a temporal resolution of 6 h. Water temperature data from the four upper layers that correspond to 9 % of the depth were used to perform this work. Future projections under the RCP 8.5 greenhouse gas emission scenario were considered.

Changes in water temperature were analyzed in terms of differences between average temperature calculated for both near (2040–2069) and far (2070–2099) future scenarios and that calculated for the historical period (1990–2019).

2.5. Determining thermal habitat suitability

As it was stated in the introduction, larval production is compromised when the water temperature is under 18 °C, being the optimal range between 20° and 25 °C (Dutertre et al., 2010; Héral and Deslous-Paoli, 1991; Mann et al., 1991; Shatkin et al., 1998). Additionally, suitable water temperature conditions must be maintained for at least two weeks before the pelagic larvae complete metamorphosis and become sessile animals (Arakawa, 1990; Rico-Villa et al., 2008; Shatkin et al., 1998). No upper limit of the water temperature tolerance range was considered, since successful larvae settlement has been reported even at 32 °C (Rico-Villa et al., 2009), and projections for the study area indicate that future water temperature will not reach that value even under the RCP8.5 scenario. According to that, favorable conditions for the presence of *M. gigas* were considered when the daily mean water temperature was higher than 18 °C for at least 15 consecutive days in July and August.

The number of consecutive days during which the average daily water temperature is equal to or >18 °C was calculated for both datasets (OISST data and downscaled data). The largest number of consecutive days for each year and each point/grid-cell was considered. The average and standard deviation were calculated for each point of the OISST dataset for the periods 1982–2001 and 2002–2020. The numerical average was also calculated for each grid cell for the historical (1990–2019), near future (2040–2069) and far future (2070–2099). Those pixels where the mean number of days is ≥15 during the study period were considered thermally suitable for the settlement of *M. gigas*.

3. Results and discussion

In Galicia, *M. gigas* was only reported in the Rías Altas in those questionnaires distributed to the guilds' technicians before the field surveys performed in 2008–2009. Pacific oysters' presence of a broad range of sizes was confirmed in different locations of the Rías Altas (Ribadeo, Foz, San Cibrao, Viveiro, O Barqueiro and Ortigueira, green dots in Fig. 3a). During this field sampling, specimens with a dorsoventral height up to 200 mm were recorded as previously shown in Fig. 2 (bottom panels), suggesting that the species established long ago. These observations are consistent with the hypothesis that their origin were the Pacific oysters inadvertently introduced during the 1980s mixed with batches of *O. edulis* spat imported from France (Molares et al., 1986). The first exploitation plans of naturalized beds of *M. gigas* were developed in Ría do Barqueiro in 2007, and the commercialization of Pacific oysters harvested in this estuary began in 2010 when 59.577 tons were sold at the local fish auctions. From 2007 to 2016, exploitation and commercialization were only performed in estuaries belonging to the Rías Altas (Fig. 3b, marked in blue), suggesting that at that time the western limit of the established populations of *M. gigas* was near Cape Ortegal (43.77° N; 7.87° W). This cape could represent a natural barrier for the dispersal of *M. gigas* on the Atlantic coast due to differences in water temperature. The northwest coast of the Iberian Peninsula is characterized by upwelling events that occur throughout the year, but

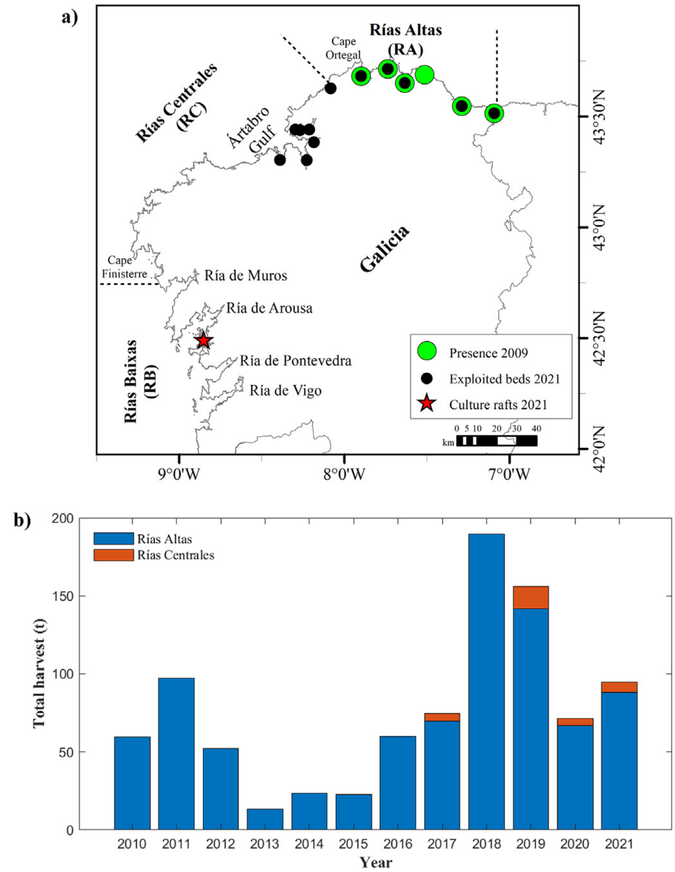

Fig. 3. Historical evolution of *M. gigas.* a) Presence along the Galician coast; b) Annual amount of *M. gigas* sold at the fish auctions in Galicia from 2009 to 2021 classified by geographical area. Blue bars indicate the amount of *M. gigas* sold in fish auctions on the north coast and orange bars on the northwest coast. Source: https://www.pescadegalicia.gal (last access: February 2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mainly during the spring-summer season (Alvarez et al., 2008; deCastro et al., 2008). However, upwelling events affecting the northwest coast are more common and intense than those affecting the northern coast (Alvarez et al., 2011). During these upwelling events, cold nutrient-rich bottom water rises to the surface and reduces water temperatures in coastal areas. The cold-upwelled water usually penetrates estuaries located on the west coast, while this only occurs during very intense events on the north coast (Alvarez et al., 2010). This produces water temperature gradients along the shoreline: the warm waters are found on the east coast of the Cantabrian Sea, and the temperature decreases towards the west, reaching minimum values between Cape Ortegal and the Rías Baixas and increasing again towards the south along the coast of Galicia (Botas et al., 1990; Gómez-Gesteira et al., 2008). This water temperature pattern has turned the northwest coast of the Iberian Peninsula into a climatic refuge for many cold-temperate species (Martínez et al., 2012).

The first sale records of fish auctions located on the Atlantic coast appeared in 2017 (Fig. 3b, marked in orange). The harvesting was progressively expanding along the northwestern coast of Galicia, and currently, the Pacific oyster is harvested on the north and northwest coasts (Fig. 3a, black dots). The reefs located on the north coast are the most productive (Fig. 3b, marked in blue), with 97.39 % of the total production between 2010 and 2020. During the last decade, the areas of harvesting increased as well as the number of oysters sold in the fish markets, peaking in 2018, when >189 tons of *M. gigas* were sold. Production data and field observations indicate that the populations located in the Rías Altas are well established and in natural expansion, while the Rías Centrales constitute an area of recent colonization where the populations are in the establishment stage (Sakai et al., 2001).

Changes in the geographical range limit of *M. gigas* over the last decade in the NW Iberian Peninsula are probably related to ocean warming. Rising water temperatures have increased the number of days that the water temperature remains above 18 °C (Fig. 4), the lower limit for the successful spawning, larval development, and settlement of *M. gigas*. The optimal thermal conditions for the settlement of the Pacific oyster (water temperature equal to or higher than 18 °C for at least 15 consecutive days) were only observed in the north coast from 1982 to 2001 (Fig. 4a and b), while more recently (2002 − 2020) these conditions also occurred in the northwestern coast of Galicia (Fig. 4c and d). The improved thermal conditions coupled with local hydrodynamics have probably favored these new settlements on the Rías Centrales (RC in Fig. 4a and c). In general, the predominant northeasterly winds in the Northwest Iberian Peninsula from March–April to September–October promote a southward surface current with an Ekman-related offshore deflection of the surface flux (Lorente et al., 2015; Varela et al., 2005). This period coincides with the spawning season of the Pacific oyster and may have facilitated the southward dispersal of oyster larvae. Sea surface temperature data indicates that 43° N represents the southern thermal range limit for the settlement of *M. gigas*; however, as far as we know, naturalized populations have not been observed further south of the Ártabro Gulf.

There are two possible reasons to explain why *M. gigas* is not naturalized between the Ártabro Gulf and Cape Finisterre: i) the improvement in water-temperature conditions has occurred at a higher rate than the expansion of the species, and ii) the shoreline of this stretch is not suitable for oyster seed settlement and reef formation because there are practically no estuaries (Fig. 1) and the coastline is exposed to high-energy waves (Carballo et al., 2014).

Although the southward displacement of the thermal limit for *M. gigas* observed over the last two decades, thermal conditions continue to be unfavorable for its recruitment in the Rías Baixas, where the Pacific oyster is cultivated with spat from the northern estuaries or imported from France. This was also confirmed in the study carried out between 2004 and 2009, when no recruitment was registered in oyster spat collectors hung on rafts and deployed on iron tables, which are located in different areas of the Ría de Arousa (Rías Baixas). However, in the face of a global warming scenario with a significant expected impact on these biologically-rich estuaries (Álvarez-Salgado et al., 2008; Des et al., 2020a, 2020b, 2021; Gestoso et al., 2016; Sousa et al., 2017, 2020), it is worth asking whether conditions will be favorable in the future for the naturalization of the Pacific oyster, when it may occur and the possible impacts.

Projections show rising water temperatures in both the near and far future (Fig. 5a, b) periods for all the Rías Baixas when compared with the historical period. The histogram of Fig. 5c shows an increase in water temperature between 0.5 and 1.5 °C for the near future and between 2 and 3 °C for the far future in >99 % of the Rías Baixas area. On average, the water temperature will rise 1.1 ± 0.2 °C and 2.5 ± 0.2 °C in the near and far future. Nevertheless, it is remarkable that the higher frequency of occurrence for the near future is between 1 and 1.5 °C (>63 % of the area) and between 2.5 and 2.8 °C (>54 % of the area) for the far future.

Modeled data shows that only the innermost areas of the Rías Baixas, mainly the estuaries of Muros, Arousa, and Vigo, were favorable for the recruitment of *M. gigas* during the historical period (Fig. 6a). Despite the presence of rafts in some of these areas with favorable conditions, such as the

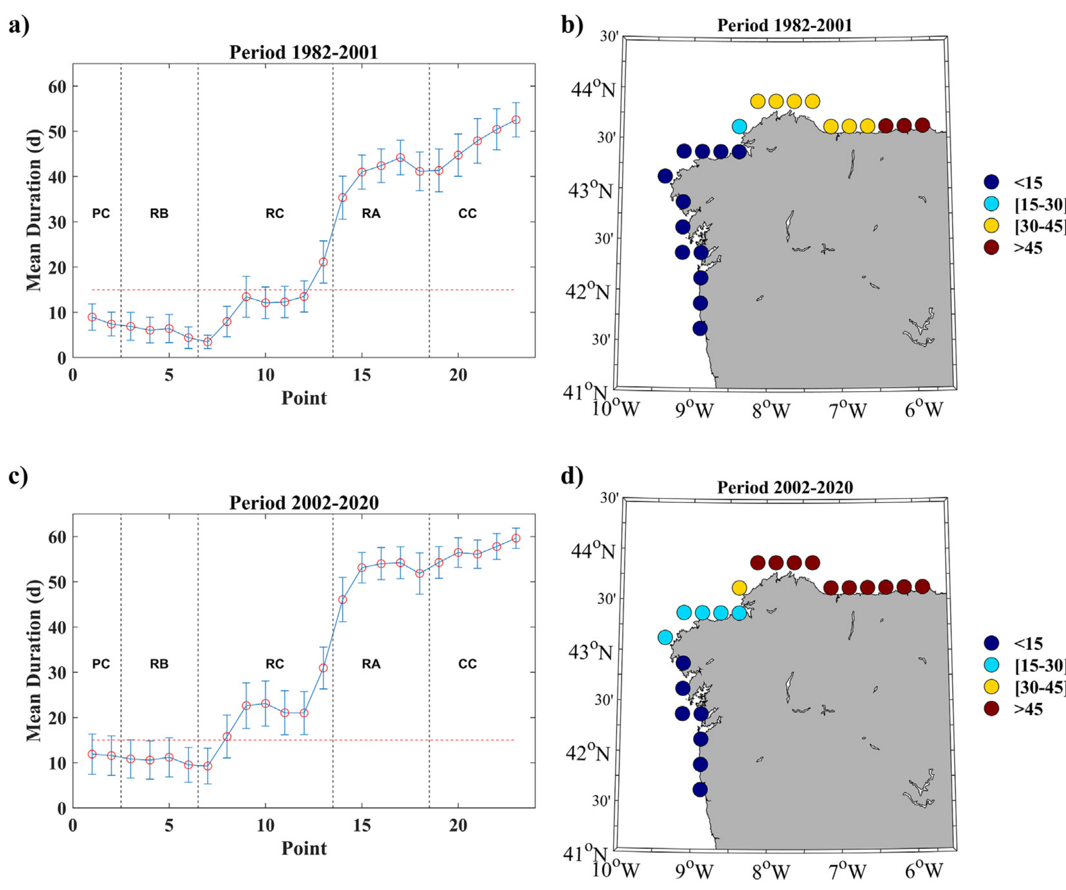

Fig. 4. Average and standard deviation of the number of consecutive days with daily mean SST overpassing 18 °C during July and August from 1982 to 2001 (a) and 2002 to 2020 (c), red dash line indicates the optimal thermal threshold for the settlement of *M. gigas*. The dashed lines in the left panels mark the limits of the zones described in Fig. 1. Right panels represent the geographical location of the points from south to north, with dot colour varying according to the average duration. PC: Portuguese Coast; RB: Rías Baixas; RC: Rías Centrales; RA: Rías Altas; CC: Cantabrian Coast. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

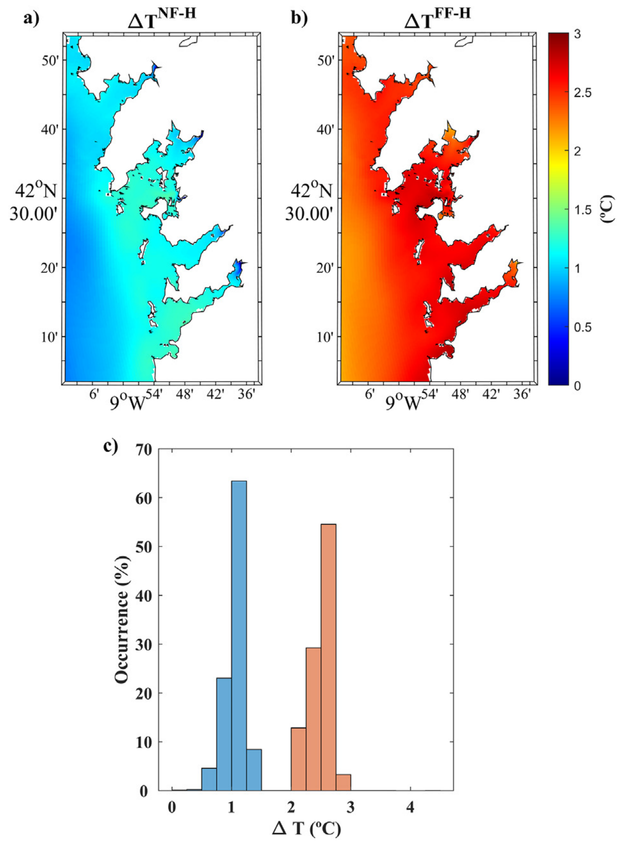

Fig. 5. Differences between predicted water temperature for the near future (a) and far future (b) regarding the historical period (Future-Historical). Histogram showing the frequency of the temperature differences shown in a (blue) and b (red) (c). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Ría de Arousa (red star marked in Fig. 3), natural recruitment has not been reported so far. During the spawning season, favorable upwelling winds are predominant, and the main direction of the surface currents is towards the ocean. This can favor the larvae transport out to sea in surface waters, which would strongly reduce recruitment (Levinton, 2011). Moreover, the high filtration pressure of the mussel stock cultured in rafts located in the Rías Baixas may produce bivalve larviphagy, *i.e.*, the feeding of bivalve larvae reducing the larval abundance and therefore limiting the recruitment success (Troost, 2010). All this is coupled with the small number of individuals cultivated in the rafts.

Thermally favorable conditions progressively extend from inner to outer and from shallower to deeper areas (Fig. 6). The projections for a mid-century show that the greatest extension of the thermally favorable areas is found in the inner and middle parts of the Arousa and Vigo estuaries (Fig. 6b). Favorable conditions may also be found in a small bay to the southwest of the Ría de Vigo and the central channel, in front of the Cíes Islands (Fig. 1). This last spot is probably related to an eddy located in the area during the summer months previously described by Barton et al. (2015). By the end of the century (Fig. 6c), thermal conditions will be favorable for the settlement of *M. gigas* practically throughout the estuaries.

The total extension of suitable areas in the Rías Baixas is expected to increase in the coming years, but the rate of increase may differ between estuaries (Fig. 7), reaching 100 % in all of them by the end of the century. Following projections, the Ría de Arousa (Fig. 1) may be the most suitable estuary for the naturalization of the Pacific oyster, since around 50 % of its total extension may be favorable for recruitment by the middle of the century, reaching up to 90 % in the 2080s and 100 % by 2100. No significant changes are expected for Pontevedra and Vigo estuaries until the 2060s. Finally, in the Ría de Muros, a very low rate of change is expected initially, with a sharp increase in the last decades of the century.

All the results indicate that *M. gigas* may undergo a naturalization process in the Rías Baixas in the future. Suitable thermal conditions can already be found in some areas, and therefore, successful settlement can occur for years to come. However, settlement by larval drift from populations located to the north is considered unlikely in a short time due to the long distance and because the ocean warming impact seems asymmetrical through the Galician coast, being more favorable in the Rías Baixas (Des et al., 2020a) and less in the Ártabro Gulf (Fuentes-Santos et al., 2021).

On the other hand, since the Pacific oyster is an ecosystem engineer (Jones et al., 1994), it is expected that it may modify the habitat structure, leading to changes in local diversity, as it may inhibit the recovery of native flat oysters, cause a decrease in fucoid algae or induce changes in the habitat chemistry (reviewed in Padilla, 2010). The Pacific oyster may also compete for settlement with mussels and clams or even live as epibiont on mussel beds as reported elsewhere (Diederich, 2005; Reise, 1998; Wrange et al., 2010), leading to trophic competition (Herbert et al., 2016). Moreover, there are negative socio-economic impacts to be considered, mainly linked to the presence of reefs due to the hard and sharp oyster shells, as they may potentially cause injuries to the public or hinder the maintenance of navigation channels for recreational boats (Herbert et al., 2016).

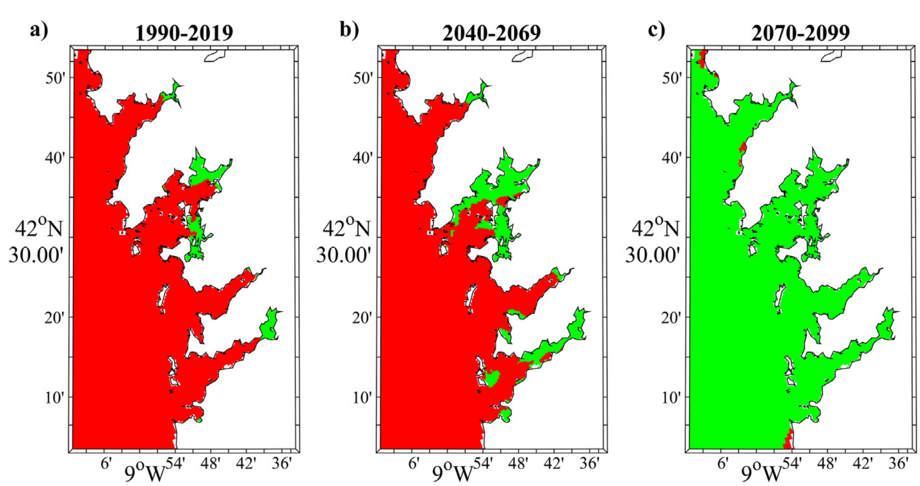

Fig. 6. Thermal suitability maps for *M. gigas* settlements in the Rías Baixas for the historical (a), near future (b) and far future (c) periods. Green colour indicates areas favorable for the settlement (daily mean water temperature ≥ 18 °C for, at least, 15 consecutive days during July and August), red colour indicates unfavorable areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

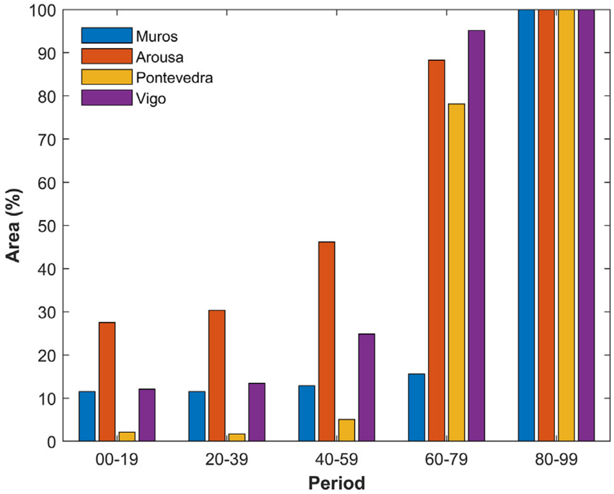

Fig. 7. Extension of the thermally favorable area for *M. gigas* settlement in the different estuaries of the Rías Baixas throughout the 21st century, in relation to the extension of each estuary, calculated in periods of 20 years.

Although the naturalization of *M. gigas* will be led by ocean warming since temperatures lower than 18 °C inhibit the successful development and settlement of the larvae (Castaños et al., 2009; Héral and Deslous-Paoli, 1991; Rico-Villa et al., 2009; Wiltshire, 2007), other environmental factors can play an important role. Changes in salinity, as well as food, calcium carbonate, and dissolved oxygen availability, are also crucial factors affecting the larval physiology and adult individuals, and it is known that climate change will affect them in a way that may hinder the naturalization process of the Pacific oyster (Gulev et al., 2021). Pack et al. (2021) have determined that salinity drops have a significant impact on the Pacific oyster while the predicted reduction of pH for the 21st century will not affect adult physiology and survival. Nevertheless, more studies are needed, particularly those related to regional and local changes, such as hypoxic events which are highly related to an increase in land-derived nitrogen inputs (Patterson et al., 2014). Further understanding of these issues and their synergetic interaction is required in order to determine the potential for *M. gigas* populations to spread.

4. Conclusions

The Pacific oyster, *M. gigas*, is a naturalized species on the north and northwest coasts of Galicia (NW Iberian Peninsula) whose recruitment and production have been favored by the current ocean warming. This has led to a significant development of harvesting activities during the last decade.

The increase in water temperature projected for the future will favor the naturalization of *M. gigas* in the Rías Baixas (southwest of Galicia). The Ría de Arousa will probably be the first of the four estuaries where *M. gigas* becomes naturalized, although favorable thermal conditions will improve substantially in Vigo, Pontevedra, and Arousa estuaries by mid-century. By the end of the century, all four estuaries are expected to be thermally favorable for this species.

Overall, Pacific oysters' naturalization will spread throughout the Rías Baixas due to ocean warming, which will imply significant changes in the habitat and the ecosystem that are difficult to predict but that are likely to cause a severe ecological and economic impact, making it necessary to implement monitoring and management strategies to mitigate its effect.

Credit authorship contribution statement

M. Des: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data Curation, Visualization, Writing - Original Draft. Funding acquisition. **J. L. Gómez-Gesteira**: Conceptualization, Methodology, Investigation, Resources, Writing - Original Draft. **M. deCastro**: Conceptualization, Methodology, Formal analysis, Investigation, Writing - review & editing, Supervision, Funding acquisition. **D. Iglesias**: Investigation, Resources, Writing - review & editing. **M.C. Sousa**: Methodology, Writing - review & editing. **G. ElSerafy**: Writing - review & editing. **M. Gómez-Gesteira**: Conceptualization, Methodology, Software, Formal analysis, Visualization, Writing - review & editing, Supervision, Project administration.

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.

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