



## Does global warming threaten small-scale bivalve fisheries in NW Spain?

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### ABSTRACT

Shellfisheries of the intertidal and shallow subtidal infaunal bivalves *Ruditapes decussatus*, *Ruditapes philippinarum*, *Venerupis corrugata* and *Cerastoderma edule* are of great socio-economic importance (in terms of landings) in Europe, specifically in the Galician Rías Baixas (NW Spain). However, ocean warming may threaten these fisheries by modifying the geographic distribution of the species and thus affecting productive areas. The present study analysed the impact of rising ocean temperature on the geographical distribution of the thermal comfort areas of these bivalves throughout the 21st century. The Delft3D model was used to downscale climate data from CORDEX and CMIP5 and was run for July and August in three future periods (2025–2049, 2050–2074 and 2075–2099) under the RCP8.5 scenario. The areas with optimal temperature conditions for shellfish harvesting located in the middle and outer parts of the rias may increase in the near future for *R. decussatus*, *V. corrugata* and *C. edule* and decrease in the far future for *R. philippinarum*. Moreover, shellfish beds located in the shallower areas of the inner parts of the Rías Baixas could be affected by increased water temperature, reducing the productive areas of the four species by the end of the century. The projected changes in thermal condition will probably lead to changes in shellfish harvesting modality (on foot or aboard vessels) with further socio-economic consequences.

### 1. Introduction

Coastal and transitional areas, including estuaries, are among the world's most productive ecosystems, producing approximately half of the global fishery catch per year (Palomares and Pauly, 2019), with small-scale fisheries contributing almost half of this catch (Elliott et al., 2019). Estuaries are important coastal environments, providing biologically productive nursery habitats for many commercially-targeted vertebrates and invertebrates species (bivalves, among others). Estuarine habitats buffer many coastal communities from the impacts of storms, rising sea levels, changes in patterns of sediment erosion and deposition and increased levels of pollutants, providing also the basis of a livelihood for millions of people (Barbier et al., 2011; Fujii, 2012; Howes et al., 2015).

In the Galician Rías (NW Iberian Peninsula), bivalves are exploited commercially in small-scale fisheries or aquaculture operations. Bivalve fisheries in the intertidal and shallow subtidal contribute an overall annual income of ~74 million €, involving ~7100 fishers (<http://www.pescadegalicia.gal>). The most important commercial species in the area

are the native clam *Ruditapes decussatus* (Linnaeus 1758), the introduced Manila clam *Ruditapes philippinarum* (Adams and Reeve, 1850), the grooved carpet shell *Venerupis corrugata* (Gmelin, 1791) and the cockle *Cerastoderma edule* (Linnaeus, 1758). The harvesting activity of these species is generally carried out by two modalities: on foot or afloat (Piñeiro-Antelo and Santos, 2021). Shellfishing on foot is mostly carried out by women in intertidal zones, and the gathered species are mainly *R. decussatus*, *R. philippinarum*, *C. edule* and, to a lesser extent, *V. corrugata*. However, shellfish gathering afloat is carried out by men in the sublittoral zone from small boats, being *V. corrugata* the main species caught in this modality (Lago, 2008; Piñeiro-Antelo and Santos, 2021).

Bivalve fisheries are strongly influenced by climatic conditions. Fluctuations in salinity and temperature cause high spatial and temporal variability in fishery catches with consequent economic losses. Episodes of severe mortality in shellfish beds in the study area were recorded in unpublished technical reports of the fishery administration (Xunta de Galicia). These reports were subsequently analysed by Parada et al. (2012) and Aranguren et al. (2014), who concluded that salinity drops and changes in water temperature were the main drivers of mortality.

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Therefore, although temperature is not the only environmental factor affecting bivalves, it is one of the determining drivers influencing the physiology and habitat distribution of these molluscs (Sobral and Widdows, 1997; Somero, 2002; Matias et al., 2009; Zippay and Helmuth, 2012). Even though the effects of temperature on physiology is species dependent, physiological rates generally increase with temperature until a threshold is met, after which performance will decline (Zittier et al., 2015). Furthermore, small increases in body temperature above optimal levels greatly reduce fitness (Deutsch et al., 2008; Martin and Huey, 2008). Abrupt short-term changes in temperature may affect the survival of bivalves (e.g. Rinde et al., 2016; Domínguez et al., 2021a), have sublethal effects on potential growth or reproductive timing and effort and, consequently, on the spatial distribution and population dynamics of the species (Bayne, 1976; Zippay and Helmuth, 2012; Filgueira et al., 2014; Domínguez et al., 2021a; Vázquez et al., 2021). In addition, even a slowly ocean warming may lead to significant and abrupt changes in the distribution and abundance of species, even when impacts on population dynamics have not been previously observed (Woodin et al., 2013). Many bivalve species are capable of adapting to long-term changes in temperature, although at some cost (Widdows and Bayne, 1971). Determining potential changes in the distribution of bivalves is of special interest for the future sustainability of shellfish beds in the context of climate change.

*Ruditapes decussatus*, *R. philippinarum*, *Venerupis corrugata* and *Cerastoderma edule* are able to survive a broad range of temperatures through physiological and behavioural mechanisms (Sobral and Widdows, 1997; Anacleto et al., 2013; Verdelhos et al., 2015; Macho et al., 2016; Domínguez et al., 2021a). However, temperature tolerance depends on the acclimation capacity (Gosling, 2008) and ecology of the species. These infaunal species live buried in the sediment at different depths, i.e. *C. edule* (~1 cm), < *R. philippinarum* (~3 cm) < *V. corrugata* (~7 cm) < *R. decussatus* (~8–10 cm) (Macho et al., 2016; Domínguez et al., 2021a), where sediment and interstitial water buffer thermal fluctuations. However, evaporative cooling becomes limited when the sediment heats and dries up during low tide, thus exposing the bivalves to long-term temperature stress. The water temperature during the summer months is very important for these species because this is when the main spawning period occurs, although changes in the solar irradiance during spring and autumn may indirectly extend such period (Fuentes-Santos et al., 2016). The spawning period of *R. decussatus* occurs between June and August, while in *R. philippinarum* and *V. corrugata* it occurs between May and July and between April to September, respectively (Vázquez et al., 2021). By contrast, *C. edule* undergoes a period of gonadal resorption in summer (Martínez-Castro and Vázquez, 2012). The duration of reproductive activity, particularly gonadal development and spawning, is directly related to temperature fluctuations (Bayne, 1976; Delgado and Pérez-Camacho, 2007a; Vázquez et al., 2021).

The global sea surface temperature (SST) has increased by on average  $0.11 \pm 0.02$  °C dec<sup>-1</sup> since 1971 (Pachauri et al., 2015), with rates of change that are not evenly distributed throughout the oceans (IPCC et al., 2021) and that vary by region. This causes populations and communities to experience specific trends in warming conditions. In the Iberian Peninsula, surrounded by both the Atlantic Ocean and the Mediterranean Sea, SST trends vary at different spatial and temporal scales (deCastro et al., 2009; Gómez-Gesteira et al., 2011; Serrano et al., 2020). In the eastern part of the Atlantic, from the Gulf of Cadiz (S Iberian Peninsula) to the Cantabrian Sea (N Iberian Peninsula), the SST increased from 0.13 to 0.35 °C dec<sup>-1</sup> in the last two decades, respectively, with non-homogeneous trends between the north and the northwest coastal areas (Serrano et al., 2020). Regarding the area adjoining the Galician Rías Baixas, the SST increase of ~0.14 °C dec<sup>-1</sup> over the last decades of the 20th century was much more intense (~0.3 °C dec<sup>-1</sup>) in spring and summer (Gómez-Gesteira et al., 2008; Gómez-Gesteira et al., 2011). More recently, a SST increase of around 0.19 °C dec<sup>-1</sup> for the period 1982–2015 has been reported by Varela et al. (2018). Regarding with projections, a SST increases of around

0.2–0.25 °C dec<sup>-1</sup> is expected for the 21st century (Varela et al., 2022).

The aim of this study was to determine how global warming, particularly changes in water temperature when the warmest temperatures occur (July–August), may affect the geographical distribution of the thermal comfort areas of *R. decussatus*, *R. philippinarum*, *V. corrugata* and *C. edule* at a spatial scale of hundreds of metres in the highly productive upwelling system of the Rías Baixas (NW Iberian Peninsula). With this aim, the Delft3D-Flow model was used to downscale the climate variables from CORDEX and CMIP5 in the Rías Baixas. The downscaling yielded bottom water temperature data with an appropriate resolution for evaluating changes in the geographical distribution of the thermal tolerance ranges. The model was run under the RCP8.5 greenhouse gas emission scenario for July and August in the historical period (1990–2019) and in near (NF, 2025–2049), mid (MF, 2050–2074), and far (FF, 2075–2099) future periods.

## 2. Methodology

### 2.1. Area of study

The Rías Baixas (Fig. 1), located at the NW Iberian Peninsula, consist of four flooded incised valleys (Evans and Prego, 2003), which lie within the NW Iberian Upwelling System (Fraga, 1981). The rias are generally divided into three parts due to the hydrodynamic and sedimentary characteristics: outer, middle and inner. The inner part is a relatively shallow area where the main river flows and is hydrodynamically dominated by river discharges. The middle part corresponds to the central area where a low-energy regime dominates, and the outer part connects the mouth of the ria to the shelf and is mainly influenced by ocean dynamics. In most cases, the presence of islands and peninsulas in the outer part protects the ria from the direct and energetic influence of the ocean swell (Vilas et al., 2005). The depth along the axis of the rias decreases gradually from the outer parts (40–60 m) to the inner parts (5–10 m) (Vilas et al., 2005).

Hydrodynamically, the Rías Baixas behave as partially-mixed estuaries with a typical positive residual circulation pattern (Taboada et al., 1998). Freshwater generally flows shelfward through the surface layers, and oceanic waters penetrate through the lower layer flowing upstream. Between April and October, the prevalence of northerly winds over the shelf favour upwelling events and enhance positive estuarine circulation in the rias (Alvarez-Salgado et al., 1993; Souto et al., 2003; Álvarez et al., 2005; Gómez-Gesteira et al., 2006; Barton et al., 2015). The occurrence of upwelling events, combined with co-varying factors such as the high nutrient inputs, the shelter from wave action and the river flow (Des et al., 2020b), support highly productive shellfish beds, especially in the inner part of the rias, near the river mouths, where riverine inputs of nutrients enhance the primary productivity of the fishing beds (Figueiras et al., 2002; Bode et al., 2009).

The tidal regime is semi-diurnal and mesotidal, with a period of approximately 12.25 h and an amplitude of between 1.3 m during neap tides and 3.4 m during spring tides (Des et al., 2021).

### 2.2. Numerical model

The Delft3D modelling open-source software ([www.os.deltares.nl](http://www.os.deltares.nl)) was used to simulate transport conditions in the Rías Baixas. Delft3D is a three-dimensional hydrodynamic model which solves the horizontal equations of momentum, continuity, transport and turbulence (Deltares, 2018). The model uses a curvilinear grid comprising an area between 41.18° to 43.50° N and 10.00° to 8.33° W (Fig. 1a). The horizontal resolution of the grid increases from the outer west boundary (2200 × 800 m) to the east, reaching 220 × 140 m in the Rías Baixas (Fig. S1). The vertical grid is composed of 16 sigma layers, divided as follows, 1st and 2nd layers 1%, 3rd 3%, 4th 4%, 5th 5%, 6th 6% and from 7th to 16th 8% of the depth.

Bathymetric data were obtained from different sources. The data for

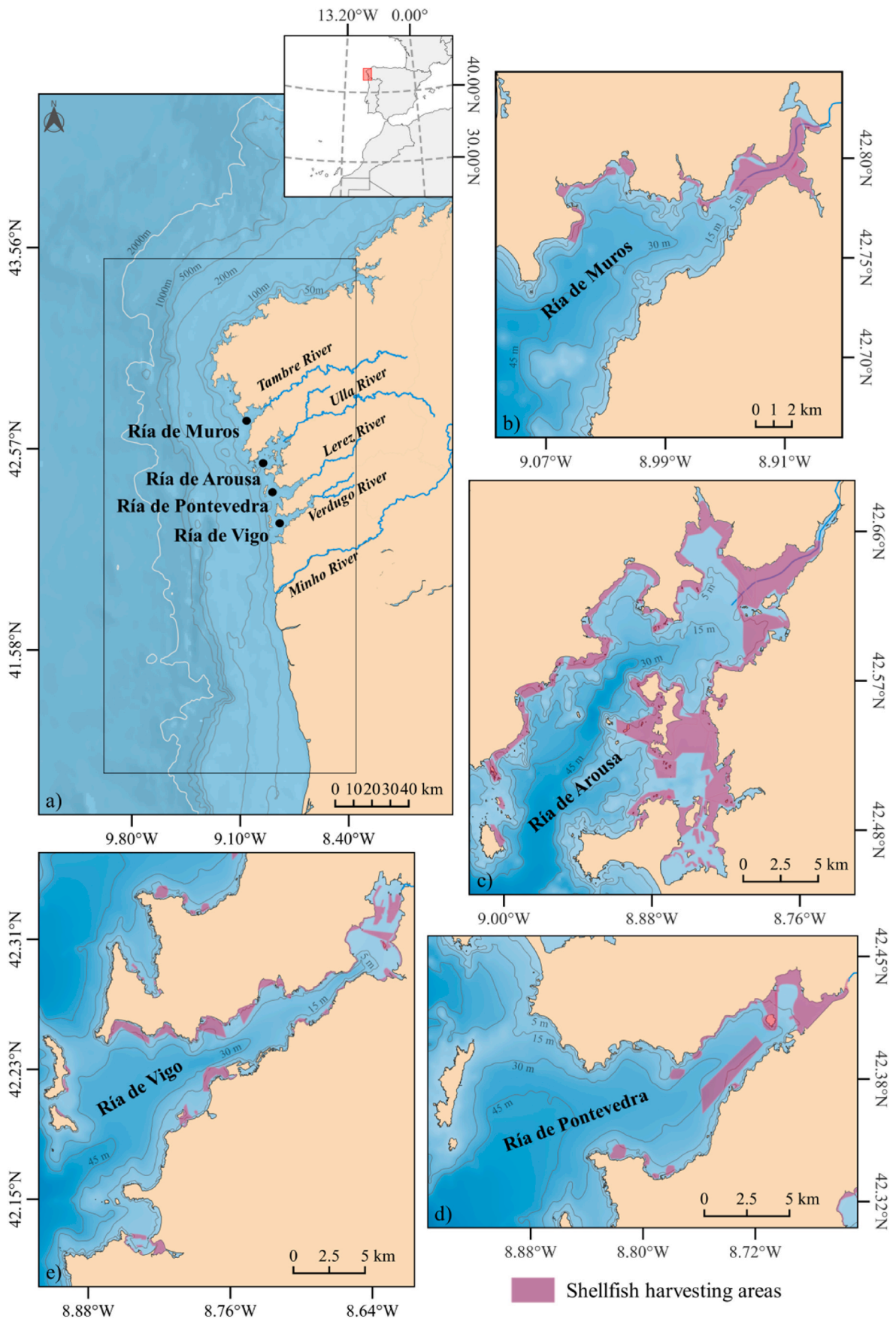


Fig. 1. Location of the study area (a). The box indicates the modelled area. Close-up views of Ría de Muros, Ría de Arousa, Ría de Pontevedra and Ría de Vigo, respectively (b–e). Shellfish harvesting areas are indicated in purple (source: <http://ww3.intecmar.gal/intecmar/>).



Muros and Arousa rias were obtained from the nautical charts of the Hydrographic Institute of the Spanish Navy. Bathymetric data with a resolution of 5m for the Vigo and Pontevedra rias were provided by the General Fishing Secretary. The data for the Minho estuary were provided by the Hydrographic Institute of the Portuguese Navy. Data from the General Bathymetric Chart of the Oceans (GBCP, <https://www.gebco.net/>) were used to fill in the gaps and cover the open ocean area.

Delft3D was forced with climate data simulated by global (GCMs) and regional (RCMs) climate models within the frameworks of the Climate Model Intercomparison Project Phase 5 (CMIP5, <https://esgf-node.lnl.gov/>) and the Coordinated Regional Climate Downscaling Experiment (CORDEX) project (<https://cordex.org/>). Due to the long time needed to run each test, the most accurate climate model reproducing historical conditions in the study area was selected. This model was determined by means of a statistical analysis similar to the one carried out by Sousa et al. (2020). As in the Sousa et al. (2020) study, MOHC-HadGEM2-ES-RCA4 showed to be the best climatic model for reproducing historical atmospheric conditions in the study area (Fig. S2). The RCP8.5 scenario was considered for future projections due to the close agreement with historical total cumulative greenhouse gas concentrations (Schwalm et al., 2020). Although it should be noted that if the necessary actions to reach the Paris agreement are implemented, the concentrations by the end of the century could be closer to other more optimistic scenarios, such as the RCP6.0 or even the RCP4.5.

Delft3D model was run for each year from the 16 of June until the end of August for the historical (H, 1990–2019) and the near (NF, 2025–2049), mid (MF, 2050–2074) and far (FF, 2075–2099) future periods. The first 2 weeks were considered as spin-up, so the study period corresponds to the months of July and August. The initial conditions for each of the runs were considered varying throughout the grid (both horizontally and vertically) and were obtained for each year from the selected climate model. In this sense, the surface boundary conditions (near-surface zonal and meridional wind components, near-surface air temperature, net solar radiation, relative humidity and sea level pressure) were obtained from the output data of the regional MOHC-HadGEM2-ES-RCA4 model. Heat exchange through the atmosphere was simulated using the “absolute flux, net solar radiation” model. Pressure and wind components were varied spatially.

The oceanic boundary was forced with transport conditions and water level. The transport conditions (salinity and water temperature) were obtained from the global MOHC-HadGEM2-ES model. The initial salinity and water temperature conditions were also retrieved from this dataset. Astronomical forcing at the oceanic boundary was introduced out of thirteen tidal harmonic constituents (M2, S2, N2, K2, K1, O1, P1, Q1, MgF, MM, M4, MS4, MN4) obtained from the model TOPEX/Poseidon Altimetry with a spatial resolution of ~25 m (<http://volkov.oce.orst.edu/tides/global.html>). Freshwater discharges were obtained from the Hype Web portal (<https://hypeweb.smhi.se/>) and imposed as fluvial open boundary conditions. A discharge reduction was applied for the near (5%), mid (10%) and far (25%) future periods following the RCP8.5 projections (<https://hypeweb.smhi.se/explore-water/climate-impacts/europe-climate-impacts/>).

Numerical simulations were carried out following the parametrization, implementation and validation performed by Des et al. (2019, 2020a) for the study area. Outputs were saved every 6h, and the water temperature corresponding to the bottom layer was averaged daily.

### 2.3. Thermal comfort index

A thermal comfort index (TCI) was calculated to analyse the effects of the summer ocean warming on *R. decussatus*, *R. philippinarum*, *V. corrugata*, and *C. edule*. The TCI indicates the percentage of time during which the mean daily bottom water temperature is within the optimal thermal range of the studied species (Des et al., 2020a). This TCI was determined based on a literature review of previous studies of each species during its reproductive period (mainly, summer months),

prioritizing those studies carried out closer to the study area (see Table 1).

The optimal thermal range ensures the best ecophysiological performance without producing negative responses during summer months. The optimal gonadal development of *R. decussatus* of individuals collected in the study area under laboratory controlled conditions of 14 °C and 18 °C, was at 18 °C (Delgado and Pérez-Camacho, 2007a). These results agree with those achieved by Matias et al. (2009, 2016), who reported great rates of spawners when water temperature ranged between 18 °C and 22 °C. Despite Serdar et al. (2007) reported a maximum growth of *R. decussatus* from 22 °C to 25.7 °C in Turkey, Sobral and Widdows (1997) and Velez et al. (2017) observed negative physiological responses in individuals collected in the study area and in the close area of the Ria Formosa (Portugal) when water temperature overpassed 25 °C. Therefore, the selected optimal thermal range for *R. decussatus* was between 18 °C to 25 °C.

In the case of *R. philippinarum*, the laboratory experiments performed by Delgado and Camacho (2007b, 2007b) showed gonadal development of this species at 14 °C, but the greatest and fastest rate of gonadal development occurred between 18 °C and 22 °C, coinciding with a greater ingestion of food. On the other hand, the maximum filtration rate of this species was reported when the temperature exceeded 15 °C (Gouilletquer and Wolowicz, 1989), which was considered the lower optimal thermal threshold for *R. philippinarum*. The upper value considered was 25 °C since Bodoy et al. (1986) and Velez et al. (2017) observed negative physiological responses at higher water temperatures.

*Venerupis corrugata* showed the best physiological rates when the water temperature was between 15 °C and 20 °C (Albentosa et al., 1994) and the optimal performance of adults and larvae at 20 °C (Albentosa et al., 1994; Joaquim et al., 2016). Thus, the optimal thermal range considered for this species was between 15 °C and 20 °C.

For *C. edule*, Compton et al. (2007) tested the lethal thermal limits of the species and determined that its optimal activity occurred when water temperature ranged between 20 °C and 23 °C. However, Navarro and Iglesias (1995) determined that the lower optimal temperature was 17 °C for adults collected close to the study area. Thus, the optimal thermal range considered for *C. edule* was from 17 to 23 °C.

The TCI was depicted in thermal comfort maps for each species and period. Three levels of thermal comfort conditions were defined on the basis of the percentage of time under comfort conditions ([0–50], [50–75] and [75–100%]). A percentage below 50% was considered a possible thermal stress situation during which the species is exposed to temperatures outside their optimal thermal threshold for at least half of the study period. The difference between the future and historical TCI was calculated as  $\Delta TCI = TCI_F - TCI_H$ , where the subscripts F and H refer to the future and historical period, respectively. Positive values indicate that comfort conditions may improve, while negative values indicate that they may worsen. Additionally, areas changing from thermally comfortable to uncomfortable ( $TCI_H \geq 50\%$  and  $TCI_F < 50\%$ ) and vice versa ( $TCI_H < 50\%$  and  $TCI_F \geq 50\%$ ) were calculated, as well as the areas where no shift is projected ( $TCI_H \geq 50\%$  and  $TCI_F \geq 50\%$  or  $TCI_H < 50\%$  and  $TCI_F < 50\%$ ).

The extent of those areas where the TCI was greater than or equal to 50%, within the appropriate depth range for each species, was calculated for each period to evaluate the potential effects of climate change on the shellfish harvesting areas. The depth range for each species was defined on the basis of the optimal distribution of the habitat (Molares et al., 2008, see Table 1). A maximum depth range of 5 m was considered for *R. decussatus*, *R. philippinarum* and *C. edule*, as these species inhabit areas between the mid-intertidal and the shallow subtidal zones. In addition, a maximum depth of 15 m was assigned to *V. corrugata*, which inhabits low-intertidal and subtidal zones.

**Table 1**

Optimum thermal tolerance thresholds (OWTT, °C) for the species analysed. Habitat information extracted from [Malham et al. \(2012\)](#) and [Macho et al. \(2016\)](#). SFG: scope for growth; ST: sediment temperature.

Species	Depth range	OWTT (°C)	Discussion	Reference
<i>R. decussatus</i>	Middle intertidal to shallow subtidal (<5 m)	18–25 °C	Normal gonadal development at 18 °C Higher condition index at 18–20 °C; higher percentage of spawners at 20–22 °C Optimum SFG at ST of 20 °C; null SFG at ST of 27 °C; negative SFG at ST of 32 °C Higher burrowing activity at ST of 32 °C No mortality at 17–21 °C; increased metabolic activity at 21 °C; 7% mortality at 25 °C Maximum growth at 22–25.7 °C (Turkey)	<a href="#">Delgado and Camacho, 2007b</a> <a href="#">Matias et al., (2009), 2016</a>  <a href="#">Sobral and Widdows (1997)</a>  <a href="#">Macho et al. (2016)</a>  <a href="#">Velez et al. (2017)</a>  <a href="#">Serdar et al. (2007)</a>
<i>R. philippinarum</i>	Middle intertidal to shallow subtidal (<5 m)	15–25 °C	Normal gonadal development at 18 and 22 °C Normal gonadal development between ST of 20–32 °C Sensitive to temperatures above 25 °C Maximum filtration rate at 15–20 °C 13% mortality at 25 °C Optimal growth at 20–24 °C (Mediterranean Sea) Optimal growth at 18–21 °C	<a href="#">Delgado and Camacho, 2007b,b</a> <a href="#">Vázquez et al. (2021)</a>  <a href="#">Bodoy et al. (1986)</a>  <a href="#">Gouletquer and Wolowicz, 1989</a>  <a href="#">Velez et al. (2017)</a> <a href="#">Solidoro et al. (2000)</a>  <a href="#">Bae et al. (2021)</a>
<i>V. corrugata</i>	Lower intertidal and subtidal (<15 m)	15–20 °C	Greater slopes in the rate/temperature at 15 °C–20 °C; Optimal SFG at 20 °C; decreased feeding at 25 °C Ingestion rate decrease at 25 °C Decreases in burrowing and siphon activity at ST ≥ 27 °C Good larval viability rate at 18 ± 1 °C and 20 ± 1 °C Optimal low threshold at 15 °C	<a href="#">Albentosa et al. (1994)</a>   <a href="#">Molares et al. (2008)</a> <a href="#">Macho et al. (2016)</a>  <a href="#">Cerviño-Otero (2011); Joaquim et al., (2016)</a> <a href="https://longline.co.uk/meta/List">https://longline.co.uk/meta/List</a>
<i>C. edule</i>	Middle intertidal to shallow subtidal (<5 m)	17–23 °C	Optimal activity at ST of 20–23 °C. Adverse effects on survivorship at ST of 28 °C	<a href="#">Compton et al., (2007); Verdelhos et al., (2015);</a>

**Table 1 (continued)**

Species	Depth range	OWTT (°C)	Discussion	Reference
			Optimal growth for larvae at 15–20 °C Optimal temperature decrease at 17 °C below a certain level of nutrient assimilation	<a href="#">Domínguez et al., (2021a)</a> <a href="#">Kingston (1974)</a>  <a href="#">Navarro and Iglesias (1995)</a>

### 3. Results and discussion

#### 3.1. Potential effects of increasing water temperature on thermal comfort areas

In general, the water thermal comfort areas (zones with TCI >50% in [Fig. 2](#)) during July–August for the historical period (1990–2019) coincided with the habitat distribution of the species where harvesting mainly takes place nowadays (purple polygons in [Fig. 1](#)). In fact, the water thermal comfort areas were mainly observed in the inner part of the rias for the intertidal species *R. decussatus*, *R. philippinarum* and *C. edule* ([Fig. 2a, b and d](#)), and in the low intertidal and shallow subtidal for *V. corrugata* ([Fig. 2c](#)).

In the study area, water temperature is mainly driven by upwelling/downwelling events and solar radiation, along with the physiography of each ria governing the local differences. Upwelling events are frequent during the summer months ([Álvarez et al., 2005](#)), and the upwelled cold water mainly affects the outer and middle parts of the rias; the bottom water temperature can drop to 13 °C near bed at the mouth of the rias ([Álvarez et al., 2005; Barton et al., 2015](#)). The areas affected by upwelling resulted thermally more favourable for *R. philippinarum* and *V. corrugata* due to the optimal lower thermal limit of these species (~15 °C) than of *R. decussatus* and *C. edule*, whose optimal lower thermal limits are 18 and 17 °C, respectively (see [Table 1](#) and references therein). The inner part of the Rías Baixas through which the main rivers flow is shallow, so atmospheric conditions therefore govern the temperature throughout the water column. Solar radiation not only heats water directly in the high and mid-intertidal zones, but also indirectly by heating sediment during low tides, thus transmitting the accumulated heat to the water with the incoming tide. This leads to the optimal upper thermal limit being exceeded for some species ([Fig. 2](#)), mainly for *V. corrugata* ([Fig. 2c](#)), whose upper thermal limit is 20 °C. These atmosphere driven areas vary among rias, probably due to differences in geographical characteristics, which may limit the extent of upwelling imprint, especially in the innermost part ([Taboada et al., 1998; Álvarez et al., 2005](#)).

Changes in the water thermal conditions projected for the far future (2075–2099) will affect the four species under study to different extents, depending on the area and the optimal thermal conditions. A decrease in thermal comfort conditions was projected in the shallower areas of the inner part of the rias for the far future ([Fig. 3](#) and [Fig. S3](#)). The TCI decrease might be ~50% for *R. decussatus* and *R. philippinarum* ([Fig. 3a and b](#), respectively) and ~75%, or even higher, for *V. corrugata* and *C. edule* ([Fig. 3c and d](#), respectively). By contrast, an increase of over 75% for *R. decussatus*, *V. corrugata* and *C. edule* and 50% for *R. philippinarum* was projected in the outer and middle part of the estuaries. This predicted pattern is mostly due to the expected 3.3 °C increase in the water temperature of the Rías Baixas by the end of the century, in agreement with previous findings ([Silva et al., 2017](#)). In addition, the outer and middle parts of the rias may become warmer due to the projected decrease in the effectiveness of upwelling events

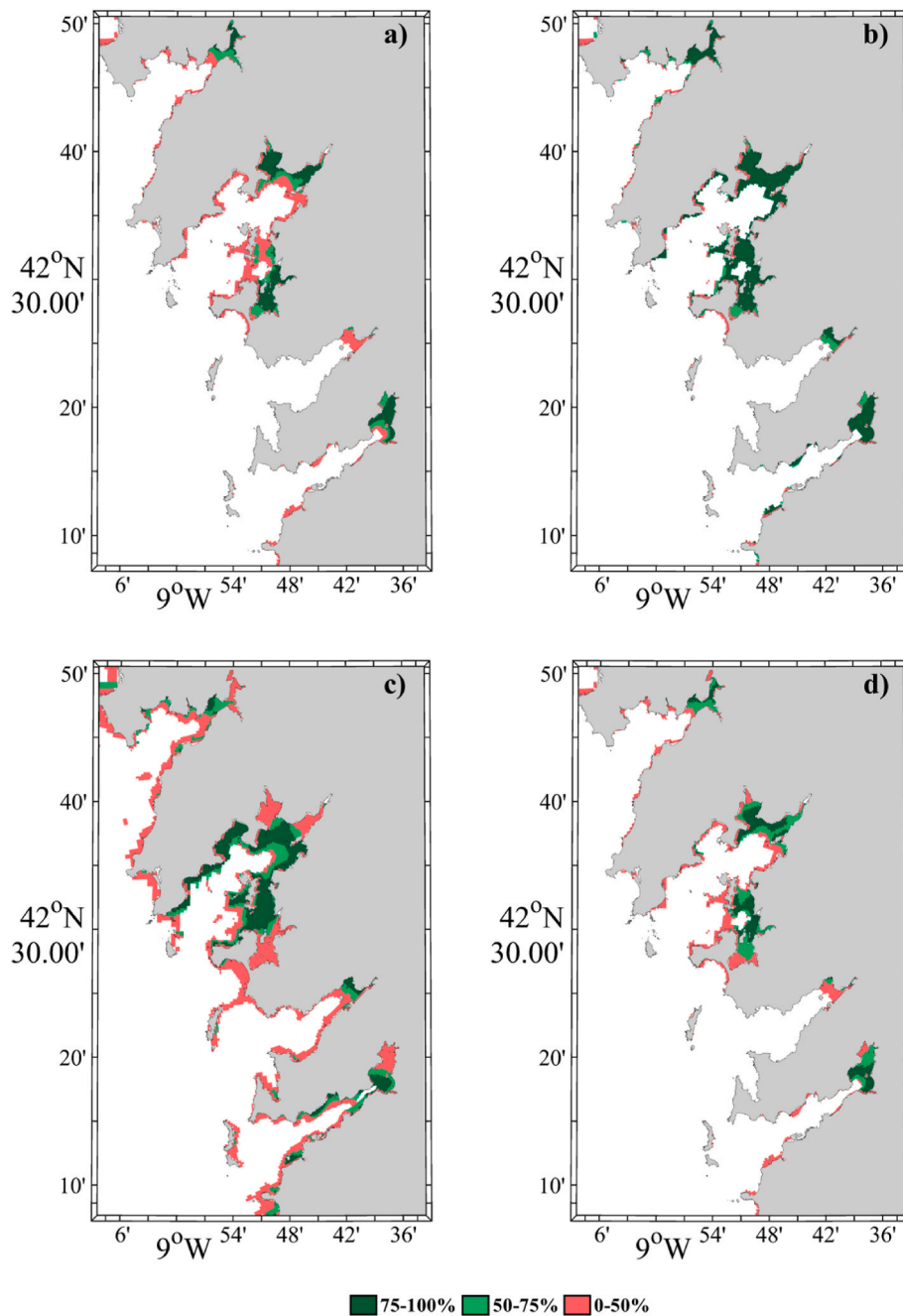


Fig. 2. Thermal comfort index (TCI, %) for *R. decussatus* (a), *R. philippinarum* (b), *V. corrugata* (c) and *C. edule* (d) during July–August for the historical period (1990–2019).

(Cordeiro Pires et al., 2016; Sousa et al., 2020). The warming would make the outer and middle zones of the rias water-thermally comfortable for the species under study as the temperature of the bottom water may frequently exceed the lower optimal thermal limit (between 15 and 18 °C) (see Table 1). Conversely, the inner part may become more vulnerable zones due to the increase in both solar radiation and air temperature (Lee et al., 2021). Thus, species such as *V. corrugata* and *C. edule* may encounter uncomfortable conditions as their optimal upper thermal limits (20 °C and 23 °C, respectively) are expected to be exceeded (see Table 1).

Even though the water temperature in the outer and middle zones of the rias became thermally comfortable, intertidal fishing beds could be placed under severe stress at low tide during atmospheric heatwave events, especially at mid-afternoon low-tide periods during summer

(Helmuth et al., 2002). In fact, mesocosms experiments showed that *C. edule* and *V. corrugata* suffered significant mortalities, as well as a dramatic decrease in scope for growth (SFG), reduced burrowing activity and underwent gonadal resorption, after two days under atmospheric heatwave conditions (Domínguez et al., 2021a; Vázquez et al., 2021). Similarly, the four species under study had a negative SFG after four days exposed to stress conditions. Further research about the impact of atmospheric heat waves, including modelling thermal transport into the sediment, is needed as such events are predicted to increase in frequency and intensity (Guerreiro et al., 2018; Lorenzo et al., 2021), giving rise to an additional stress to the increase of mean SST.

Areas changing from thermally comfortable to uncomfortable and vice versa are depicted in Fig. 4. Generally, the comfortable extension might decrease in the inner part of the rias and increase in the outer part.

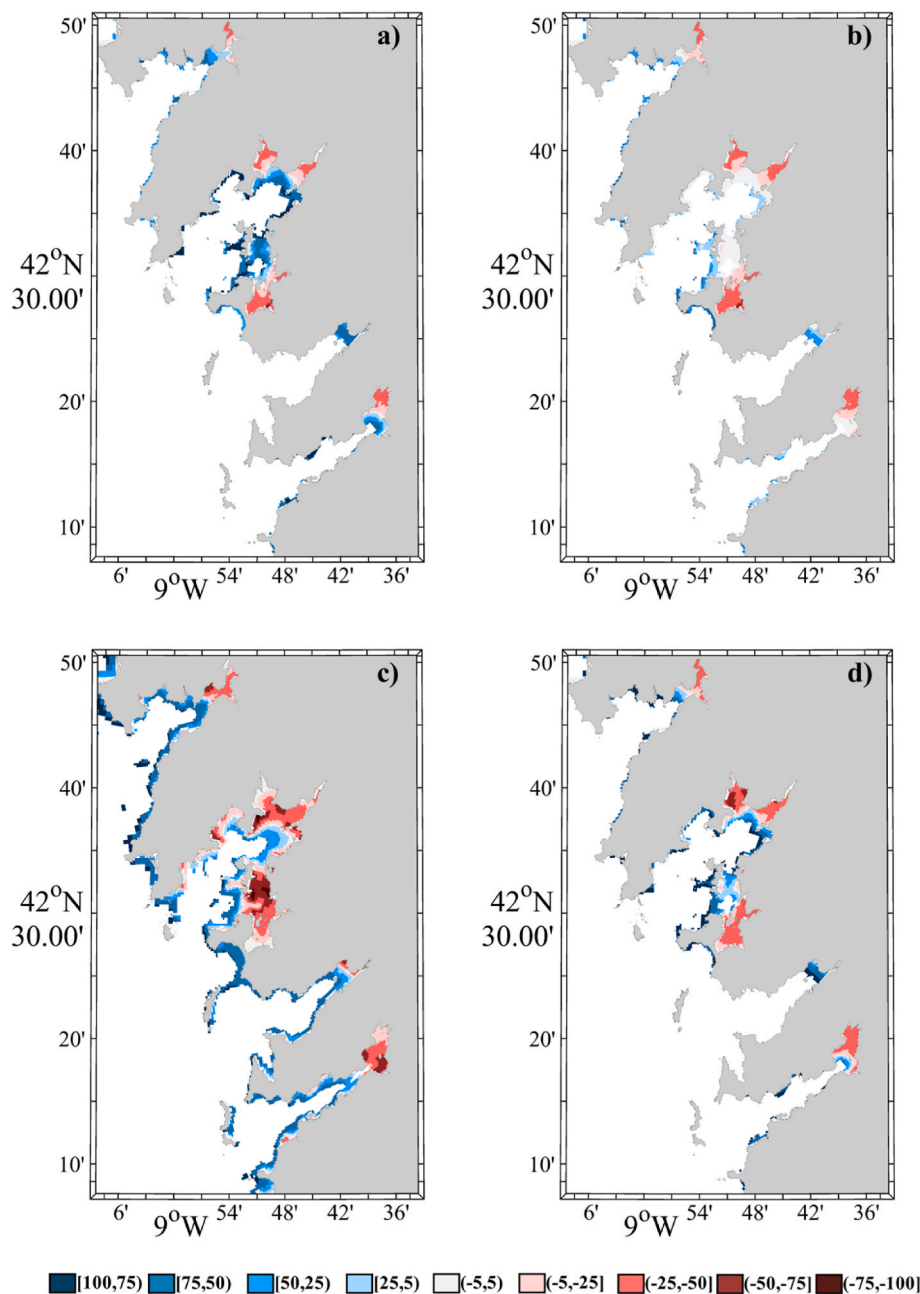


Fig. 3. Changes in the TCI (%) between the far future (2075–2099) and the historical period (1990–2019) for (a) *R. decussatus*, (b) *R. philippinarum*, (c) *V. corrugata* and (d) *C. edule* calculated as  $\Delta TCI = TCI_{FF} - TCI_H$ , where the subscripts FF and H indicate far future and the historical period, respectively.

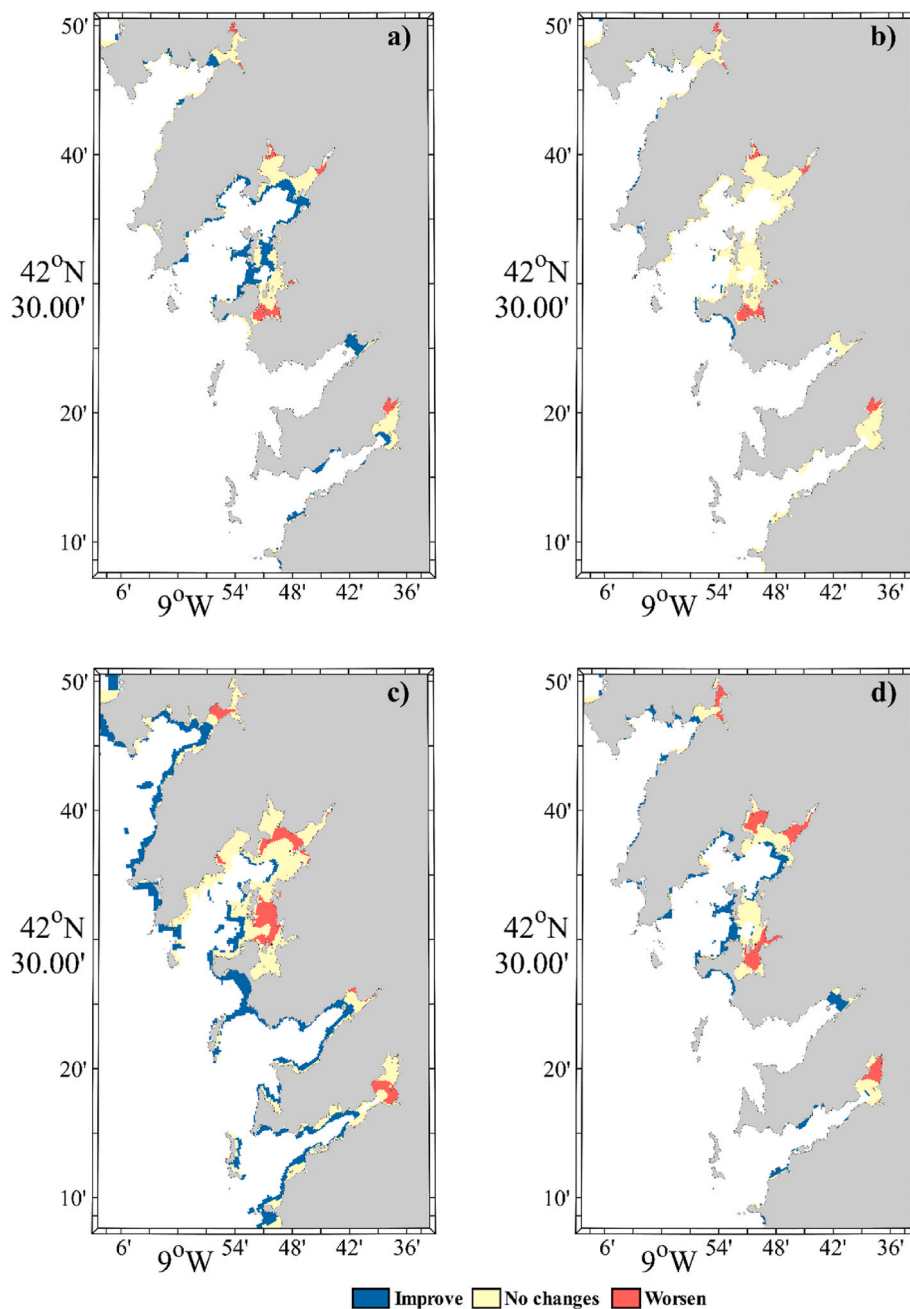
Neither positive nor negative changes are expected in most of the rias, that is, the comfortable areas will continue to be comfortable by the end of the century, and the currently uncomfortable areas will continue to be uncomfortable, especially for *R. philippinarum* (Fig. 4b).

Changes in the TCI for the near and mid future (Figs. 5 and 6, respectively; see also Figs. S4 and S5) showed similar, although less intense, patterns to those obtained for the far future. Thus, for the near future, a decrease in the TCI was projected in the shallower areas of the inner part of the rias with values below  $\sim 25\%$  for all species. In addition, an increase of between 5% and 25% was projected for *R. decussatus*, *R. philippinarum* and *C. edule* (Fig. 5a, b and d), and an increase greater than 50% was projected for *V. corrugata* (Fig. 5c) in the outer and middle part of the estuaries. For the mid-future, a decrease in the TCI of less than 50% was projected for all bivalve species in the inner part of the rias. Finally, an increase of up to 50% was projected for *R. decussatus*, *R.*

*philippinarum* and *C. edule* (Fig. 6a, b and c), and  $\sim 75\%$  for *V. corrugata* (Fig. 6c) in the outer and middle part of the rias.

Overall, according to the TCI, thermal comfort areas of the rias may move from the shallow areas of the inner part to those of the middle and outer parts throughout the 21st century. The shellfish harvesting areas in the innermost part of the rias will very likely have uncomfortable thermal conditions for species such as *V. corrugata* and *C. edule*. Moreover, the productivity of shellfish beds in relation to *R. decussatus* and *R. philippinarum* could also be affected in the inner and shallower areas of Ría de Vigo and Ría de Arousa. This thermal pattern, warmer in the inner part compared to the middle-outer parts of the rias, has been described in recent studies of the impact of climate change on mussels (Silva et al., 2017; Des et al., 2020a) and macroalgae (Des et al., 2020b).





**Fig. 4.** Changes in thermally comfortable ( $\text{TCI} \geq 50\%$ ) and uncomfortable ( $\text{TCI} < 50\%$ ) areas between historical (1990–2019) and far future (2075–2099) for (a) *R. decussatus*, (b) *R. philippinarum*, (c) *V. corrugata* and (d) *C. edule*. Blue/red colours represent areas where the TCI will shift from uncomfortable to comfortable and vice versa. “No changes” implies that the TCI will remain in the same class for both periods.

### 3.2. Changes in extension of thermal comfort areas

The obtained total extension of the thermal comfort area determined for the historical period was 68.44 km<sup>2</sup> for *R. decussatus*, 111.60 km<sup>2</sup> for *R. philippinarum*, 128.39 km<sup>2</sup> for *V. corrugata* and 73.38 km<sup>2</sup> for *C. edule* (Table 2, column H). In particular, the introduced clam *R. philippinarum* occupies 97% of the total available area (115.44 km<sup>2</sup>, column TA in Table 2) due to its wider optimal thermal threshold (15–25 °C). The total extension of the thermal comfort area of harvesting *R. decussatus* and *C. edule* is expected to increase at different rates throughout the 21st century due to the difference in their upper comfort limits, i.e. 25 °C for *R. decussatus* and 23 °C for *C. edule* (see Table 1). This increase may be slightly greater for *C. edule* (7.35 km<sup>2</sup> vs 6.56 km<sup>2</sup>) in the near future, similar for both species (~15.7 km<sup>2</sup>) in the mid future and greater for

*R. decussatus* (28.83 km<sup>2</sup>) in the far future when the increase in the total area may be negligible for *C. edule* (1.05 km<sup>2</sup>). The total area is also expected to increase for *V. corrugata* in the future relative to the historical period. This increase may be greater in the near future (43.44 km<sup>2</sup>) than in the mid (37.34 km<sup>2</sup>) and far future (~11 km<sup>2</sup>). This pattern, which is different from those previously described for *R. decussatus* and *C. edule*, is mainly due to the smaller lower and upper optimal comfort limits for *V. corrugata* and the fact that this species can be harvested at depths of up to 15 m deep (Table 1). By contrast, the total extent of thermal comfort areas for *R. philippinarum* shows a negligible increase in the near future (1.53 km<sup>2</sup>), no change in the mid future, and a decrease (–9.85 km<sup>2</sup>) in the far future, despite the wider thermal tolerance (15–25 °C, Table 1). This pattern could be explained by the fact that as a result of the increase in water temperature during



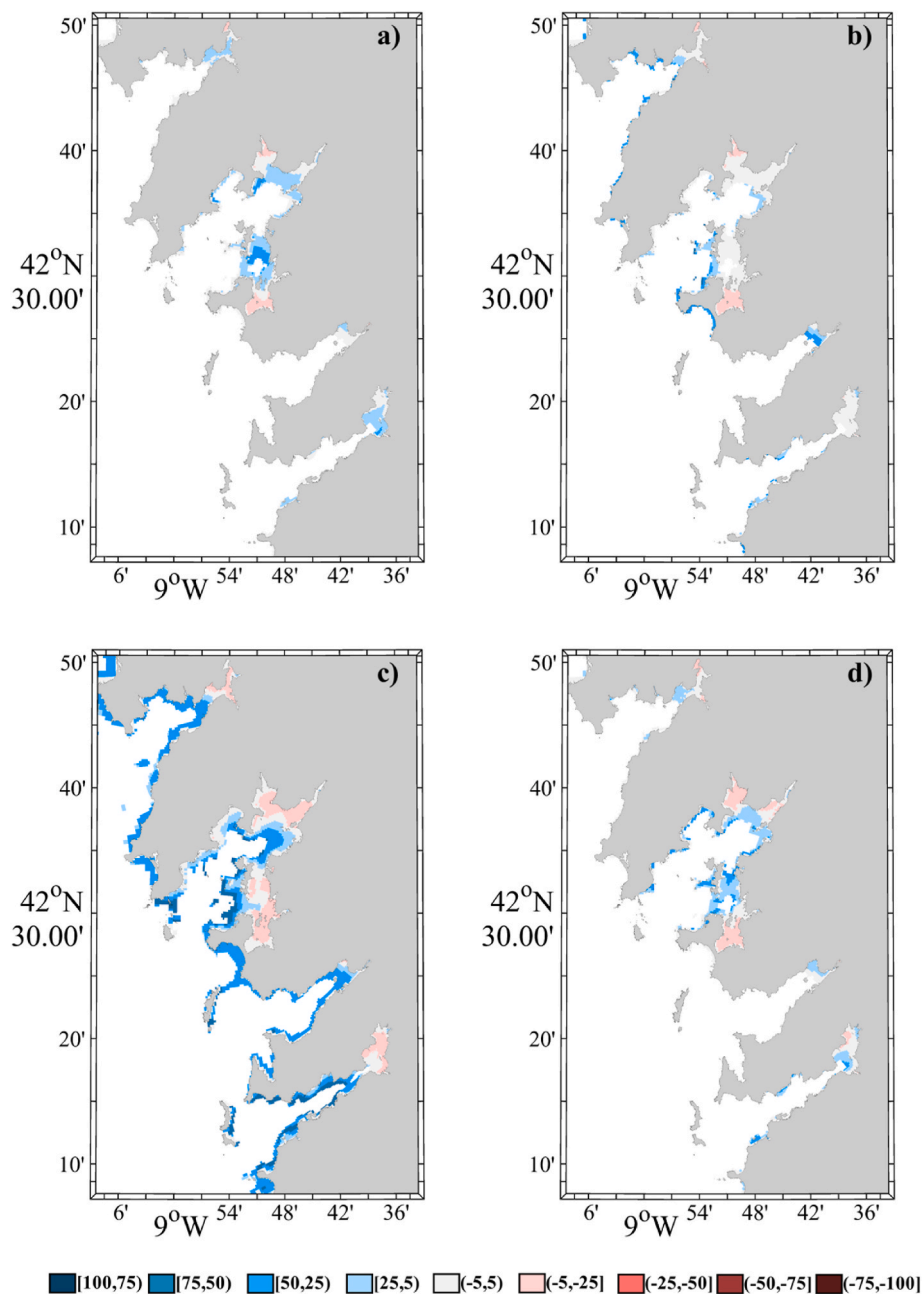


Fig. 5. Changes in the TCI (%) between the near future (2025–2049) and the historical period (1990–2019) for (a) *R. decussatus*, (b) *R. philippinarum*, (c) *V. corrugata* and (d) *C. edule* calculated as  $\Delta TCI = TCI_{NF} - TCI_H$ , where the subscripts NF and H indicate near future and the historical period, respectively.

the 21st century the number of days during which the upper thermal comfort limit was exceeded could not be compensated by the number of days in which the lower thermal comfort limit was exceeded. Nonetheless, *R. philippinarum* was predicted to be the species with the largest harvesting area by the end of the century. However, the present study only considered changes in extent related to thermal comfort areas. Although projections display an increase in water-thermally comfortable areas during the 21st century. Other factors that determine distribution of these species such as type of sediment, hydrodynamics, food or predation may also play a part in shaping the predicted extension of the area (e.g. Ramón, 2003; Aranguren et al., 2014; Kang et al., 2016; Domínguez et al., 2021b). For instance, the suitability of outer parts of the rías as productive areas for bivalve populations might be limited by sediment type. The productive areas of bivalves are characterized by muddy or fine sand sediments with high values of organic matter

(Bidegain et al., 2015), which cannot be found nearshore in these zones (Vilas, 2002). Moreover, a larger abundance of predators in the outer parts of rías (Gestoso et al., 2014) could narrow or constrict the ecological niche of these bivalves.

The bivalve species under study are of great economic importance for artisanal fisheries in Galicia (Molares et al., 2008; Macho et al., 2016; Vázquez et al., 2021), making a relatively large contribution to the economy of the region in recent years, despite the restrictions imposed due to the COVID-19 pandemic and a 14% reduction in the value of catches (Villasante et al., 2021), i.e. around 57 million euros in 2020 and 2021 ([www.pescasgalicia.com](http://www.pescasgalicia.com)). Prolonged thermal stress conditions as shown by future projections for the shallow areas of the inner parts, would result in less productive shellfish beds and may lead to a drastic decrease in catches. Although these bivalves are able to deal with unfavourable thermal conditions by adapting physiological and

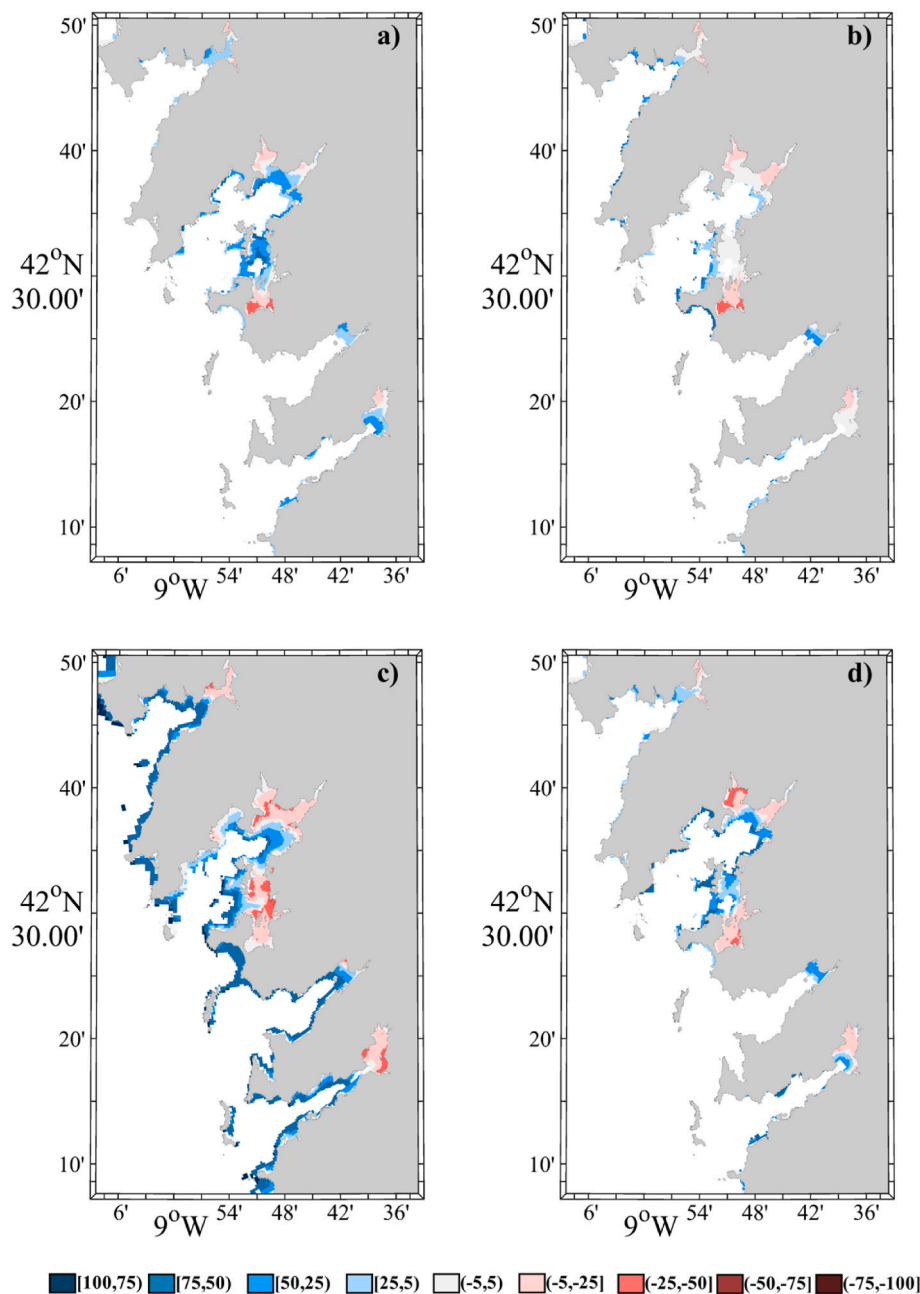


Fig. 6. Changes in the TCI (%) between the mid future (2050–2075) and the historical period (1990–2019) for (a) *R. decussatus*, (b) *R. philippinarum*, (c) *V. corrugata* and (d) *C. edule* calculated as  $\Delta TCI = TCI_{MF} - TCI_H$ , where the subscripts MF and H indicate mid future and the historical period, respectively.

behavioural mechanisms (Sobral and Widdows, 1997; Woodin et al., 2020; Domínguez et al., 2021a), sustained periods during which threshold thermal limits are exceeded may have not only lethal, but also sublethal effects on the growth potential, leading to e.g. a delay in the time required for the species to reach commercial size (e.g. Albertosa et al., 1994; Sobral and Widdows, 1997; Verdelhos et al., 2015; Macho et al., 2016; Domínguez et al., 2021a). Furthermore, the decrease in thermal comfort conditions in shallow areas projected by numerical simulations may be particularly relevant for those species in which the peak spawning period occurs in late spring and summer, i.e. *R. decussatus*, *R. philippinarum* and *V. corrugata*, as temperature increases may reduce reproductive success in bivalves through diverse mechanisms such as changes in timing and duration of reproduction and the number and size of gametes (Ojea et al., 2008; Petes et al., 2008; Cerriño-Otero, 2011). Such alterations are not trivial as they can lead to

failures in the recruitment in shellfish beds (Vázquez et al., 2021).

Changes in the distribution of the thermal comfort areas of the infaunal bivalve species *R. decussatus*, *R. philippinarum*, *V. corrugata* and *C. edule* support the current evidence that climate change may alter important ecosystems such as the Rías Baixas (Des et al., 2020 a,b). Based on observed patterns, productive sites are likely to change in the future, inducing socioeconomic changes. These changes may particularly affect women, as historically harvesting in intertidal zones has mainly been done by women on foot, while men have carried out harvesting from aboard fishing vessels in deeper areas (Piñeiro-Antelo and Santos, 2021). In addition, future changes in freshwater input, which is larger during winter months and affects mostly the inner zone of the rias, would result in a sudden salinity drops (Des et al., 2021) adding further pressure on the sector. Short periods of salinity below 15 ppt have been shown to cause an important stress, i.e. reduction of pumping activity,

Table 2

Extent of area (km<sup>2</sup>) above the bathymetric distribution of *R. decussatus* (5m), *R. philippinarum* (5m), *V. corrugata* (15m) and *C. edule* (5m) where the comfort index is exceeded 50% of the time. H=Historical period (1990–2019); NF=Near Future (2025–2049); MF = Mid Future (2050–2074); FF=Far Future (2075–2099).  $\Delta A$  represents the increase in the extent of the area for the future relative to the historical period. TA is the total area above 5 or 15 m, depending on the species.

	H	NF	$\Delta A^{NF-H}$	MF	$\Delta A^{MF-H}$	FF	$\Delta A^{FF-H}$	TA
<b><i>R. decussatus</i></b>								
Muros	9.78	10.22	0.44	10.92	1.14	11.38	1.60	14.15
Arousa	43.88	48.07	4.19	52.86	8.98	56.38	12.50	67.49
Pontevedra	0.40	0.73	0.33	1.24	0.83	4.43	4.03	4.43
Vigo	14.38	15.98	1.60	19.04	4.66	25.09	10.71	29.37
TOTAL	68.44	75.00	6.56	84.05	15.61	97.27	28.83	115.44
<b><i>R. philippinarum</i></b>								
Muros	13.63	14.15	0.52	13.96	0.33	12.46	-1.16	14.15
Arousa	65.83	65.22	-0.61	63.92	-1.91	58.33	-7.51	67.49
Pontevedra	4.43	4.43	0.00	4.43	0.00	4.43	0.00	4.43
Vigo	27.71	29.34	1.62	29.30	1.59	26.53	-1.18	29.37
TOTAL	111.60	113.14	1.53	111.62	0.01	101.76	-9.85	115.44
<b><i>V. corrugata</i></b>								
Muros	12.33	32.47	20.14	32.82	20.49	29.84	17.51	40.53
Arousa	89.12	101.88	12.76	97.56	8.44	79.05	-10.06	136.78
Pontevedra	7.51	18.70	11.19	18.56	11.05	17.89	10.38	18.80
Vigo	19.42	18.78	-0.65	16.79	-2.63	12.75	-6.67	29.37
TOTAL	128.39	171.82	43.44	165.73	37.34	139.54	11.15	225.48
<b><i>C. edule</i></b>								
Muros	9.79	9.84	0.05	10.15	0.36	8.88	-0.91	14.15
Arousa	47.13	50.34	3.21	52.86	5.16	39.56	-7.57	67.49
Pontevedra	1.16	2.26	1.10	3.73	2.57	4.43	3.28	4.43
Vigo	15.30	18.29	2.99	22.89	7.58	21.55	6.24	29.37
TOTAL	73.38	80.73	7.35	89.05	15.68	74.42	1.05	115.44

SFG, burrowing ability and disrupted reproductive cycles (Domínguez et al., 2020; Vázquez et al., 2021).

Although the increase of water temperature is the main factor affecting bivalve comfort and production, other environmental drivers that often exhibit local patterns of variability should not be ignored. For instance, air and sediment temperature, especially under heatwave conditions during low tide, can affect the performance of bivalves differently as the different species present different burrowing abilities (Domínguez et al., 2021a). Ocean acidification, as a major accompanying effect of global climate change, impairs physiological processes related to shell calcification and may also impact shellfisheries as productive coastal areas exhibit significant local changes in seawater  $pCO_2$  (Narita et al., 2012; Gestoso et al., 2016; Padin et al., 2020). Despite sea level rise is not uniform and varies regionally, it may also have important consequences on productive coastal communities (IPCC et al., 2014), particularly on the Galician coast as intertidal fishing beds may be affected by flooding (Toubes et al., 2017) that could change the location of productive sites. Finally, human-induced changes due to sprawling urbanization and coastal development, chemical pollutants, as well as the emergence of invasive species (Des et al., 2022) and parasitic diseases may be also essential drivers of change in these systems, contributing to future shifts in the structure and composition of estuarine communities (Kennish, 2002; Scavia et al., 2002; Mieszkowska et al., 2013; Scanes et al., 2020) and affecting the productivity of the shellfish beds.

Additional numerical and experimental research should be conducted to take into account all these factors for a better understanding of the impacts and consequences of climate change on shellfisheries productivity.

#### 4. Conclusions

The geographical distribution of the thermal comfort areas for *R. decussatus*, *R. philippinarum*, *V. corrugata* and *C. edule* in the Galician Rías Baixas during summer (July–August) was analysed. Bottom water temperature was evaluated both historically (1990–2019) and for the near (2025–2049), mid (2050–2074), and far (2075–2099) future periods under the RCP8.5 scenario by using the Delft3D-Flow model.

Historically, thermal comfort areas for *R. decussatus*, *R. philippinarum*

and *C. edule* were mainly observed in shallow areas located in the inner part of the rias. Comfortable areas were also observed for *R. philippinarum* and *V. corrugata* in the low intertidal and shallow subtidal areas in the middle and outer parts due to their optimal lower thermal limit of 15 °C.

The thermal comfort index of the shellfish harvesting areas in the middle and outer parts may increase throughout the 21st century relative to the historical period for *R. decussatus*, *V. corrugata* and *C. edule*. The increase would be greater for the near and mid future than for the far future for *V. corrugata* and *C. edule*. By contrast, a decrease in the thermal comfort index for the distribution area of *R. philippinarum* is expected, especially for the far future, although this may remain the most widespread species. Overall, the findings indicate an increase of the extension of comfort areas towards the outer and middle parts of the rias. By contrast, the inner part of the rias could be negatively impacted by the increase in water temperature by the end of the 21st century, with a decrease in productive shellfish beds. This could result in economic losses for the shellfishing sector, as most of the productive banks are located in the inner part of the estuaries, and would induce socioeconomic changes, especially for women who traditionally carry out harvesting on foot in the intertidal zones. Therefore, the information obtained is important to help policy-makers in the future management of this activity.

#### CRedit author statement

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## 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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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2022.105707>.

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