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LETTER

Projecting expected growth period of bivalves in a coastal temperate sea

Petra Zemunik Selak,[1] Cléa Denamiel,[2,3] Melita Peharda,[1] Bernd R. Schöne,[4] Julien Thébault,[5] Hana Uvanović,[1] Krešimir Markulin,[1] Ivica Vilibić[2,3]*

[1]Institute of Oceanography and Fisheries, Split, Croatia; [2]Division for Marine and Environmental Research, Ruđer Bošković Institute, Zagreb, Croatia; [3]Institute for Adriatic Crops and Karst Reclamation, Split, Croatia; [4]Institute of Geosciences, University of Mainz, Mainz, Germany; [5]Univ Brest, CNRS, IRD, Ifremer, LEMAR, Plouzane, France

Scientific Significance Statement

Climate change is transforming coastal ecosystems; however the extent of its impact is not fully understood. This study offers insights into the growth of bivalve species at the end of this century by integrating the sclerochronological approach provided by shell measurements with the climatological aspect presented by projections of the state-of-the-art climate model. This innovative method introduces a promising strategy for forecasting future trends in bivalve growth phenology, which may be extended to other marine species across various coastal environments.

Abstract

The impact of climate warming on coastal benthic fauna is already observed, but forecasting their long-term fate remains challenging. This study uses $\delta^{18}O_{shell}$ data of specimens of five bivalve species collected at six locations and results from kilometer-scale atmosphere–ocean climate model for the time intervals of 1987–2017 and 2070–2100, to estimate changes in bivalve growth phenology. All species will benefit from climate warming during winter, experiencing a longer growing season than currently. The growth of *Aequipecten opercularis*, *Flexopecten glaber*, and *Pecten jacobaeus* will decrease in summer, resulting in up to 3 months of reduced growth per year. *Glycymeris pilosa* and *Venus verrucosa* in the southern Adriatic Sea will be more affected than those in the north, with up to 4 months longer annual growth. These findings can inform adaptation plans for bivalve management in the Adriatic Sea but also in areas where the studied species are present.

***Correspondence**: ivilibic@irb.hr

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Author Contribution Statement: P.Z.S. and C.D. co-led the entire manuscript effort and contributed equally. C.D., M.P., and I.V. came up with the research question and designed the study approach. C.D. designed and implemented the atmosphere–ocean model. M.P., B.R.S., J.T., H.U., and K.M. obtained shell isotope data. P.Z.S. and C.D. conducted the statistical analyses and prepared visuals. P.Z.S., C.D., and I.V. wrote the manuscript. M.P., B.R.S., J.T., H.U., and K.M. reviewed and edited the manuscript. P.Z.S. and C.D. contributed equally to this work.

Petra Zemunik Selak and Cléa Denamiel contributed equally and are listed as co-first authors.

Data Availability Statement: All the data (bivalve stable oxygen isotope data, eastern Adriatic Sea temperature data, Adriatic Sea and Coast (AdriSC) model results) are archived in the Open Science Framework public repository and are available at: https://osf.io/ecqu3 (Denamiel et al., 2023).

Additional Supporting Information may be found in the online version of this article.

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Understanding the impact of climate warming on fisheries and aquaculture systems has been highlighted as a priority in the latest report of the Intergovernmental Panel on Climate Change (https://www.ipcc.ch/assessment-report/ar6/, last accessed: 22 January 2024). However, predicting the impact of climate change on bivalve species remains challenging. Recent studies (Froehlich et al. 2018; Cubillo et al. 2021; Tan et al. 2022; Gallagher and Albano 2023) have attempted to forecast the global effects of climate change on coastal benthic fauna, yet they relied on regional and global models which often fail to accurately reproduce the thermohaline and biogeochemical conditions in coastal environments (Holt et al. 2009; Reale et al. 2020). Bivalves record temperature and salinity changes in their shells in the form of stable oxygen isotopes ($\delta^{18}O_{shell}$; e.g., Goodwin et al. 2003; Vihtakari et al. 2016; Kubota et al. 2017). In settings characterized by stronger variations in ocean temperature than salinity $\delta^{18}O_{shell}$ data can thus provide reliable temperature estimates (Mook and Vogel 1968; Schöne et al. 2004; Wanamaker et al. 2007). Consequently, a sclerochronological approach can provide insight into bivalve growth seasonality (e.g., Vihtakari et al. 2016; Branscombe et al. 2021; Ezgeta-Balić et al. 2022).

The Adriatic Sea, which presents a complex coastal topography along its eastern coast (Fig. 1) is a particularly interesting region for the reproduction and projection of the growing season duration of bivalves. The Adriatic Sea and Coast (AdriSC; Denamiel et al. 2019) kilometer-scale climate model, with resolutions an order of magnitude higher than the available regional climate models (e.g., Med-CORDEX ensemble; Soto-Navarro et al. 2020), has been specifically designed to accurately represent the Adriatic coastal dynamics under historical (1987–2017) and extreme warming (2070–2100) time interval for a representative concentration pathways (RCP) 8.5 greenhouse scenario conditions. Previous research has indeed demonstrated that the horizontal resolutions of 3-km in the atmosphere and 1-km in the ocean used in the AdriSC model are essential to reproduce the bora wind (Grisogono and Belušić 2009) driving the Adriatic dense water dynamics (Denamiel et al. 2021*a*) and the Adriatic thermohaline circulation (Pranić et al. 2023). Recent studies (Peharda et al., 2019*a*,*b*; Johnson et al., 2021; Uvanović et al. 2021; Ezgeta-Balić et al. 2022) have demonstrated that five bivalve species living in the Adriatic Sea (i.e., *Aequipecten opercularis*, *Flexopecten glaber*, *Pecten jacobaeus*, *Glycymeris pilosa*, and *Venus verrucosa*) form their shells near oxygen isotopic equilibrium with the ambient seawater. These species were chosen because of their longevity (*G. pilosa*) and commercial importance (other four species). Consequently, their $\delta^{18}O_{shell}$ values can be used for robust water temperature reconstructions and, combined with the AdriSC climate model results, trustable reproduction and projection of the expected growth of these five species under historical and extreme warming conditions can be achieved, as demonstrated in studies by Abe (2021) in Japan and Steeves et al. (2018) along the Atlantic Canadian coast.

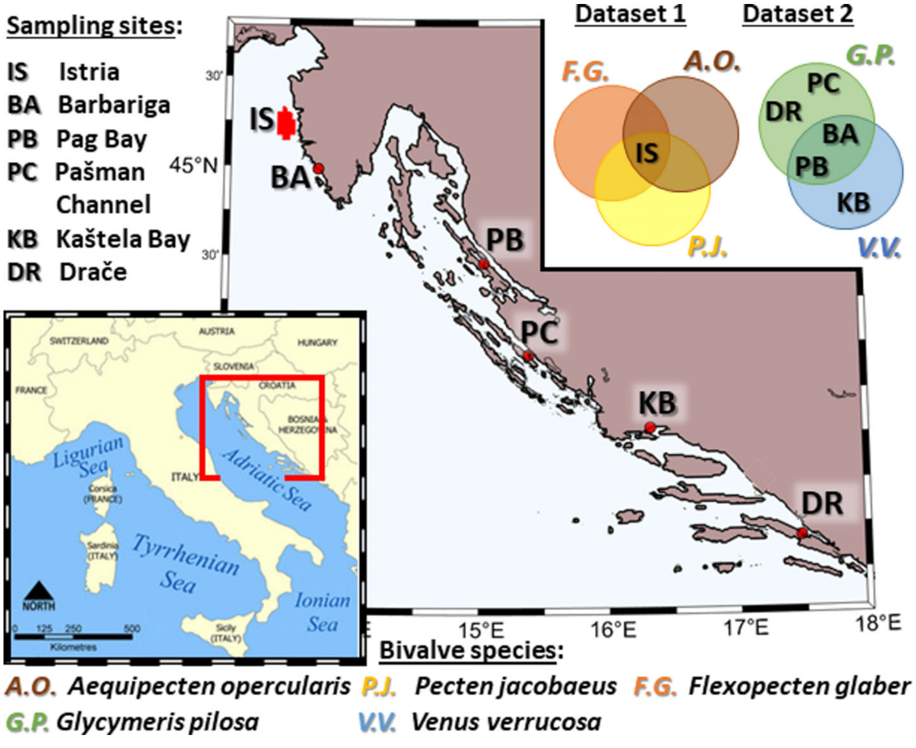

Fig. 1. Geographical location of the eastern Adriatic coast, locations of the bivalve sampling sites and description of the two datasets depending on both sampling site locations and bivalve species.

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In this study, we propose a more comprehensive assessment of the impact of extreme warming on the growth of five bivalve species along the eastern Adriatic coast, based on a methodology that may be generalized to other marine species, coastal seas, and climate scenarios. Our primary objective is to provide a preliminary assessment of the locations and species that will potentially either benefit from climate change or not be suitable for fisheries and aquaculture. Based on these results, we will further discuss the potential adaption plans for the commercial exploitation of bivalves along the eastern Adriatic Sea.

Material and methods

AdriSC climate model

The AdriSC climate model (Denamiel et al. 2019) is the first atmosphere–ocean kilometer-scale climate model implemented in the world. It is based on the coupling between the weather research and forecasting (Skamarock et al. 2005) model at up to 3-km horizontal resolution (using 58 vertical levels) and the regional ocean modeling system (Shchepetkin and McWilliams 2009) at up to 1-km horizontal resolution (using 35 vertical levels). Two different AdriSC climate simulations were performed.

The historical simulation was forced with reanalysis products and covers the time interval 1987–2017 (Denamiel et al. 2021*b*; Pranić et al. 2021). The evaluation of the model demonstrated that the AdriSC 1-km ocean results could reproduce key processes driving the Adriatic thermohaline circulation (Denamiel et al. 2022; Pranić et al. 2023). Additionally, in this study, the evaluation was extended by using the observations collected at the bivalve sampling sites (Supporting Information Table S1; Fig. S1) and, overall, confirmed the skills of the AdriSC model in reproducing the temperatures along the eastern Adriatic coast.

The extreme warming simulation, covering the time interval 2070–2100, was performed under the RCP 8.5 greenhouse emission scenario using the pseudo-global warming (PGW) methodology to downscale the LMDZ4-NEMOMED8 regional climate model (Hourdin et al. 2006; Beuvier et al. 2010) from the Med-CORDEX ensemble (Soto-Navarro et al. 2020). The PGW methodology (Schär et al. 1996; Denamiel et al. 2020) consists in calculating the climatological changes based on the differences between future scenario (here for 2070–2100) and historical (here for 1987–2017) results from global or regional climate model and imposing it, as forcing, on top of the reanalysis products. Consequently, the main drawback of the PGW methodology is that it might miss potential changes in intra-annual and inter-annual variability. However, its main advantage consists in projecting the impact of climate change on the atmosphere–ocean dynamics at an unprecedented spatial resolution compared with traditional global and regional models, and for a reduced numerical cost.

Stable oxygen isotope data

Along the eastern Adriatic coast, about 1650 carbonate samples from 32 shells collected at six different sampling sites were previously extracted and analyzed for five bivalve species (Peharda et al. 2019*a*, 2019*b*; Uvanović et al. 2021; Ezgeta-Balić et al. 2022) in order to analyze their stable oxygen isotope composition ($\delta^{18}O_{shell}$, reported on the Vienna Pee Dee Belemnite scale as ‰ V-PDB). These species include three pectinids in Dataset 1—the Mediterranean scallop, *P. jacobaeus*, the queen scallop, *A. opercularis*, and the smooth scallop *F. glaber*—as well as, in Dataset 2—the long-lived hairy bittersweet (Dataset 2.1), *G. pilosa*, and the commercially important warty venus (Dataset 2.2), *V. verrucosa*. The sampling sites, depths, gears, periods and number of specimens, as well as the previously published studies are fully described in Fig. 1 and Table 1 and in section S1 of the Supporting Information.

In this study, seawater salinity and temperature time-series reproduced by the AdriSC model at different sampling sites were employed to compute the expected $\delta^{18}O_{shell}$ chronology (hereafter $\delta^{18}O_{exp}$) for the time intervals 1987–2017 and 2070–2100. For Dataset 1, the AdriSC results were extracted and averaged over the entire region (off Istra; see Fig. 1) and depth ranges covered by the beam trawl, while, for Dataset 2, the values were extracted at the model grid points with the nearest location and depth of the sampling sites. Validation of the AdriSC data on in situ temperature loggers is provided in section S2 of the Supporting Information. Model and $\delta^{18}O_{shell}$ data are available in the Open Science Framework repository (Denamiel et al. 2023).

As the mineralogy of the bivalve species differs (i.e., calcitic and aragonitic for respectively Datasets 1 and 2), different paleothermometry equations were used. For Dataset 1, the Friedman and O'Neil (1977) formula derived from the O'Neil et al. (1969) equation was used to compute the expected $\delta^{18}O_{shell}$ ($\delta^{18}O_{exp}$) chronology with the AdriSC temperature (T in °C):

$$\delta^{18}O_{\mathrm{exp}} = \left(1000 + \delta^{18}O_{\mathrm{water}}\right) \times e^{\left[2780\times(T+273.15)^{-2}-0.00289\right]} - 1000 \tag{1}$$

Because the oxygen isotope composition of the water was not monitored over the lifespan of the studied specimens, $\delta^{18}O_{water}$ values (reported relative to V-SMOW) were reconstructed from the AdriSC salinity (S, at transect marked in Fig. 1, Peharda et al. 2019*a*) using the equation derived from Stenni et al. (1995):

$$\delta^{18}O_{\mathrm{water}} = 0.366\,S - 12.568, \quad r^2 = 0.964 \tag{2}$$

The conversion from the V-SMOW scale to V-PDB was done with the equation of Coplen et al. (1983):

$$\delta^{18}O_{\mathrm{exp-V-PDB}} = 0.97002\,\delta^{18}O_{\mathrm{exp-V-SMOW}} - 29.98 \tag{3}$$

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Table 1. Description of the different Datasets used in the study. The last column specifies the time interval covered by the isotope data of the studied shells.

Dataset	Species	Sites	Coordinates	Depths	Gears	# Specimens	Time interval
1	*A. opercularis*[a]	Istria	45°08′58″ to 45°23′08″N	25–35 m	Beam trawl	2	2016–2018
	F. glaber[a]		13°17′05″ to 13°24′04″E			2	
	P. jacobaeus[a,b]					2	2016–2018
						3	2009–2013
2.1	*Glycymeris pilosa*	Barbariga[b]	44°59′07.47″N 13°44′19.22″E	10–11 m	SCUBA divers	3	2011–2013
		Pag Bay[c]	44°27′42.0″N 15°01′36.0″E	5–7 m		4	2006–2015
		Pašman Channel[c]	43°56′52.68″N 15°23′15.03″E	2–3 m		2	2013–2015
		Drače[c]	42°56′10.54″N 17°28′23.71″E	4–5 m		3	2003–2012
2.2	*Venus verrucosa*[d]	Barbariga	44°59′07.47″N 13°44′19.22″E	10–11 m		3	2010–2014
		Pag Bay	44°29′42.9″N 14°59′16.0″E	4–6 m		3	2012–2017
		Kaštela	43°33′01.47″N 16°20′50.79″E	2.5–4 m		5	2011–2016

[a] Ezgeta-Balić et al. (2022).
[b] Peharda et al. (2019*a*).
[c] Peharda et al. (2019*b*).
[d] Uvanović et al. (2021).

For Dataset 2, the empirically developed equation of Grossman and Ku (1986) with a V-SMOW to V-PDB scale correction of −0.27‰ (after Dettman et al. 1999) was used to compute the expected $\delta^{18}O_{shell}$ chronology based on the AdriSC temperature (T in °C):

$$\delta^{18}O_{exp} = \frac{20.6 - T}{4.34} + \delta^{18}O_{water} - 0.27 \tag{4}$$

Except at Barbariga where Eq. 2 was used, the $\delta^{18}O_{water}$ values were reconstructed from the AdriSC salinity with the equation given in Purroy et al. (2018):

$$\delta^{18}O_{water} = 0.23\,S - 7.54 \tag{5}$$

The species-specific range of $\delta^{18}O_{shell}$ values was determined from the minimum and maximum $\delta^{18}O_{shell}$ values measured in the studied specimens (Judd et al. 2018). The shell growth phenology was given by the number of days during which $\delta^{18}O_{exp}$ fell within the range of $\delta^{18}O_{shell}$ values in each year, averaged over the historical (1987–2017) and extreme warming (2070–2100) periods. Analogously, monthly growth days were computed as the number of days when $\delta^{18}O_{exp}$ fell within the corresponding range in each month of a year, averaged over both periods.

Results

For each dataset (1, 2.1, and 2.2), the impact of climate change on the eastern Adriatic bivalve growth periods is quantified, separately for the present (1987–2017) and future (2070–2100) for each species at each sampling site. This assessment considers the range between the minimum and maximum $\delta^{18}O_{shell}$, applied to the probability density functions of $\delta^{18}O_{exp}$, along with annual and monthly days of shell growth.

For Dataset 1, *A. opercularis*, *F. glaber*, and *P. jacobaeus* are likely to be adversely affected by extreme warming due to less favorable conditions for their growth (Fig. 2). Specifically, *A. opercularis* experiences a shortening of the growing season under extreme warming, as indicated by the shift from historical conditions, where both winter (right) and summer (left) peaks in $\delta^{18}O_{exp}$ distribution supported growth, to a scenario where only the winter peak aligns with favorable conditions. For *F. glaber* and *P. jacobaeus*, in which current growth ranges are shifted toward even colder conditions, this tendency is even more pronounced. In fact, for *F. glaber*, the growth range does not include the warm season peak even in the historical distribution, hence, no growth can be expected during summer, which is likely to be even longer in the future. In terms of annual growth days, *P. jacobaeus* is likely to experience the most severe drop under extreme warming with only 255 d of favorable conditions compared with 319 d under historical conditions. For *F. glaber* and *A. opercularis* the decrease in the duration of the main growing season is less severe (i.e., from 230 to 152 d and from 259 to 224 d, respectively). The monthly overview of the growth shows that the colder season is likely to become more favorable for the growth of all species. *A. opercularis* will potentially benefit the most between February and March, with ~ 24 more days of shell growth per month while, under historical

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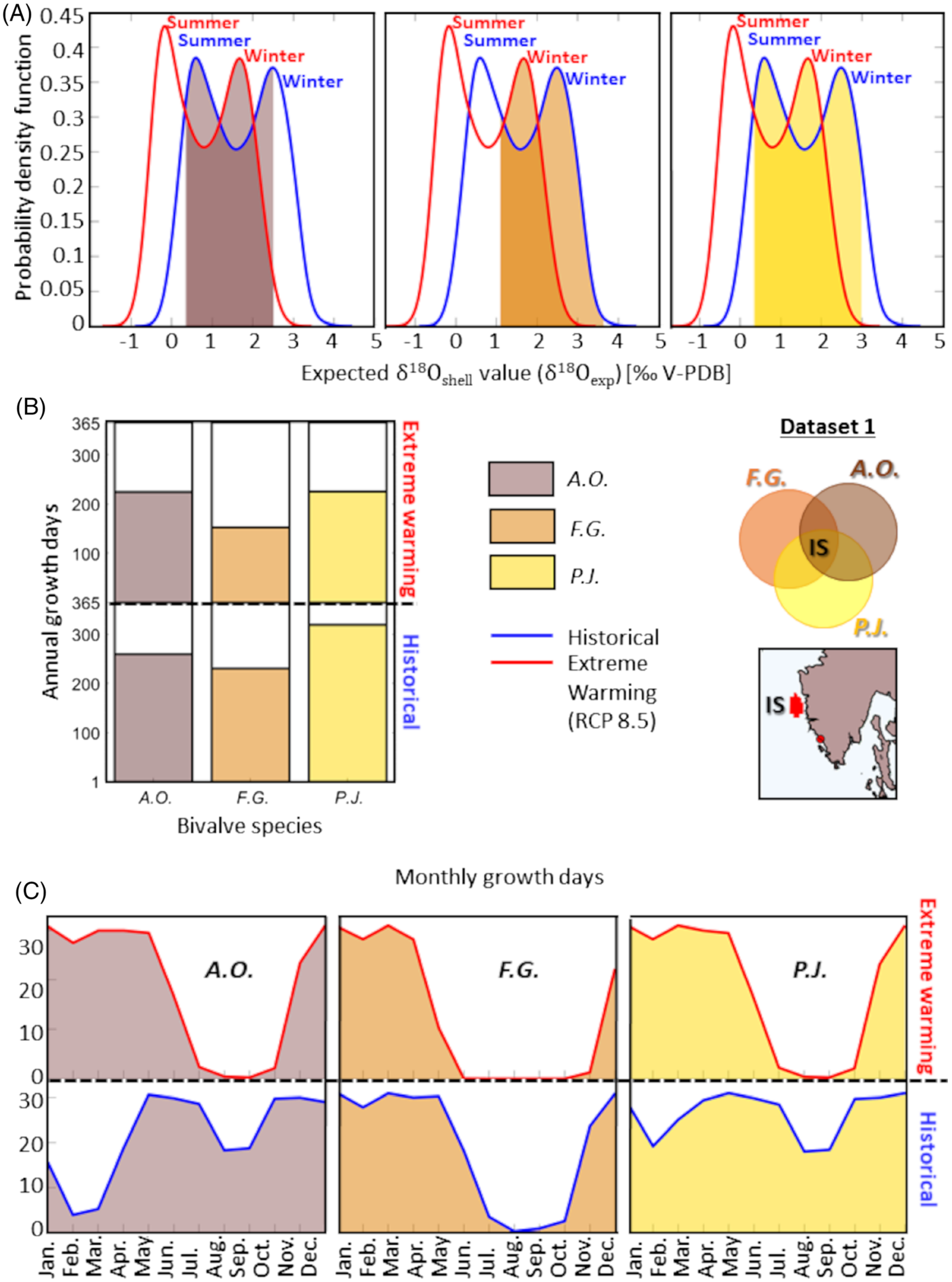

Fig. 2. Impact of climate change on shell growth of the bivalves species, *Aequipecten opercularis* (A.O.), *Flexopecten glaber* (F.G.), and *Pecten jacobaeus* (P.J.) (= Dataset 1 species) along Istria (IS) for conditions during 1987–2017 (= "Historical," blue) and for conditions during 2070–2100 (= "Extreme warming," red). (**A**) Distributions of the reconstructed shell oxygen stable isotope data ($\delta^{18}O_{exp}$ values) with conditions favorable to growth derived from observed $\delta^{18}O_{shell}$ (shaded), (**B**) duration of the annual growing season, and (**C**) duration of the monthly growing season.

conditions, shells deposited almost no material during this period of the year. The growth of Dataset 1 species will, however, substantially decrease during the warmer season (from May to October). This will likely far more affect the growth of *A. opercularis* and *P. jacobaeus*, with favorable conditions occurring throughout the entire year during

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historical times, than *F. glaber* that was restricted to the annual thermal minimum. Consequently, *A. opercularis* and *P. jacobaeus* will potentially have an up to 3 months shorter annual growing season.

In Dataset 2, $\delta^{18}O_{shell}$ values for both *G. pilosa* (Fig. 3) and *V. verrucosa* (Fig. 4) range from negative to positive. This is in contrast with Dataset 1 species which displayed only positive values. Consequently, Dataset 2 species can thrive in warm

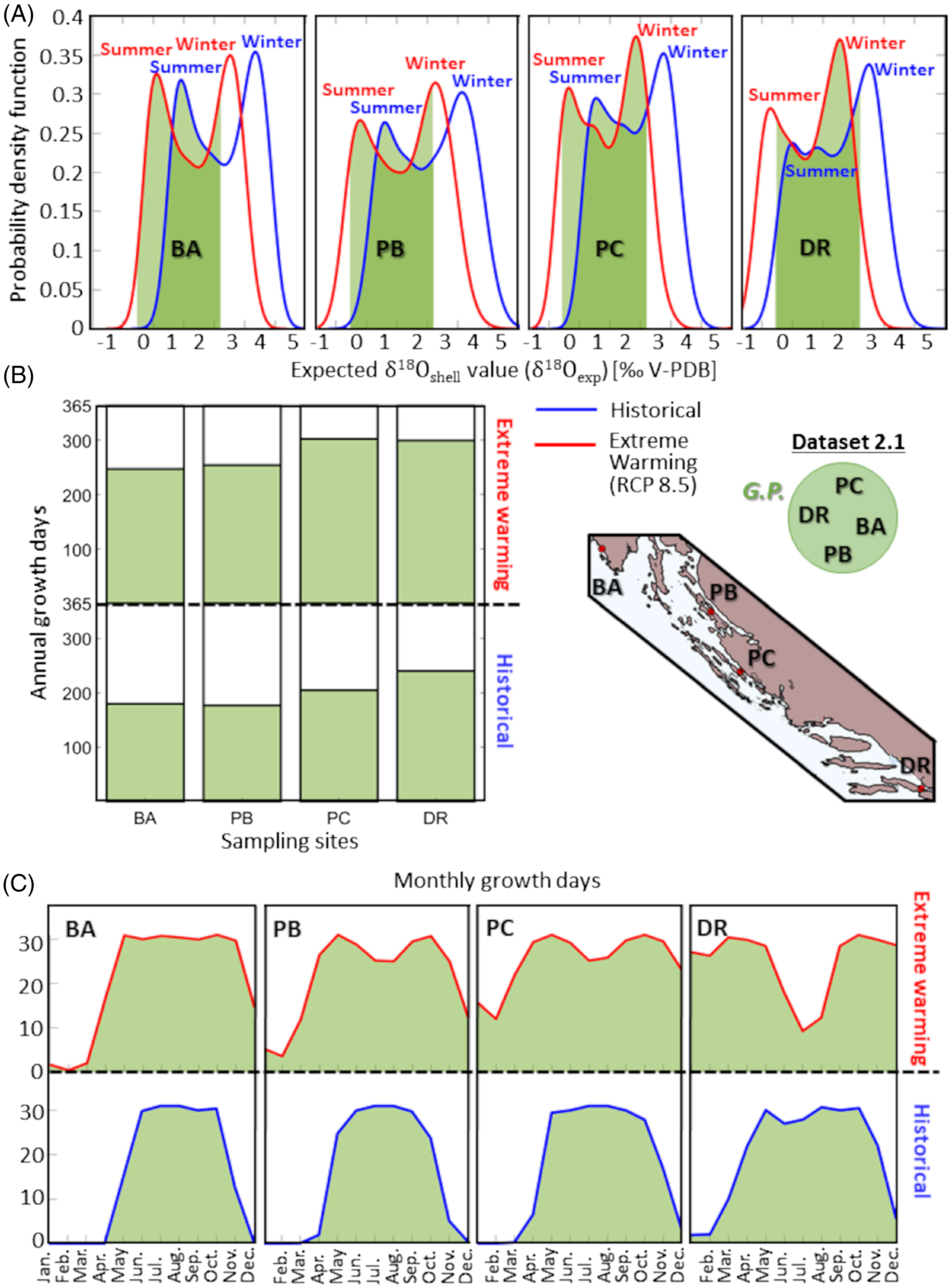

Fig. 3. Dataset 2.1: *Glycymeris pilosa* (G.P.) at Barbariga (BA), Pag Bay (PB), Pašman Channel (PC), and Drače (DR). For explanation see caption of Fig. 2.

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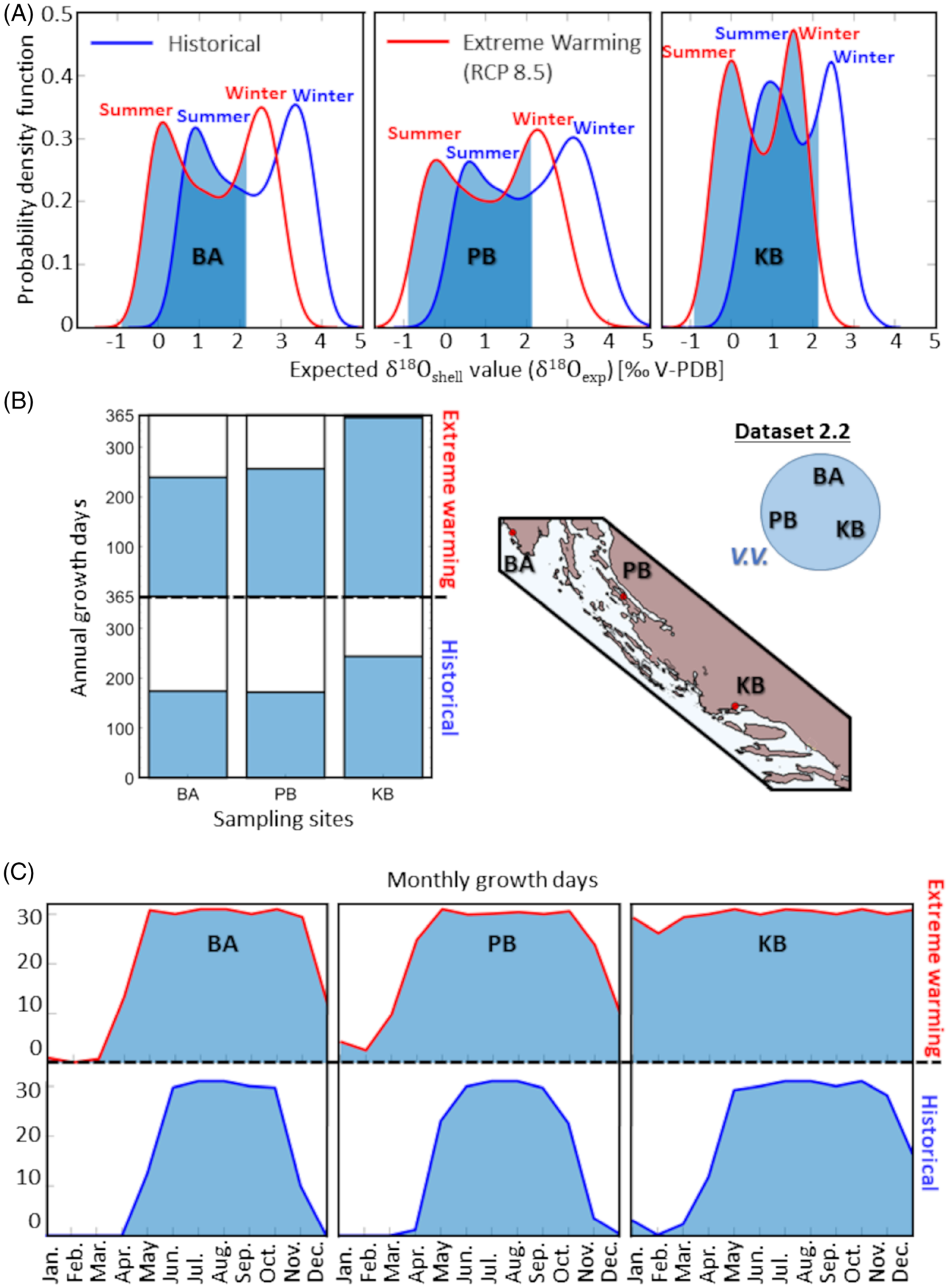

Fig. 4. Dataset 2.2: *Venus verrucosa* (V.V.) at Barbariga (BA), Pag Bay (PB), and Kaštela Bay (KB). For explanation see caption of Fig. 2.

waters and are expected to have a longer growing season under extreme warming. Further, Dataset 2 species in the southern Adriatic (e.g., Kaštela Bay and Drače) are likely to benefit more from extreme warming than those living in the north. Indeed, the temperatures along the eastern Adriatic coast will likely be warmer by up to 2°C, and about 0.4°C on average, in the south than in the north (Supporting Information Table S2; Fig. S2). Additionally, the warming is likely to

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be stronger at shallower than at deeper sites. This will potentially result in an up to 4 months longer annual growing season for *V. verrucosa* in Kaštela Bay than at Barbariga under extreme warming. Furthermore, for *G. pilosa* (Fig. 3), $\delta^{18}O_{exp}$ distributions in historical and extreme warming conditions at Barbariga and Pag Bay show nearly equal peaks in summer and winter, while a more distinct peak during the winter season is present at Pašman Channel and Drače. This indicates both different historical thermohaline conditions and varying impacts of climate change at each location. Additionally, the effect of extreme warming will be the strongest in Pašman Channel, with a more than 3 months longer growing season. The growth of this species was restricted from May to November in historical times and it will likely be extended to the entire year, especially in the central and southern Adriatic (Pašman Channel and Drače) while, in the north (Barbariga and Pag Bay), the shell growth will still be relatively limited during winter months. *V. verrucosa* has fairly similar growth conditions as *G. pilosa* (Fig. 4). In Kaštela Bay, where conditions were most optimal for growth during the past, with 244 d of shell growth per year, this species will presumably have the ability to grow throughout the entire year. The increase is also evident in the northern locations (from 174 to 240 growth days at Barbariga and from 172 to 257 growth days at Pag Bay), although less pronounced as for *G. pilosa*. Consequently, species from Dataset 2 would clearly benefit from climate warming, which predicts an extended growing season and favorable thermal conditions for growth.

Discussion

Our preliminary study is based on the unique combination of $\delta^{18}O_{shell}$ data of five bivalve species and the AdriSC kilometer-scale atmosphere–ocean climate model results for historical and extreme warming conditions. Overall, it reveals a substantial influence of extreme warming on the expected duration of all bivalve growing seasons that can be summarized as follows:

- At all sites the five studied species will likely benefit from climate warming during the colder season, i.e., they will grow longer than currently between November and April.
- The expected growing season of scallops (Dataset 1 species) will likely substantially decrease during summer, i.e., between May and October, resulting in an up to 3 months shorter growing season.
- *G. pilosa* and *V. verrucosa* (Dataset 2 species) in the south and at shallower habitats will likely be more impacted by climate warming than those living in the north and deeper habitats, resulting in an up to 4 months' longer growth season.

However, this study presents several limitations. First, the evaluation of the AdriSC temperatures (Table S1; Fig. S1) shows that the results should be interpreted with some caution, particularly at Drače, where the model results deviate the most from the observations. Second, the climate uncertainty derived from ensembles of simulations forced by multiple global climate models under multiple warming scenarios (Semenov and Stratonovitch 2010) is not considered. Third, the $\delta^{18}O_{shell}$ thresholds defining the conditions favorable for bivalve growth are derived from a small number of specimens, particularly for Dataset 1 (e.g., only two specimens of *A. opercularis* and *F. glaber*; Table 1), which might impact their accuracy. Fourth, in contrast to the study by Abe (2021), our results do not account for the impact of extreme warming on the food availability (Norkko et al. 2005) derived from either the primary production (e.g., Bonitz et al. 2018) or the acidification (e.g., Tan et al. 2019). Lastly, no adaption of the investigated species to the new climate is assumed as no information is available, although some bivalve species are found to better adapt if inhabiting zones prone to higher temperature oscillations (Zhang et al. 2020). Despite the crucial need to reproduce these processes in complex coastal environments (Mishra et al. 2023), no kilometer-scale biogeochemical climate model has yet been implemented (Ani and Robson 2021). Therefore, our analyses could only use the reconstructed $\delta^{18}O_{exp}$ values. The reconstructed $\delta^{18}O_{exp}$ values are, however, in a good agreement with the measured $\delta^{18}O_{shell}$ values, as demonstrated in previous research (Peharda et al. 2019*a*,*b*; Uvanović et al. 2021; Ezgeta-Balić et al. 2022) that employed the alignment technique described in the Methods. Although different climate models were used in these studies, the AdriSC model was successfully employed in Ezgeta-Balić et al. (2022).

In terms of bivalve management along the eastern Adriatic Sea, *P. jacobaeus* is commercially the most important scallop species in the Adriatic (Mattei and Pellizzato 1996; Peharda et al., 2019*a*; Ezgeta-Balić et al., 2022). In the last 40 years, due to a combination of overfishing, decline in eutrophication (Iveša et al. 2016) and positive temperature trends (Vilibić et al. 2019), its biomass has already declined (Mazzoldi et al. 2014). As its main growing season could further be reduced by 30%, its accelerated decline or eventual vanishing could occur by the end of this century in the northern Adriatic. Owing to a high nutritional quality, *A. opercularis* has been proposed for human consumption (Kovačić et al. 2023), with winter and spring being the most suitable period of the year for the harvest. However, our results indicate a substantial change in its growing season, posing a question if and how this species can adapt to that. *F. glaber*, which grows particularly fast and is free of diseases, could also be farmed (Marčeta et al. 2016). However, due to its sensitivity to warming and heavy metal pollution (Nardi et al. 2018; Telahigue et al. 2022) and the projected shortening of its growing season by 3 months, its commercial exploitation may never be possible. Our results indicate that, among the three

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studied scallop species, *F. glaber* is expected to be most impacted by climate warming scenarios. In contrast, *G. pilosa* which, due to its longevity is regarded as an archive for environmental change in the Mediterranean (Peharda et al. 2016), and *V. verrucosa* which has a high commercial value and occurs in the entire Mediterranean Sea (Arneri et al. 1998; Poppe and Goto 2000), will benefit from extreme warming with an up to 45% longer growing season along the southeastern Adriatic coast, where *V. verrucosa* could successfully be exploited in the future.

To the date, is has not been assessed how the growing season of the target species vary across latitudes or (paleo)climates. However, for *Mercenaria mercenaria* it has been found that variations in growth rate over different latitudes do not affect the shell δ^{18}O values (Elliot et al. 2003), while latitudinal changes in temperature were the major factor in shaping growth rate (Palmer et al. 2021). Similarly, *P. maximus* exhibits a latitudinal reduction of the growth due to a shorter phenology (Chauvaud et al. 2012). Assuming the same for the species investigated here, a migration to higher latitudes may be a way for preserving bivalves for which a substantial decline in growth in the future climate is envisaged. Changes in growth dynamics, for these, as well as other bivalve species, will potentially have impact on the marine food webs. Bivalve predators belong to different taxa, including echinoderms, crustaceans, gastropods, cephalopods, and fish (see Gosling 2015). Thereby, it can be expected that a wide range of marine organisms will be impacted by changes in seawater temperature.

If generalized, this study might lead to better adaptation plans (e.g., Roman et al. 1999; Papa et al. 2021; Marčeta et al. 2022) for possible cultivation of the studied bivalve species, along the eastern Adriatic Sea, as well as in other areas where these species live. Furthermore, similar scenarios of changes in growth patterns may occur for other bivalve species in temperate coastal areas around the world, which may constitute a growing portion of the food production in the future (Jennings et al. 2016; Tan et al. 2020; Willer et al. 2021).

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