

ORIGINAL ARTICLE

# Age and growth of *Pecten jacobaeus* in the eastern Adriatic Sea – why location matters?

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**Abstract:** Bivalves deposit shell material during their lifetime, and many species' growth patterns and age can be determined from their growth increments. Shell growth varies through ontogeny and can also have temporal and spatial variations dependent on the environmental conditions. Some scallop species (family Pectinidae) have clearly visible annual growth lines on the external surfaces of their shells that enable reliable analysis of growth patterns. *Pecten jacobaeus*, a commercially important scallop species that lives in Mediterranean coastal waters, is one of them. In this study, we analysed variations in growth and age of *P. jacobaeus* specimens collected from five locations in the eastern part of the Adriatic Sea. To obtain insights into spatial variations in feeding ecology, nitrogen and carbon isotopes were analysed in mussel tissues. Sampling was conducted in late 2023 and the first half of 2024, and between 45 and 60 specimens were collected at each location. In the northeast Adriatic (Istria), samples were collected by beam trawl fishing vessels, while at other locations (Iž, Maslenica, Prokljan, Pelješac) SCUBA divers were engaged. The shell length of analysed specimens varied from 44.6 to 149.5 mm, while their estimated age ranged from one to 12 years. The data on age and shell length were fitted to the von Bertalanffy growth function. Growth was also estimated using the Gulland-Holt plot, and a relative growth functions were constructed. Results of this study contribute to the understanding of *P. jacobaeus* growth dynamics and have potential applications in fisheries management and conservation.

**Keywords:** scallops; Mediterranean; fisheries; Bivalvia; marine ecology; stable isotopes

**Sažetak:** STAROST I RAST VRSTE *PECTEN JACOBAEUS* U ISTOČNOM DIJELU JADRANSKOG MORA – ZAŠTO JE VAŽNA LOKACIJA? Školjkaši tijekom svog života talože ljuštorni materijal, a obrasci rasta i starost mnogih vrsta mogu se odrediti iz njihovih zona prirasta. Rast ljuštura varira tijekom ontogeneze i može imati vremenske i prostorne varijacije ovisno o uvjetima okoliša. Neke vrste kapica (porodica Pectinidae) imaju jasno vidljive godišnje linije rasta na vanjskim površinama svojih ljuštura koje omogućuju pouzdanu analizu obrazaca rasta. *Pecten jacobaeus*, komercijalno važna vrsta kapice koja živi u priobalnim područjima Mediterana, jedna je od njih. U ovom istraživanju analizirali smo varijacije u rastu i starosti primjeraka *P. jacobaeus* prikupljenih s pet lokacija u istočnom dijelu Jadranskog mora. Kako bi se dobio uvid u prostorne varijacije u ekologiji hranjenja, analizirani su izotopi dušika i ugljika u mišićnom tkivu. Uzorkovanje je provedeno krajem 2023. godine i u prvoj polovici 2024. godine, a na svakoj lokaciji prikupljeno je između 45 i 60 primjeraka. Na sjeveroistočnom Jadranu (Istra) uzorci su prikupljeni dredžom, dok su na drugim lokacijama (Iž, Maslenica, Prokljan, Pelješac) uzorke prikupili ronionci. Dužina ljuštura analiziranih primjeraka kretala se od 44,6 do 149,5 mm, dok se njihova procijenjena starost kretala od jedne do 12 godina. Podaci o starosti i dužini ljuštura prilagođeni su von Bertalanffyjevoj funkciji rasta. Rast je također procijenjen pomoću Gulland-Holtovog dijagrama, a konstruirane su i relativne funkcije rasta. Rezultati ovog istraživanja doprinose razumijevanju dinamike rasta *P. jacobaeus* i imaju potencijalnu primjenu u upravljanju i očuvanju ribarstva.

**Ključne riječi:** kapice; Sredozemno more; ribarstvo; Bivalvia; ekologija mora; stabilni izotopi

## INTRODUCTION

The Mediterranean scallop *Pecten jacobaeus* (Linnaeus, 1758) is a relatively large-sized (up to ~ 15 cm; Poppe and Goto, 2000) commercially important bivalve species (Mattei and Pellizzato, 1996). According to official Eurostat statistics, *P. jacobaeus* is harvested in several European Union countries, with annual catches decreasing from 277 tonnes in 2016 to 118 tonnes in 2023. Although these catch quantities are relatively small in

comparison to other marine taxa, due to their high market price and negative trends, *P. jacobaeus* represents an important taxon for fisheries science. The Adriatic Sea is a particularly important region, as over 99% of *P. jacobaeus* catches originate from Italy and Croatia (Eurostat, 2025).

The sustainable management of living marine resources depends on our understanding of their life histories, including age and growth patterns (see King, 1995). As bivalves deposit shell material during their lifetime,

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the age and growth of many bivalve species can be determined by analysing their growth increments (see Richardson, 2001). For most species, reliable age estimates require analysis of growth patterns in shell cross sections, which is a time-consuming and costly method (e.g., Ezgeta-Balić *et al.*, 2011; Brocas *et al.*, 2013; Peharda *et al.*, 2023). However, some scallop species, including *P. jacobaeus* and great scallop *P. maximus* (Linnaeus, 1758), have clearly visible annual growth rings on the external surfaces of both the left (upper, flat) and right (lower, concave) valve, and their analysis enables a reliable estimate of age and growth (e.g., Mason, 1957; Peharda *et al.*, 2003; Chauvaud *et al.*, 2012). Despite this, age and growth analysis are still limited to a relatively small number of scallop species, and/or geographic areas and periods.

Age and growth of *P. jacobaeus* have been previously studied at several locations in the Adriatic Sea, however, most studies date back to the 1990s and 2000s. In 1996, Mattei and Pellizzato published data on *P. jacobaeus* from the Italian part of the northern Adriatic Sea. Their study applied age estimates based on shell lengths, which is not considered a reliable method for relatively long-lived species (see King, 1995); therefore, their results related to age estimates need to be interpreted with caution. However, they raised valid concerns that the North Adriatic stock of *P. jacobaeus* was already threatened by overexploitation in the 1990s and pointed out the need for future studies. In 2003, Peharda *et al.* published results on the age and growth of *P. jacobaeus* from the Croatian part of the northern Adriatic Sea based on analysis of annual growth lines on the external shell surface. This ageing method was earlier applied by other authors and in other parts of the eastern Adriatic Sea, including the Krka River estuary (Marguš *et al.*, 1992) and the Mljet lakes on the island of Mljet (Onofri and Marguš, 1995).

In the last few years, two sclerochronological studies on the seasonality of growth patterns in *P. jacobaeus* were published. Peharda *et al.* (2019) and Ezgeta-Balić *et al.* (2021) applied the analysis of stable oxygen isotope ( $\delta^{18}\text{O}$ ) to obtain a high-resolution insight into *P. jacobaeus* growth patterns on specimens from the north Adriatic. Their results show a slowdown/cessation in growth during the warmer part of the year. A similar approach was used by Danise *et al.* (2024) on fossil *P. jacobaeus* shells from the Pliocene, who also pointed out a summer growth slowdown. With current and future climate warming, the growth of *P. jacobaeus* is expected to further decrease during summer, resulting in several months of reduced growth *per year* (Zemunik Selak *et al.*, 2024). Such changes in growth dynamics will need to be taken into consideration for the sustainable management of *P. jacobaeus* populations.

These studies provide important background data, especially for the north Adriatic *P. jacobaeus* population that is under exploitation by the beam trawl fishery (see Ezgeta-Balić *et al.*, 2021). However, in order to under-

stand the spatial and temporal variations in the growth dynamics of *P. jacobaeus*, it is important to obtain data from different locations, especially due to the patchy distribution and high environmental heterogeneity in the eastern Adriatic. Therefore, the objectives of this study were to (i) estimate the age of *P. jacobaeus* specimens collected from different locations in the eastern Adriatic Sea, (ii) estimate their growth parameters, and (iii) relate growth patterns to environmental conditions.

## MATERIAL AND METHODS

### Study area and sample collections

*Pecten jacobaeus* specimens were collected from five locations in the eastern Adriatic (Fig. 1). These locations were chosen to cover geographic and habitat diversity, following consultations with local fishermen, and do not include some historical areas of the scallop fishery. For example, the Kaštela Bay has been known for the harvesting of different bivalve species, including *P. jacobaeus* (Ivica Matijaca, personal communication). However, in recent years, *P. jacobaeus* is very rare there, and thereby sampling for this study was not possible. Location Istria is in the northern Adriatic Sea and is under exploitation by commercial beam trawlers (see Ezgeta-Balić *et al.*, 2021). Maslenica is a narrow channel connecting the Velebit Channel with the Novigrad Sea, an area well known for mussel aquaculture (Milošević *et al.*, 2024). This location is characterised by strong currents and inflow of freshwater from the nearby river Zrmanja (Fiket *et al.*, 2017; Hasan *et al.*, 2020). Iž is in the area between the Dalmatian islands, is pristine and not considered to be under direct anthropogenic influences. Prokljan is a part of the Krka river estuary, which is a productive area known for mussel aquaculture and the presence of different scallop species, thanks to previous research by Marguš and his collaborators (e.g., Marguš *et al.*, 1992, 1993; Marguš, 1994). Pelješac location is in the northern part of this peninsula, close to a well-known bivalve aquaculture site, Mali Ston Bay, and is under the influence of the river Neretva (Viličić *et al.*, 1994).

At the northernmost location (the west coast of the Istrian peninsula), sampling was conducted in November 2023 during the regular beam trawl fishing activity. The water depth in this area ranged between 25 and 35 m, and this location is further referred to as Istria in the text. At the remaining four locations, *P. jacobaeus* specimens were collected by commercial SCUBA divers (Table 1). At these four locations, samples for the analysis of surface sediments were also collected using plastic containers, and they were frozen ( $-20\text{ }^{\circ}\text{C}$ ) until laboratory analysis. Three sediment samples were collected per location at different depths where *P. jacobaeus* were found, to gain insight into the range of conditions. At all locations, sampling depths exceeded 10 m.

After collection, specimens were transported to the Institute of Oceanography and Fisheries and processed



**Fig. 1.** Map of study area with sampling locations indicated in red.

within 24 h. In the laboratory, muscle tissue samples (~0.5 g) were carefully cut from six individuals *per* location and stored frozen for later stable isotope analysis. Soft tissue and epibiontic organisms were carefully removed from all collected scallop shells, and they were

cleaned with tap water and left to air-dry. Each shell was individually marked, and its shell length (anterior-posterior) and height (dorsal-ventral) were measured with a digital calliper to the nearest 0.1 mm. Shell dry weight was determined using a scale with a precision of 0.01 g.

**Table 1.** Sampling dates, sampling depth, number of specimens (N) and corresponding morphometric measurements, including mean values and standard deviation, and minimal and maximal values presented in brackets.

| Location  | Sampling date              | Depth (m)           | N  | Shell length (mm)               | Shell height (mm)             | Shell weight (g)                   |
|-----------|----------------------------|---------------------|----|---------------------------------|-------------------------------|------------------------------------|
| Istria    | 15.11.2023.                | 25 – 35             | 50 | 105.1 ± 4.3<br>(98.6 – 116.9)   | 89.4 ± 3.8<br>(81.7 – 96.8)   | 55.61 ± 6.75<br>(41.85 – 71.58)    |
| Maslenica | 6.11.2023.                 | 13 – 38             | 60 | 131.1 ± 11.1<br>(104.2 – 149.5) | 113.8 ± 9.1<br>(93.5 – 128.9) | 101.10 ± 20.53<br>(61.01 – 149.52) |
| Iž        | 11.1.2024.                 | 15 – 42             | 48 | 109.6 ± 12.6<br>(72.7 – 136.4)  | 95.6 ± 11.1<br>(63.0 – 120.3) | 68.37 ± 17.33<br>(28.47 – 124.18)  |
| Prokljan  | 8.11.2023.<br>30.11.2023.  | 11 – 18;<br>10 – 25 | 53 | 105.6 ± 16.5<br>(44.6 – 139.7)  | 91.1 ± 13.7<br>(39.2 – 121.4) | 63.50 ± 19.58<br>(7.00 – 122.03)   |
| Pelješac  | 13.11.2023.<br>15.06.2024. | 20 – 30             | 50 | 97.6 ± 9.2<br>(78.3 – 123.6)    | 84.9 ± 7.4<br>(70.9 – 105.4)  | 52.33 ± 10.40<br>(33.90 – 88.90)   |



## Age and growth analysis

Shells were aged based on the number of growth rings on the external shell surface (Fig. 2). Both valves were examined, and during analysis we took into account that the first scars and rings are often missing (see Tang 1941; Mason 1957; Minchin and Mathers 1982; Richardson, 2001). Disturbance rings were distinguished from the annual ones as they did not have a regular shape (Fig. 2) and did not extend from the anterior to the posterior part of the shell. Furthermore, the distribution of striae varied between disturbance and annual rings, with striae being equally spaced on either side of the disturbance ring (Mason, 1957; Owen *et al.*, 2002). The distance between the umbo and each clearly visible annual ring was measured with the digital caliper to the nearest 0.1 mm. Growth parameters were estimated using two approaches. First, age data obtained for each analysed shell were fitted to the relative von Bertalanffy growth function  $L_t = L_{inf} (1 - e^{-k(t)})$ , where  $L_t$  is the shell length at time  $t$ ,  $L_{inf}$  is the asymptotic shell length, and  $k$  is the curvature parameter (Beverton and

Holt, 1957). Furthermore, the obtained shell height data were used for the construction of a Gulland-Holt plot, where growth rates are plotted against the mean height (Gulland and Holt, 1959). This method is based on the analysis of adjacent growth lines, without the need to know their ordinal numbers, and is therefore suitable for verifying growth parameters in cases where the first growth lines are not clearly visible. In this method, the growth parameters are estimated using a numerical value of the slope ( $k$ ) and the x-axis intercept ( $H_{inf}$ ). As it is not possible to calculate a value of  $t_0$  using this method, this constant was omitted from the von Bertalanffy equation, and a relative growth curve was constructed (Sparre and Venema, 1998). The growth performance index ( $\Phi$ ) was estimated using the equation:  $\Phi = \log K + 2 * \log H_{inf}$  (see also Sparre and Venema, 1998).

According to a study by Peharda *et al.* (2019), in the North Adriatic, *P. jacobaeus* forms distinct annual growth lines during the September to November period. Since there is no data for other parts of the Adriatic Sea, we assumed that the growth line is deposited at similar periods at different locations.



**Fig. 2.** The shell of *Pecten jacobaeus*: illustration of annual growth rings on the external shell surface of both shell valves, shell from Prokljan (upper panel), illustration of disturbance lines, shell from Istria (lower panel). Annual growth rings are indicated by black arrows, disturbance lines with red arrows. Scale bar 1 cm.

## Stable isotope analysis

The subsample of scallop muscle tissue was dried at 60 °C for 48 hours. The dried tissue was then ground and homogenised using a mortar and pestle. For the stable isotope analysis of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , approximately 1 mg of each prepared sample was placed into tin capsules. The samples were analysed in a commercial laboratory - the Stable Isotope Facility at the University of California, Davis, United States. Stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) were measured using a PDZ Europa ANCA-GSL elemental analyser coupled to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, United Kingdom).

## Surface sediment analysis

In the laboratory, the surface sediments were first freeze-dried. Then, the weighed dry sediment sample was soaked in distilled water and sieved on a 0.5 mm sieve, and particles larger than 0.5 mm were air dried and sieved on a sieve set (1, 2 and 4 mm). The suspension with particles smaller than 0.5 mm was determined using a laser diffraction particle size analyser (Mastersizer 3000e). The results of grain size analysis were used to create a cumulative curve, where the x-axis represents grain size, while the y-axis represents the cumulative percentage. At the boundary between clay, silt, sand and gravel-sized particles (4, 63 and 2000  $\mu\text{m}$ ), cumulative percentages were obtained, and the content of gravel, sand, silt and clay particles was calculated.

The gravimetric method was used to determine the organic matter and carbonate content. Organic matter content was determined as weight loss after treating the sediment samples with  $\text{H}_2\text{O}_2$  and then heating them for six hours at a temperature of 450 °C. Carbonate content, presented as  $\text{CaCO}_3$ , was calculated from the weight of the sediment before and after treatment with 4M HCl for two hours (Loring and Rantala, 1992).

## Hydrographic data

For three sampling locations, including Istria, Iž, and Pelješac, daily mean temperature and salinity values were obtained for the depths of shell collection for the period from 2019 to 2023. Ocean environmental parameters were modelled using the 3D high-resolution (500 m horizontal) numerical model ROMS nested within a larger Adriatic Sea ROMS domain with spatial resolution of 2 km, sharing 20 vertical “s” levels (terrain following coordinates for the vertical dimension). The model was used in numerous Adriatic studies and thoroughly validated with available observations (e.g., CTD profiles and satellite SST in Janeković *et al.*, 2010, 2014, 2020; Vilibić *et al.*, 2016). The model used realistic atmospheric forcing, lateral open boundary conditions, and freshwater input from 41 rivers, providing accurate estimates for all model state variables. Due to remote

and specific geomorphological features for Maslenica and Prokljan locations, which were outside of the model domain, it was not possible to obtain reliable modelled data.

## Statistics

The relationship between shell length and height was analysed using a regression equation. One-way ANOVA was applied for the analysis of  $\delta^{13}\text{C}_{\text{muscle}}$  with respect to sampling location, following Leven’s test for homogeneity of variance. Non-parametric Kruskal-Wallis and Mann-Whitney pairwise tests were used for testing differences in  $\delta^{15}\text{N}_{\text{muscle}}$ . Analysis was performed in PAST statistical program. Graphs were prepared using Excel and SigmaPlot 15.0 software.

## RESULTS

### Age and growth

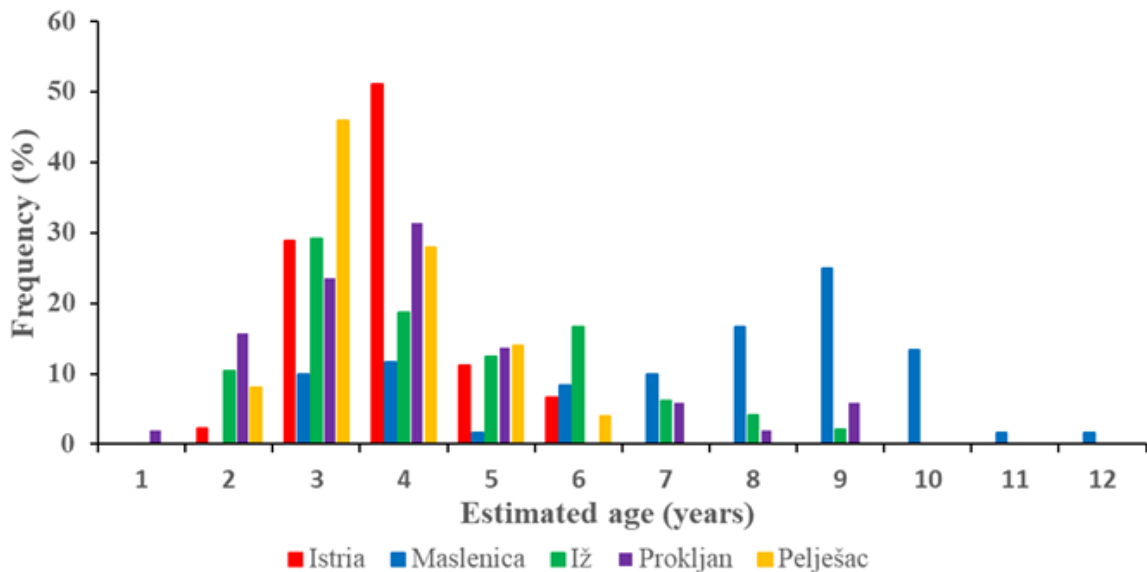
The shell lengths of the analysed specimens ranged from 44.6 to 149.5 mm, while their weights ranged from 7.0 to 149.52 g. The smallest shell was from Prokljan, while the largest one was collected from the Maslenica location. The morphometric data according to sample location are presented in Table 1, and the relationship between shell length and shell height is presented in Table 2. The highest variation in shell shape was observed for shells from Istria ( $r^2 = 0.697$ ).

Some shells did not have clearly visible annual growth lines, and these were excluded from the analysis. Out of these, five were from Istria, and two from Prokljan. In the overall samples, age classes from three to five dominated (Fig. 3). Specimens from Istria and Pelješac had a maximal estimated age of six years, while for Iž and Prokljan locations, the maximal estimated age was nine years. Maslenica was characterised by the oldest individual, which includes a total of 33 individuals (55%) in age classes eight to 10, and one individual in age classes 11 and 12 years. Many shells from Istria had pronounced disturbance lines, which hampered analysis and might have had an impact on age and growth estimates from this location.

Variations in shell growth were observed both within and between sampling locations. Within location vari-

**Table 2.** Relationship between shell length (L) and height (H) according to sampling location.

| Location  | $L = a \cdot H + b$          | $r^2$ |
|-----------|------------------------------|-------|
| Istria    | $L = 0.946 \cdot H + 20.482$ | 0.697 |
| Maslenica | $L = 1.166 \cdot H + 1.697$  | 0.944 |
| Iž        | $L = 1.123 \cdot H + 2.334$  | 0.957 |
| Prokljan  | $L = 1.202 \cdot H - 3.994$  | 0.980 |
| Pelješac  | $L = 1.231 \cdot H - 7.001$  | 0.956 |



**Fig. 3.** Age frequency histogram of *Pecten jacobaeus* according to sampling location.

ations are evident from the dispersal of data points for individual shells presented in Fig. 4A-E. The comparison of the relative von Bertalanffy growth equations (presented in Fig. 4F) illustrates variation between the sampling locations. According to these results, shells from Istria had the fastest shell growth during the first two years of life, followed by a pronounced slowdown. At this location, shells reached a minimal conservation shell length of 10 cm by the third year of life. The slowest growth during early ontogeny was that of shells from Pelješac, which reached 10 cm in their fourth year. Shells from Maslenica exhibited rapid shell growth ( $k = 0.50$ ) and the highest value of asymptotic length ( $L_{inf} = 138.3$  mm).

Gulland-Holt analysis obtained similar growth pattern results with respect to locations (Table 3), with the exception of growth patterns during early ontogeny, that is, during the first three years of life, when shells from Prokljan had the fastest growth (Fig. 5). After that period, shells from Iž and Prokljan had similar growth rates that were faster than those of shells from Istria and Pelješac, and slower than those of shells from Maslenica.

### Stable isotopes

The highest  $\delta^{15}\text{N}_{\text{muscle}}$  values were recorded for samples from Prokljan ( $8.29 \pm 0.41$  ‰), while the lowest ones were for samples from Pelješac ( $4.33 \pm 0.26$  ‰). The observed differences between locations were statistically significant (Kruskal-Wallis test  $\chi^2=24.37$ ,  $p<0.001$ : Pelješac < Iž = Istria < Prokljan; Maslenica = Istria; Maslenica < Iž). Statistical difference between locations was also observed for  $\delta^{13}\text{C}_{\text{muscle}}$  values (one-way ANOVA,  $F=21.12$ ,  $df=4$ ,  $p<0.001$ , Istria = Maslenica < Iž = Prokljan < Pelješac). Samples from Pelješac were

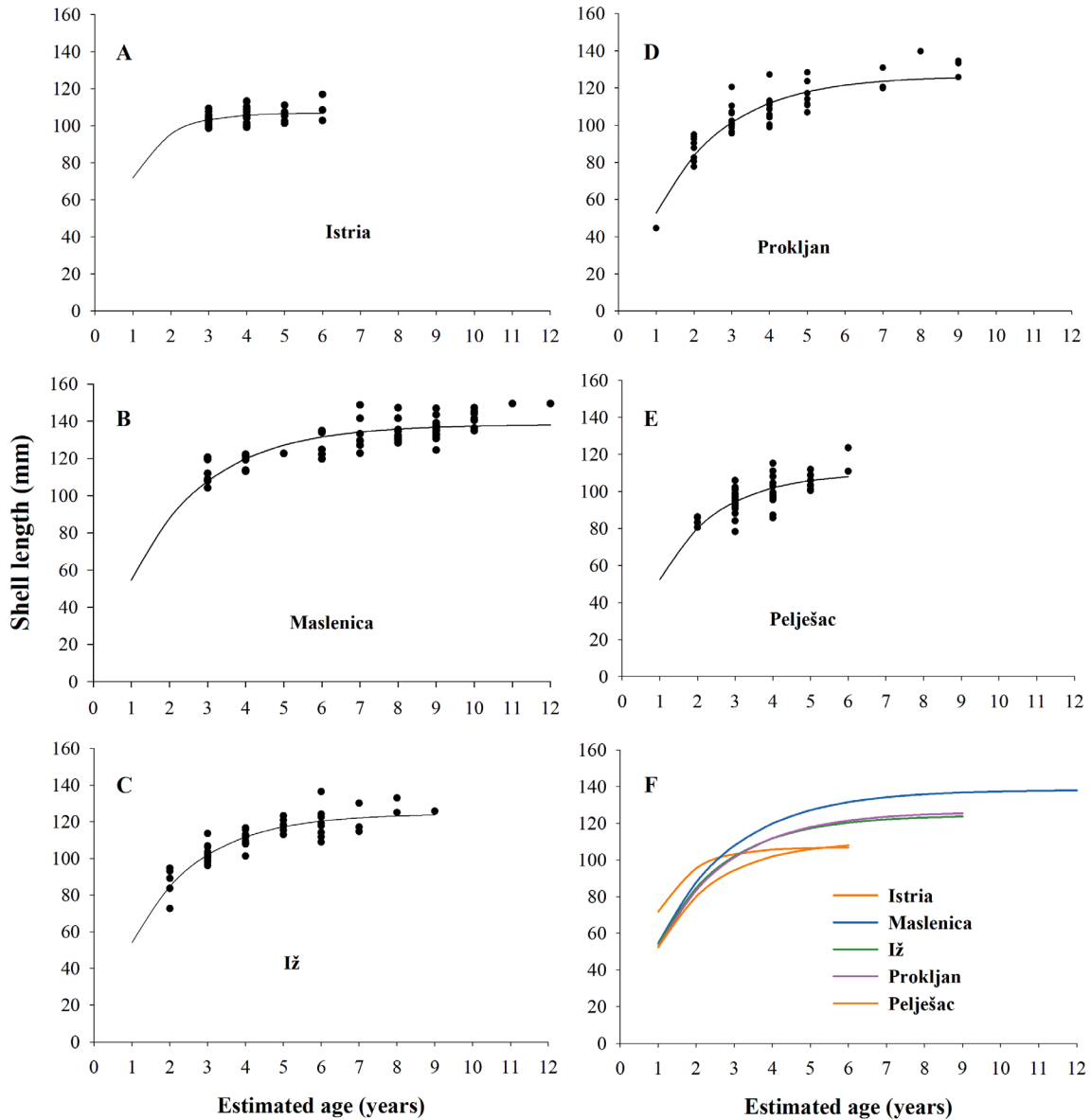
characterised with the highest  $\delta^{13}\text{C}_{\text{muscle}}$  values ( $-18.64 \pm 0.32$  ‰), while those from Istria and Maslenica had mean  $\delta^{13}\text{C}_{\text{muscle}}$  values of  $<-20$  ‰ (Fig. 6).

### Sediment characteristics

Sediment characteristics varied with respect to sampling location, with the highest percentage of sand particles in sediment samples from location Iž (>75%; Suppl. Fig. 1). Samples from Prokljan showed the most variations and were characterised by a pronounced decrease in the contribution of sand particles with respect to depth, with a minimal value of 5.4% at 18 m depth. An increase in organic matter content and a decrease in carbonate percentage accompanied this transition in Prokljan. Samples from Iž had the lowest organic matter content. The percentage of carbonates showed less variation with respect to the sampling location.

### Hydrography

Minimal values of the modelled mean daily seawater temperatures varied between locations (see Suppl. Fig. 2A), and increased from north to south, 9.9 °C (Istria; March 2022), 11.7 °C (Iž; March 2022) and 12.5 °C (Pelješac; February 2022). A similar trend was observed for maximal (22.9, 23.5 and 24.2 °C, respectively) and mean annual (16.2, 17.4, and 17.8 °C, respectively) values. Salinity values did not have a clear seasonal and spatial distribution and were most variable for Pelješac locations (see Suppl. Fig. 2B) due to the Neretva River proximity. At Istria mean daily modelled salinity values ranged from 37.54 to 38.85, at Iž from 38.27 to 38.99 and at Pelješac from 37.22 to 39.18.



**Fig. 4.** Shell length at age data according to sampling location fitted with relative von Bertalanffy growth equations. Istria  $L_{\infty} = 106.95(1 - e^{-1.11t})$  (A), Maslenica  $L_{\infty} = 138.29(1 - e^{-0.50t})$  (B), Iž  $L_{\infty} = 124.41(1 - e^{-0.57t})$  (C), Prokljan  $L_{\infty} = 126.47(1 - e^{-0.54t})$  (D), Pelješac  $L_{\infty} = 110.24(1 - e^{-0.65t})$  (E), von Bertalanffy growth equations for all sampling locations (F).

## DISCUSSION

The present study contributes to the understanding of the current state of *Pecten jacobaeus* age and growth dynamics in the eastern Adriatic Sea. The multi-location approach we applied enables comparison and insight into the variability of growth patterns. Results are especially important for the North Adriatic Sea (location Istria), where the most intense *P. jacobaeus* exploitation is taking place. In our study, the largest *P. jacobaeus* from that area had a shell length of only 11.7 cm, which is smaller than the values recorded in previous studies in this region (Cetinić and Soldo, 1999; Peharda *et al.*, 2003; Ezgeta-Balić *et al.*, 2021). It is important to note

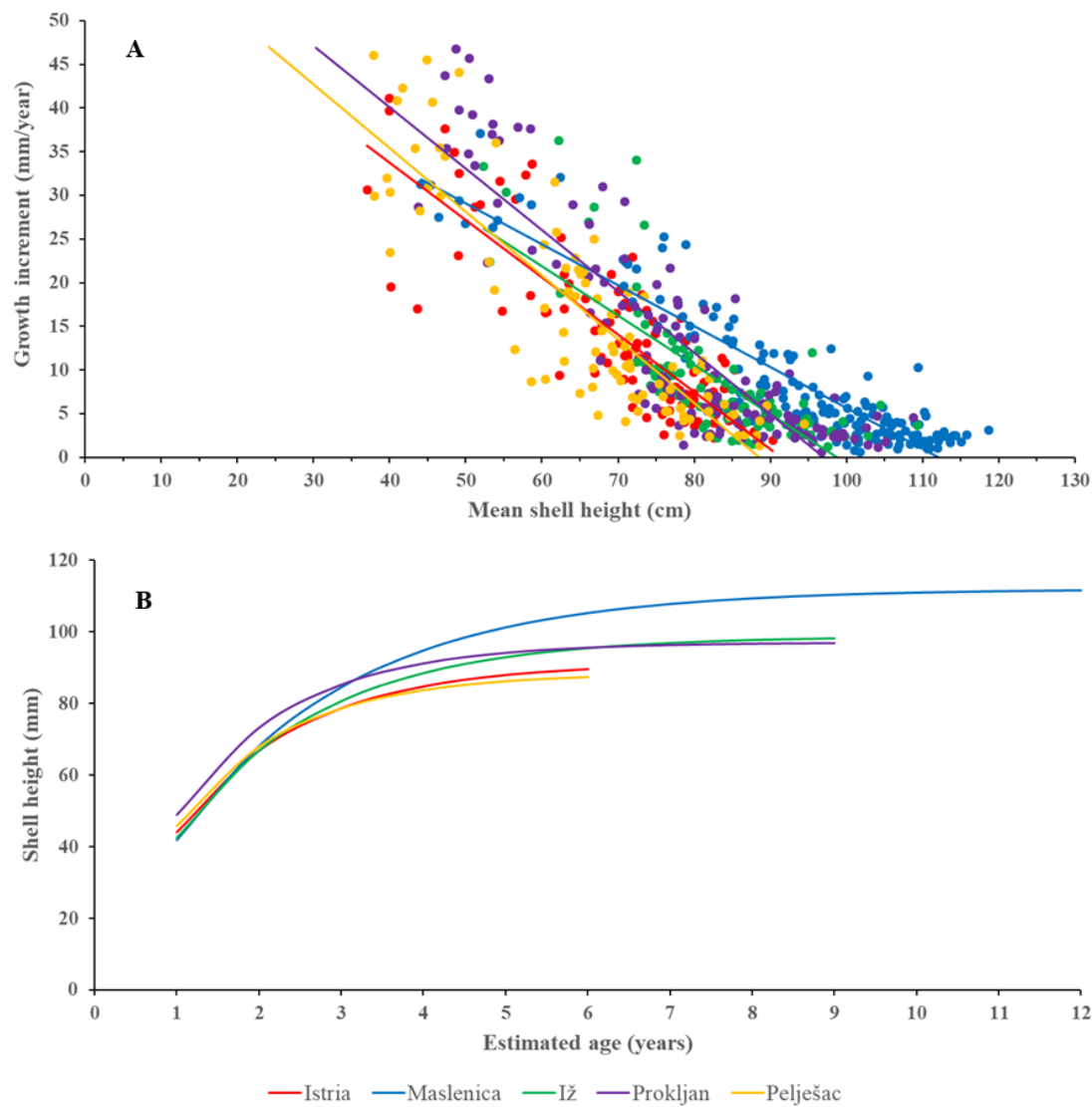
that the analysis was based on a subsample of the total catch, which implies that larger and older specimens may have been present but not included in the examined sample. In a study by Cetinić and Soldo (1999), specimens from the northern Adriatic had shell lengths of up to 15 cm, whereas the largest shell analysed by Peharda *et al.* (2003) measured 14.2 cm. In a more recent study by Ezgeta-Balić *et al.* (2021), the largest specimen had a shell length of 13.2 cm, and a very few specimens were larger than 12 cm. These results indicate changes in *P. jacobaeus* population size structure over the last few decades and support Ezgeta-Balić *et al.* (2021)'s observation that the current level of exploitation might not be sustainable. The results on age structure further sup-



**Table 3.** Gulland-Holt equations constructed from measurements of clearly visible growth rings on the external shell surface.  $L_{inf}$  data calculated from  $H_{inf}$  and the regression equation between shell length and height according to sampling location (see Table 2). N – number of specimens;  $H_{inf}$  – asymptotic shell height; K – growth coefficient;  $\emptyset$  – growth performance index;  $L_{inf}$  – asymptotic shell length.

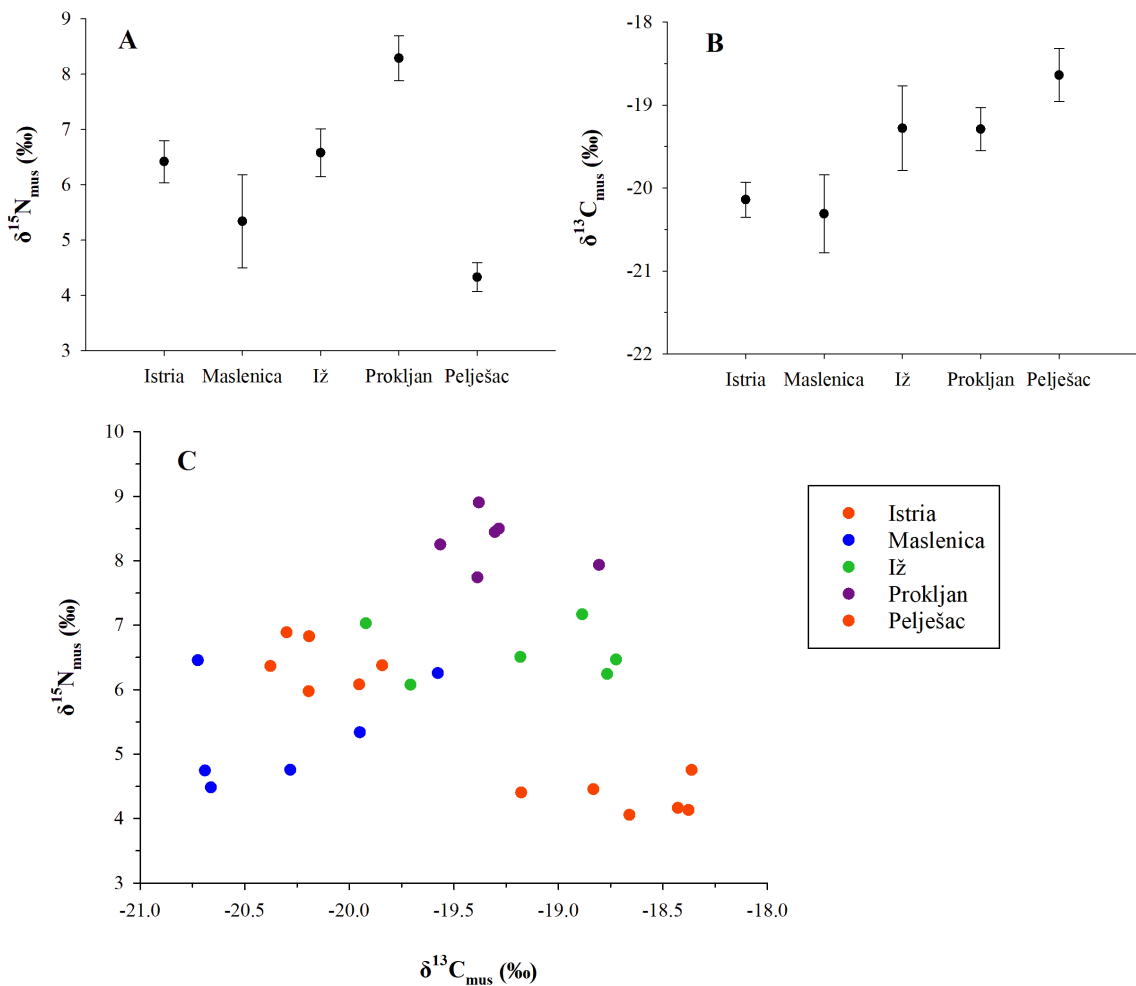
|           | N   | Equation             | R <sup>2</sup> | p       | $H_{inf}$ (mm) | K year <sup>-1</sup> | $\emptyset$ | $L_{inf}$ (mm) |
|-----------|-----|----------------------|----------------|---------|----------------|----------------------|-------------|----------------|
| Istria    | 100 | Y = -0.656X + 60.045 | 0.719          | < 0.001 | 91.5           | 0.656                | 3.740       | 107.03         |
| Maslenica | 156 | Y = -0.469X + 52.547 | 0.853          | < 0.001 | 112.1          | 0.469                | 3.770       | 132.41         |
| Iž        | 103 | Y = -0.566X + 55.854 | 0.614          | < 0.001 | 98.7           | 0.566                | 3.741       | 113.17         |
| Prokljan  | 125 | Y = -0.703X + 68.197 | 0.763          | < 0.001 | 97.0           | 0.703                | 3.821       | 112.61         |
| Pelješac  | 91  | Y = -0.730X + 64.642 | 0.730          | < 0.001 | 88.5           | 0.730                | 3.758       | 101.98         |

port this concern. In a study by Peharda *et al.* (2003), the maximal estimated age of analysed specimens from the north-eastern Adriatic was 13 years. In addition, in their study, 20% of shells larger than 98 mm (the smallest one collected in the current study) had an estimated age of seven years or more. In comparison, in the current



**Fig. 5.** Gulland-Holt plot based on measurements of clearly visible growth rings on the external shell surface (A), relative von Bertalanffy growth equations based on Gulland-Holt plot (B).





**Fig. 6.** Variations of stable isotope values of *Pecten jacobaeus* muscle tissues according to sampling location;  $\delta^{15}\text{N}_{\text{mus}}$  (A),  $\delta^{13}\text{C}_{\text{mus}}$  (B), dual isotope values (C).

study, the maximal estimated age of specimens from Istria was only six years. Furthermore, many of them had pronounced disturbance lines (scars) on their shells that are most likely caused by the beam trawl fishery. This aligns with the observation of Ezgeta-Balić *et al.* (2021), who noted that smaller *P. jacobaeus* specimens are caught in beam trawl nets, due to a large amount of megazoobenthos discards, and are returned to the sea after each tow. The presence of scars might indicate that these specimens survived the return to the sea, although their growth pattern is disturbed.

The length and age structure of the analysed specimens varied with respect to sampling location, most likely pointing out different levels of exploitation. The northern Adriatic is the only region in the eastern Adriatic Sea where scallop harvesting from the fishing vessel, that is by beam trawler, is permitted (see Ezgeta-Balić *et al.*, 2021). In other areas, scallops are commercially harvested by SCUBA divers with special permits for that type of fishery (Official Gazette, 30/2021). As scallops

prefer areas below the thermocline and sandy substrate (Poppe and Goto, 2000), which are relatively rare in the eastern Adriatic, their distribution is patchy and restricted to the North Adriatic (Piccinetti *et al.*, 1986) and relatively small areas (see research by Marguš *et al.*, 1992; Onofri and Marguš, 1995). Furthermore, scallops have prolonged larval phases lasting up to four weeks (Peña *et al.*, 1996), which can cause their high dispersal and can potentially hinder repopulation of certain locations, potentially leading to local extinctions. Although length and age data for three of the four southern sampling locations show a more diverse population age structure than those from Istria, data from Pelješac do point out that *P. jacobaeus* populations are exposed to anthropogenic and/or environmental impacts in different parts of the Adriatic Sea.

The minimal conservation reference size of *P. jacobaeus* is 10 cm (EU Regulation 2015/812), and according to the results of our study, this shell length was attained by the third year of life at most study locations.

Exceptions were shells from Pelješac, which were characterised by slower growth. This is the most southern location, and it is possible that higher seawater temperatures (see Lipizer *et al.*, 2014 and Suppl. Fig. 2), inhibited shell growth during summer months. Previous studies (Peharda *et al.*, 2019; Ezgeta-Balić *et al.*, 2022; Danise *et al.*, 2024) showed that *P. jacobaeus* has reduced growth during the warmer part of the year, and it is possible that at the Pelješac location, the growing season is shorter than at other, more northern, locations.

Stable isotope analysis was not previously conducted on soft tissue of *Pecten jacobaeus*, therefore, we compared our results with those for other bivalve species in the Adriatic Sea, as well as the results obtained for closely related *P. maximus* from the Atlantic Ocean. Muscle tissue of specimens from Pelješac was characterised by the lowest  $\delta^{15}\text{N}_{\text{mus}}$  values ( $\sim 4\text{‰}$ ), while those of shells from Prokljan were the highest ( $\sim 8\text{‰}$ ). In a study on *P. maximus*, Lorrain *et al.* (2002) observed  $\delta^{15}\text{N}_{\text{mus}}$  values above  $9\text{‰}$ . With respect to other taxa in the Adriatic Sea, similar spatial variations in  $\delta^{15}\text{N}_{\text{mus}}$  were previously observed in *Mytilus galloprovincialis*, with values for specimens from a coastal location near Tribunj (the middle coastal Adriatic) of  $\sim 3\text{‰}$ , and those from a bivalve aquaculture farm in the Krka River estuary, that is close to Prokljan location, of  $\sim 7\text{‰}$  (see Peharda *et al.*, 2024). However, stable isotopes reflect specific environmental features and are thus not always directly comparable. Still, they provide a valuable baseline for food web research, given their position at the base of the food webs. A detailed analysis of *P. jacobaeus* feeding ecology is beyond the scope of this study, as our sampling was conducted only on one occasion, and the data on suspended particulate organic matter were not analysed, which would provide insight into the availability of food. However, the obtained data do provide insight into spatial variability and contribute to  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  data for bivalve soft tissue, serving as a baseline for further research on marine food webs in the Adriatic Sea.

Micro-growth increments, that is, distances between individual striae on the external shell surface of scallops, have been analysed in some species, including, for example, *Pecten maximus* (Chauvaud *et al.*, 2012) and *Aequipecten opercularis* (Johnson *et al.*, 2021). Their daily periodicity has been validated, and it was demonstrated that their analysis provides a high-resolution insight into variations in shell growth. To the best of our knowledge, only published results on micro-growth increments in *P. jacobaeus* are those of Danise *et al.* (2024) on fossil specimens from the Pliocene. Their analysis concentrated on the 2<sup>nd</sup> and 3<sup>rd</sup> annual cycle, the period of early ontogeny with relatively intensive growth. Future studies should adopt such an approach to live-collected *P. jacobaeus* and attempt to validate the periodicity of striae formation and compare growth dynamics between different locations and environmental conditions.

## CONCLUSIONS

This study demonstrated that the same bivalve species can exhibit different growth dynamics depending on the sampling site, likely influenced by environmental factors. Differences in maximum age of *Pecten jacobaeus* were also observed between areas, particularly in regions with more intensive exploitation of the species. However, these findings should be interpreted with caution, as the current analysis was based on a limited sample size. Future studies should include a larger number of *P. jacobaeus* specimens to allow for more robust conclusions. When dealing with a commercially exploited bivalve species, it is crucial to understand such spatial differences in life-history traits to enable effective and sustainable management.

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## Declaration of competing interest

Given her role as Acta Adriatica Editor-in-Chief, Melita Peharda had no involvement in the peer review of this article and had no access to information regarding its peer review. Full responsibility for the editorial process for this article was delegated to another journal editor.

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