Marine Environmental Research 134 (2018) 138–149

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Drivers of shell growth of the bivalve, *Callista chione* (L. 1758) – Combined environmental and biological factors

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ARTICLE INFO

Keywords:
Bivalve mollusk
Seasonal shell growth patterns
Stable isotopes
Sclerochronology
Environment
Biology
Life history traits

ABSTRACT

Seasonal shell growth patterns were analyzed using the stable oxygen and carbon isotope values of live-collected specimens of the bivalve *Callista chione* from two sites in the Adriatic Sea (Pag and Cetina, Croatia). Micromilling was performed on the shell surface of three shells per site and shell oxygen isotopes of the powder samples were measured. The timing and rate of seasonal shell growth was determined by aligning the $\delta^{18}O_{shell}$-derived temperatures so that the best fit was achieved with the instrumental temperature curve. According to the data, shells grew only at very low rates or not at all during the winter months, i.e., between January and March. Shell growth slowdown/shutdown temperatures varied among sites, i.e., 13.6 °C at Pag and 16.6 °C at Cetina, indicating that temperature was not the only driver of shell growth. Likely, seasonal differences in seawater temperature and food supply were the major component explaining contrasting growth rates of *C. chione* at two study sites. Decreasing shell growth rates were also associated with the onset of gametogenesis suggesting a major energy reallocation toward reproduction rather than growth. These results highlight the need to combine sclerochronological analyses with ecological studies to understand life history traits of bivalves as archives of environmental variables.

1. Introduction

Shells of bivalve mollusks are increasingly used to reconstruct past climates. Environmental variables are encoded in shells in the form of geochemical properties, shell growth rate, and shell microstructure. To make use of these proxy records, it is crucial to properly align them in time. In turn, this requires knowledge of the timing and rate of seasonal shell growth and identifies causes thereof. Previous studies identified several drivers that influence the timing and rate of shell growth of bivalves including temperature (Brocas et al., 2013; Goodwin et al., 2001a; Jones et al., 1983; Royer et al., 2013; Schöne et al., 2005a), food supply and quality (Brey, 1995; Broom and Mason, 1978; Sato, 1997; Witbaard, 1996), salinity (Koike, 1980; Marsden and Pilkington, 1995) and latitude (Chauvaud et al., 2012; Hall et al., 1974; Jones et al., 1989), but also reproduction (Jones, 1980; Okaniwa et al., 2010; Sato, 1995), and genetically determined thresholds (Hall et al., 1974). Depending on species and habitat, environmental or physiological factors are more relevant for shell growth (Jones, 1980; Nishida et al., 2012; Richardson, 2001; Vihtakari et al., 2016; Witbaard, 1996).

In iteroparous (multiple reproductive cycles) marine bivalves, there is no clear rule on how much energy is allocated toward growth (Jokela and Mutikainen, 1995). Whereas most species maximize growth at the expense of reproduction (Sebens, 1987), others do the opposite and preferentially allocate energy resources to gamete production instead of growth, e.g., *Chlamys islandica*, *Anodonta piscinalis* or *Arctica islandica* (Jokela and Mutikainen, 1995; Jones, 1980; Schöne et al., 2005b; Vahl, 1981). Still others such as *Cerastoderma edule* (Seed and Brown, 1978, 1977) gain sufficient energy for both growth and reproduction provided there is an adequate food supply. Seasonal shell growth patterns should therefore not only record changes in temperature, food, spawning or other stressful factors (Cardoso et al., 2007), but potentially also the seasonal energy allocation to gamete production. A comprehensive study of the main drivers of shell growth, considering the physical and chemical environment as well as the ecology and biology, in particular physiological factors, is therefore a research priority to interpret the geochemical proxy record of bivalve shells.

In the present study we studied the limiting drivers for shell growth of *Callista chione*. This iteroparous burrowing venerid bivalve inhabits Atlantic and Mediterranean waters and is of high commercial importance and plays an important role in benthic ecosystems. According

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https://doi.org/10.1016/j.marenvres.2018.01.011
Received 22 May 2017; Received in revised form 15 January 2018; Accepted 16 January 2018

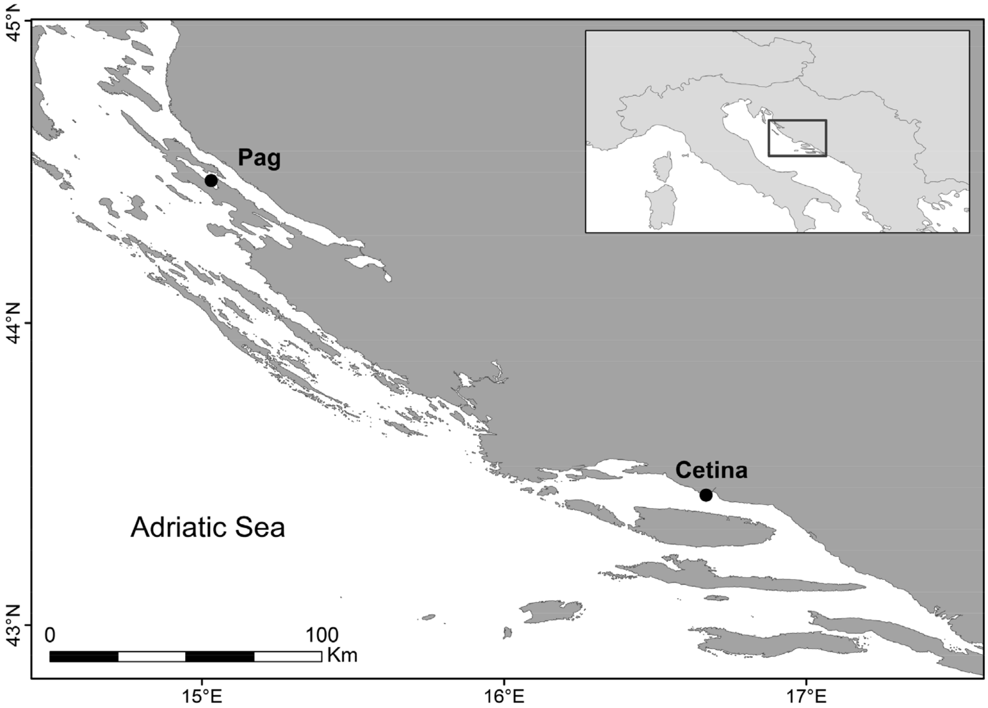

Fig. 1. Map showing sampling locations in the eastern Adriatic Sea.

to previous findings, it has a relatively long life span of over 40 years (Ezgeta-Balić et al., 2011; Galimany et al., 2015; Hall et al., 1974; Metaxatos, 2004; Tirado et al., 2002). Since *C. chione* forms distinct periodic growth patterns on the external shell surface as well as in cross-sections (Ezgeta-Balić et al., 2011; Hall et al., 1974), it is potentially a valuable species for the reconstruction of environmental and physiological conditions. Here, shell growth patterns and high-resolution stable isotope analyses were used to determine the timing and rate of seasonal shell growth and life history traits of this species. Furthermore, the shell ultrastructure was studied to gain insights into biomineralization processes.

2. Material & methods

2.1. Sample collection

Specimens of *Callista chione* were collected alive by SCUBA and skin diving (3–5 m depth) from two sites in the eastern Adriatic Sea, i.e., Pag (44.46167° N, 15.02667° E) and Cetina (43.43694° N, 16.68722° E) (Fig. 1). In Pag, specimens were collected in June 2015, October 2015, and June 2016, while all studied specimens from Cetina were collected in October 2015. The right valve of three shells from each site was used for sclerochronological analysis. Based on shell length and previous knowledge of their reproduction cycle (pers. obs.), all individuals were determined as sexually mature. Shells AC1 to AC3 from Pag measured 45.2 mm, 47.8 mm and 36.4 mm in length, respectively, whereas those from Cetina (CC1 to CC3) measured 53.9 mm, 52.7 mm and 50.6 mm, respectively. Each sample was cut along the axis of maximum growth using a Struers Labotom 3 saw, and determination of ontogenetic age was performed by counting major, presumably annual, growth bands in shell cross-sections (Fig. 2).

2.2. Instrumental and ecological data

Seawater temperature was measured by data loggers (Tinytag, Gemini®) deployed at each sampling locality in a water depth of 3–5 m. The loggers recorded water temperature between May 2014 and October 2015 on an hourly basis (own observation by AP). During the same time interval and at each sampling locality, salinity was measured once per month with a YSI probe at same water depths. Monthly precipitation was computed from daily data of meteorological stations at Pag and Cetina (Split) obtained from the Meteorological and Hydrological Service of the Republic of Croatia. Biological variables (own observation by AP) were used in relationship to shell growth patterns. These variables include data on food origin and quality based on stable carbon isotope values ($\delta^{13}C_{SPM}$) and the C:N molar ratio ($C:N_{SPM}$) of the suspended particulate matter (SPM), respectively, and on the gonadal development (gonadosomatic index - GSI, and body mass index - BMI).

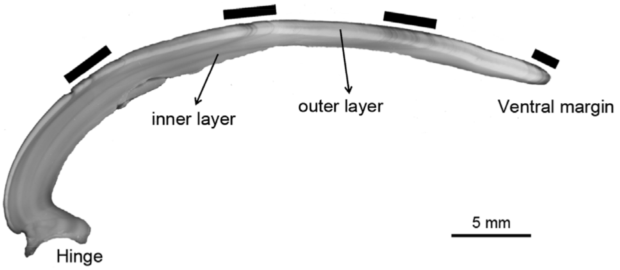

Fig. 2. Cross-section of *Callista chione* CC2 specimen collected on 3 October 2015 (length: 52.7 mm). Black rectangles indicate annually formed growth bands.

In coastal marine environments, the $\delta^{13}C$ values of the particulate organic matter can be driven by phytoplankton dynamics (Miller and Page, 2012). Typically, phytoplankton has a carbon isotopic value of ~ -22‰ (Fry and Sherr, 1984; Harmelin-Vivien et al., 2008). Therefore, the temporal pattern of $\delta^{13}C$ in the suspended particulate matter can be used as a tracer of phytoplankton blooms (Cifuentes et al., 1988). Another proxy is the C:N ratio of phytoplankton composition, which is approximately 6 (Redfield, 1958). Based on this value, fresh marine particulate matter can be discriminated from either more degraded or terrestrial material, providing an insight into the quality of suspended particles.

Seawater samples were collected ~ 0.5 m above the seafloor using a Niskin bottle (between 10 — 20 L) and vacuum filtered in the laboratory. Prior to filtration water containers were gently agitated to homogenize seawater and filters were rinsed with distilled water. Pre-