Estuarine, Coastal and Shelf Science 92 (2011) 19–26

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

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

Seasonal variability in somatic and reproductive investment of the bivalve *Scrobicularia plana* (da Costa, 1778) along a latitudinal gradient

Sílvia Santos [a],*, Joana F.M.F. Cardoso [a,b], Célia Carvalho [a], Pieternella C. Luttikhuizen [a], Henk W. van der Veer [a]

[a] *NIOZ – Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg Texel, The Netherlands*
[b] *CIMAR/CIIMAR – Centro Interdisciplinar de Investigação Marinha e Ambiental – Universidade do Porto, Rua dos Bragas, 289, 4050-123 Porto, Portugal*

ARTICLE INFO

Article history:
Received 3 August 2010
Accepted 5 December 2010
Available online 14 December 2010

Keywords:
Scrobicularia plana
seasonal cycle
life history
latitude
temperature

ABSTRACT

Monthly investment in soma and gonads in the bivalve *Scrobicularia plana* is described for three populations along its distributional range: Minho estuary, Portugal; Westerschelde estuary, The Netherlands and Buvika estuary, Norway. Seasonal cycles in body mass (BMI), somatic mass (SMI) and gonadal mass (GMI) indices were observed for all populations. In Portugal, BMI and SMI peaked in mid-autumn, while in The Netherlands both indices were at their highest in mid-spring. Norway showed a different pattern with two distinct peaks: one in mid-autumn and a second peak in spring. GMI reached maximum values in July in Portugal and Netherlands and in June in Norway. Overall, mean BMI and SMI were lower in Portugal while mean GMI was lower in Norway. The spawning period lasted the whole summer in Portugal, but was shorter (only two months) in The Netherlands and Norway. The reproductive investment in The Netherlands was significantly higher than in Portugal and Norway, with the lowest values being observed in Norway. Differences in annual cycles between populations were attributed to environmental factors, namely temperature and food availability. Temperature seems important in shaping the reproductive pattern with more northern populations showing shorter reproductive periods starting later in the year, and a lower reproductive output. In addition, winter water temperatures can explain the lower mean body and somatic mass values observed in Portugal. Food availability influenced the physiological performance of the species with peaks in somatic mass coinciding with phytoplankton blooms. This relation between physiological performance and environmental factors influences *S. plana* distribution, densities and even survival, with natural consequences on its commercial importance.

1. Introduction

Bivalves are a main component of the intertidal benthic faunal communities, with top–down effects on sediment characteristics and primary producers, and bottom–up effects on a variety of invertebrate, fish and shorebird predators (Piersma and Beukema, 1993; Raffaelli and Hawkins, 1996; Seitz and Lipcius, 2001; Tulp et al., 2010). They can be found in a variety of habitats where they are exposed to temporal and spatial differences in the environmental conditions, influencing physiological processes in these organisms. Two of the main abiotic factors are temperature and food availability, affecting physiological rates (Clarke, 1987; Sprung, 1991; Masilamoni et al., 2002) and reproduction (MacDonald and Thompson, 1986; De Goeij and Honkoop, 2003; Burke et al., 2008). Other factors such as salinity, water flow, immersion time and sediment type seem to be more important at a local scale (Warwick et al., 1991; Dame, 1996; Bocher et al., 2007). Therefore, it is expected that the general inverse trend of temperature and food availability with latitude (Thorson, 1950; Barry and Carleton, 2001; Pidwirny, 2006; Jansen et al., 2007), will be reflected in the physiological performance of bivalves.

Latitudinal trends in the physiological performance of marine invertebrates are commonly observed. Studies showed that egg and larval size, initial energy reserves of eggs and larvae and reproductive effort tend to increase with increasing latitude, and fecundity, age at first maturity and reproductive output (Clarke, 1987; Thatje et al., 2004; Ward and Hirst, 2007) as well as growth and mortality tend to decrease (Contreras and Jaramillo, 2003; Petracco et al., 2010). Some hypotheses are still under debate (e.g. Mileikovsky, 1971; Pearse et al., 1991; Arntz and Gili, 2001; Gallardo and Penchaszadeh, 2001; Laptikhovsky, 2005), such as “Thorson’s rule”, which suggests that the occurrence of species with pelagic

---

* Corresponding author.
E-mail address: silvia.santos@nioz.nl (S. Santos).

0272-7714/$ – see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecss.2010.12.005

planktotrophic larvae decreases with latitude due to increased food seasonality and lower temperatures in colder areas (Thorson, 1950). Therefore, knowledge of large-scale patterns of growth and reproduction in marine invertebrates and the factors determining them is essential for understanding spatial patterns of population dynamics and for management of commercially exploited species. This requires species with a large distributional range such as for instance the peppery furrow shell, *Scrobicularia plana.*

Scrobicularia plana is an important species in shallow water benthic communities (Keegan, 1986) and commercially exploited in several European countries (Langston et al., 2007). It ranges from the Norwegian Sea in the north, along the Atlantic coast into the Mediterranean until Senegal (Tebble, 1976). *S. plana* usually remains confined to the upper intertidal (Hughes, 1970; Orvain et al., 2007), not being very common in subtidal areas (Dekker, 1989) and preferably inhabiting muddy sediments (Bocher et al., 2007). It burrows to a depth of 5–20 cm (Akberali and Davenport, 1981) and can act both as a deposit and as a suspension feeder, although it behaves mainly as a deposit-feeder when emersion periods are long (Hughes, 1970). The species has been found in salinities ranging from 11 (Green, 1957) to 34.5 PSU (Freeman and Rigler, 1957), suggesting a higher tolerance to low salinities than most common estuarine bivalves (Spooner and Moore, 1940). *S. plana* occurs in areas with water temperature regimes ranging from 6–15.5 °C in North Wales (Hughes, 1971) to 13–28 °C in Morocco (Bazaïri et al., 2003), and 10–27 °C in the Mediterranean (Casagranda and Boudouresque, 2005). In the intertidal, organisms may need to cope with even a larger spatial and temporal variation in temperature (Harrison and Phizacklea, 1987).

Although studies on growth and reproduction are available for *Scrobicularia plana* (Paes-da-Franca, 1956; Hughes, 1971; Bachelet, 1981; Worrall et al., 1983; Zwarts, 1991; Sola, 1997; Guerreiro, 1998), none of these assessed the reproductive output in a quantitative way and in relation to somatic mass, which is essential to determine the allocation strategies of a population to growth and reproduction. Therefore, we studied growth and reproduction patterns of three populations along a latitudinal gradient, from Norway (Trondheim) to the north of Portugal (Caminha). The aim was to interrogate spatial and temporal variation in growth and reproduction by analyzing: (1) body and somatic mass cycles; (2) reproductive strategies (by assessing the seasonal patterns in gonadal mass) and (3) mass allocation to growth and reproduction (by following changes in somatic and gonadal cycles throughout the year).

2. Materials and methods

2.1. Field sampling

Scrobicularia plana was collected at three different locations along the European coast (Fig. 1): Minho estuary, Portugal (N41°52′46″, E08°50′14″); Westerschelde estuary, The Netherlands (N51°21′01″, E03°44′01″); and Buvika estuary, Norway (N63°18′42″, E10°10′12″). Sites were exposed for 3–4 hours per day in Portugal and Norway and 7–8 hours per day in The Netherlands. Sampling took place once a month over a total period of 2 years: between April 2007 and May 2008 in Portugal, June 2008 and September 2009 in The Netherlands, and from April 2008 to April 2009 in Norway. At each sampling, around 50 individuals were randomly collected by hand at each location, in an area of 1–2 km^2. They were then transported to the laboratory the same day, stored overnight in seawater at 5 °C and processed within the next 24 h.

At each location, sediment surface temperature was recorded every 15 min. during the sampling period with loggers (StowAway® TidbiT®). Since there was an overestimation of low water temperatures due to the intertidal location and structure of the logger, mean monthly temperatures were calculated using only high water data. In addition, long-term data series of sea surface water temperatures were obtained from subtidal areas in the vicinity of the sampling stations. Data were obtained for Portugal by the “CISL Research Data Archive” (via http://dss.ucar.edu/), for the Netherlands by “Rijkswaterstaat” (via http://www.waterbase.nl), and for Norway by J.-A. Sneli (pers. comm.).

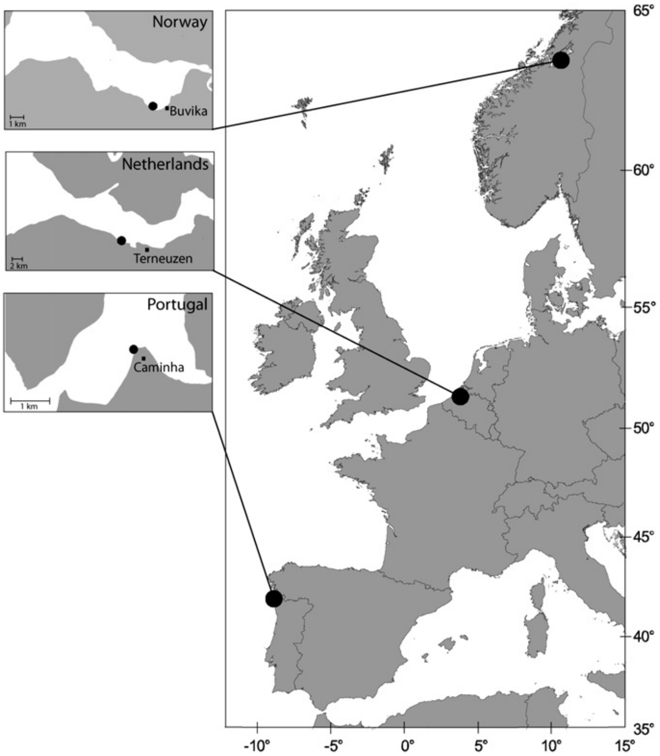

Fig. 1. Sampling locations of *Scrobicularia plana* along the European coast: Minho estuary, Portugal; Westerschelde estuary, The Netherlands; Buvika estuary, Norway.

2.2. Data analysis

For each specimen, shell length was measured to the nearest 0.01 mm with electronic callipers, after which bivalves were opened and reproductive tissue was separated from the somatic mass under a binocular microscope (10×). For both gonadal and somatic tissues, ash-free dry mass (AFDM) was determined to the nearest 0.01 mg, as the difference in dry and ash mass by first drying for 48 h at 60 °C followed by incineration for 2 h at 580 °C. In order to determine body condition, the body mass index (BMI) was calculated as the total body AFDM (soma + gonads) divided by cubic shell length. To follow the investment in somatic and gonadal mass, the somatic mass index (SMI) and the gonadal mass index (GMI) were estimated as the AFDM of the soma, or gonads respectively, divided by cubic shell length. Mass was divided by cubic shell length to allow comparison in terms of condition between animals of different sizes. If more than 50 individuals were collected, the extra animals were burnt as a whole and only information regarding BMI, and not SMI or GMI, would be available. The relative investment in reproduction compared to body mass was calculated as the gonadosomatic ratio (GSR), i.e. the gonadal AFDM divided by the total body AFDM.

ANOVA was performed to test for differences in seasonality of BMI, SMI and GMI between locations. Due to the lack of independence between samples from each month within location, monthly