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Age and growth in three populations of *Dosinia exoleta* (Bivalvia: Veneridae) from the Portuguese coast

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Abstract The present study aimed at estimating the age and growth in three populations of *Dosinia exoleta* from the Portuguese coast (Aveiro in the north, Setúbal in the southwest and Faro in the south). Two techniques were compared to ascertain the most suitable method for ageing *D. exoleta*. Growth marks on the shell surface and acetate peel replicas of sectioned shells were the techniques applied. Two hypotheses were tested: growth parameters present latitudinal variation along the Portuguese coast; growth parameters are influenced by the fishing exploitation. Shell surface rings proved inappropriate for ageing this species, whereas acetate peels provided realistic estimates of the von Bertalanffy growth parameters (K, L_∞ and t_0). A latitudinal gradient in growth rate was detected, with a clear southward increase in the growth coefficient (K) of *D. exoleta* (Faro > Setúbal and Aveiro) indicating that warmer waters in southern Portugal provide optimal conditions for the growth of this species. Fishing exploitation in northern Portugal targets larger individuals and leaves behind a younger population of smaller individuals, decreasing the asymptotic shell length (L_∞) of *D. exoleta* from Aveiro. The overall growth performance was compared among populations of *D. exoleta* and with other venerid species worldwide.

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Introduction

The rayed artemis or mature dosinia (*Dosinia exoleta* Linnaeus, 1758) is distributed from the Norwegian and Baltic Seas, southwards to the Iberian Peninsula, into the Mediterranean, and along the western coast of Africa to Senegal and Gabon (Tebble 1966). This species burrows deeply in sand, mud and gravel bottoms, from the intertidal zone to 70 m depth (Poppe and Goto 1993; Macedo et al. 1999), but can be found up to 150 m depth (Anon 2001). In Portugal, *D. exoleta* is among the target species of the bivalve dredging fleet operating in the northern coast, whereas along the southwestern and southern coasts, it constitutes a by-catch species of the dredge fishery (Gaspar et al. 2007). Fishery exploitation in the northern coast started around 2007 and since then annual landings ranged between a maximum of 37.0 tons in 2007 and a minimum of 9.4 tons in 2010 (DGPA 2012). The latest statistics available on the landings of *D. exoleta* in northern Portugal (Matosinhos wholesale market) reported total landings of 15.3 tons in 2011, corresponding to an overall value for first sale of 15.3 thousand euro (DGPA 2012).

Knowledge on the age and growth of commercially exploited bivalve species is a crucial requirement for the successful management of the fishery (Gaspar et al. 2004). In bivalves, growth rings on the shell surface have been widely used to make inferences about age and growth rate (Deval 2001). Although being the most quick and economic method, in some species it is difficult to discern real seasonal growth rings from false rings caused by gonad development and spawning, diseases, extreme temperatures, storms and

damage during dredging (Gaspar et al. 1995, 2004; Richardson 2001; Keller et al. 2002; Moura et al. 2009). These constraints have been overcome by analysing internal shell microgrowth banding patterns revealed in acetate peel replicas of sectioned shells (Jones et al. 1990; Ramón and Richardson 1992; Richardson 2001). Although being a time-consuming method, internal growth lines visible in acetate peel replicas generally provide a reliable record of the age and growth history of individuals (Anwar et al. 1990). However, some problems in the identification of the annual ring may also occur, especially in long-lived species. In older specimens, the umbonal region is usually eroded, making impossible to identify the first growth rings (Gaspar et al. 2004). In addition, in older individuals growth becomes slower and the later growth rings are deposited very close together at the shell margin, making them hardly discernible (Deval and Oray 1998; Ezgeta-Balić et al. 2011). Furthermore, in some years clearly defined rings may not be formed (Anwar et al. 1990). In some species, age can also be estimated by counting the growth lines visible in acetate peel replicas of the umbonal region of the shell (e.g. Anwar et al. 1990; Ridgway et al. 2011; Peharda et al. 2012).

Information on the age and growth rate of *D. exoleta* is very scarce and limited to studies on population dynamics performed in Norway by Tunberg (1979). Initially, this author attempted to find annually deposited growth marks in the shells, using surface rings and acetate peels, but both ageing techniques were unsuccessful (Tunberg 1979). Later, an in situ experiment with marked individuals was performed, but results were not satisfactory due to disturbance of the studied specimens and to the weakness of the regression analysis (Tunberg 1983a). Once again, both surface rings and acetate peels were analysed; however, it was impossible to establish an acceptable correlation between the number of growth marks and individual age (Tunberg 1983a).

Taking into account the current scarcity of information, this study aimed at improving the knowledge on the age and growth of *D. exoleta* by providing data on shell banding, age and growth rate estimates for three populations from the Portuguese coast (Aveiro in the north, Setúbal in the southwest and Faro in the south). Two techniques (surface rings and acetate peels) were employed and compared in order to ascertain which is the most suitable for ageing this species. This study allowed assessing the occurrence of latitudinal variation in the growth parameters of *D. exoleta* along the Portuguese coast, as well as comparing growth parameters between fishery-exploited (Aveiro) and unexploited (Setúbal and Faro) populations of this species. Finally, the overall growth performance (OGP) was compared among populations of *D. exoleta* and with analogous information available for other venerid species worldwide.

Materials and methods

Samples of *D. exoleta* were collected between May and June 2010 in three areas along the Portuguese coast: Aveiro ($40°59'$–$41°03'$N) in the northern coast, Setúbal ($38°23'$–$38°27'$N) in the southwestern coast and Faro ($36°58'$–$36°59'$N) in the southern coast (Fig. 1). Individuals were caught by the IPMA's RV "Diplodus" operating bivalve dredges on sandy bottoms between 8 and 12 m depth in the southern coast, 8 and 15 m depth in the southwestern coast and between 15 and 30 m depth in the northern. Following the usual fishing procedures, the dredges were towed for 15 min at a constant speed of 2 knots. The dredges used were identical to those operated by the commercial fleet. In brief, the dredge weighs around 40 kg and consists of a rigid iron structure with a toothed lower bar (15 cm tooth length with an angle of $20°$). The catch is retained in a net bag 2.5 m long with diamond mesh size of 25 mm for further details on the dredge design, characteristics and dimensions, see (Gaspar et al. 2003); (Leitão et al. 2009).

In order to assess its influence on the growth of *D. exoleta*, data on seawater temperature along the Portuguese coast were provided by the Hydrographical Institute (IH). For this purpose were gathered data monitored during 2010 by the oceanographic buoys closest to the bivalve collecting sites (buoys of Leixões in the northern coast, Sines in the southwestern coast and Faro in the southern coast). Mean annual temperature was compared between study areas through analysis of variance (ANOVA). If ANOVA assumptions (normality of data and homogeneity of variances) were not met, the nonparametric Kruskal–Wallis test (ANOVA on ranks) was performed. Whenever significant differences were detected by ANOVA or Kruskal–Wallis test, pairwise multiple comparisons were made using Tukey or Dunn's tests, respectively (Zar 1999). Statistical analyses were performed with the software package SigmaStat© (version 3.5) with significance considered for $P < 0.05$.

In the laboratory, a total of 50 individuals from each collecting site were measured for shell length (SL) (maximum distance along the anterior–posterior axis) to the nearest 0.1 mm using a digital calliper. Specimens analysed were within the following SL (ranges Aveiro = 40.4–46.8 mm (42.5 ± 1.7 mm); Setúbal = 41.7–52.0 mm (46.7 ± 3.1 mm); Faro = 36.9–44.3 mm (41.0 ± 2.1 mm)). Subsequently, for estimating age and growth, the rings deposited on the external surface of the shells were counted and measured with the digital calliper. In addition, the internal structure of each shell was analysed using acetate peel replicas of polished and etched sections of resin-embedded valves, following the technique previously adopted with success in other commercially exploited bivalve species from the Portuguese coast (for
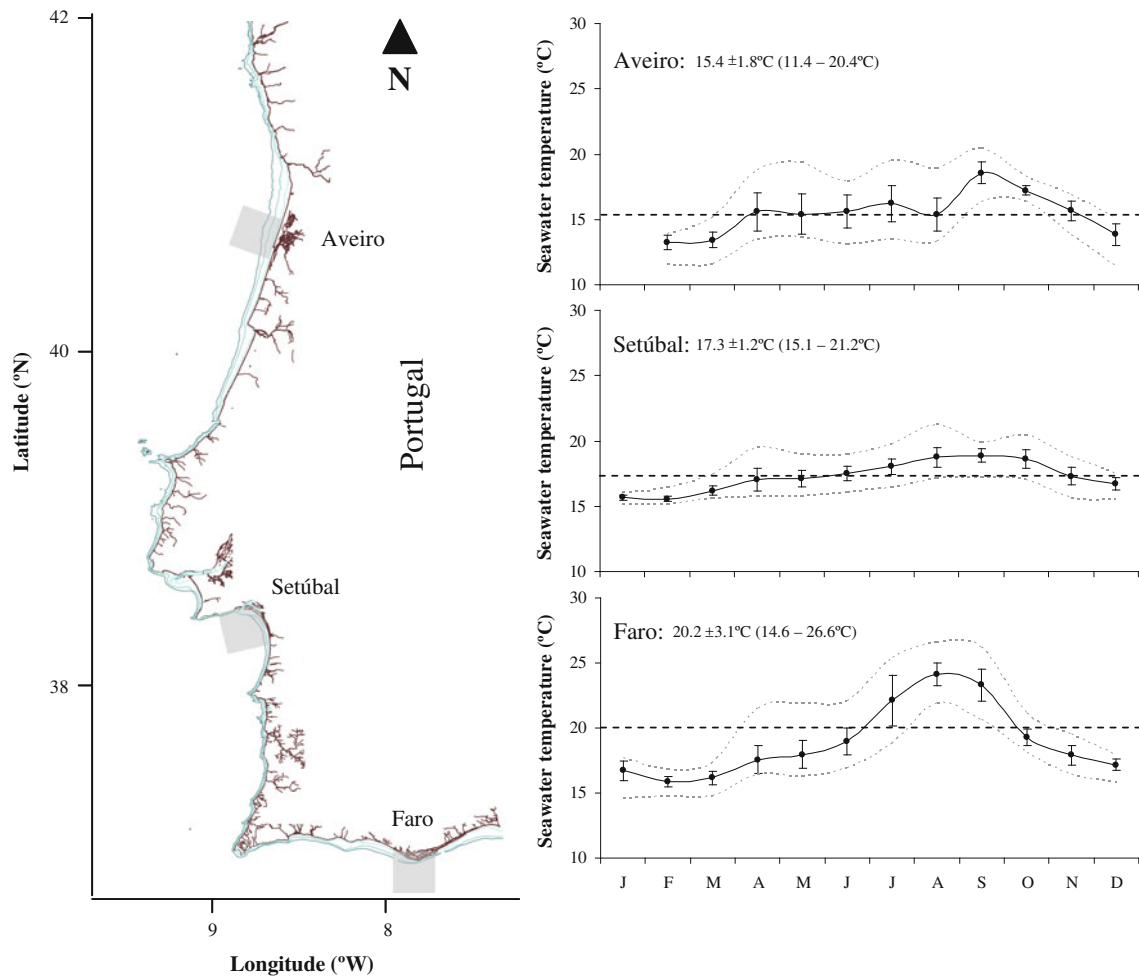
Fig. 1 Geographical location and seawater temperature at the collecting sites for *Dosinia exoleta* along the Portuguese coast (Aveiro, Setúbal and Faro). *Shadow squares* denote the collecting sites. Seawater temperature monitored during 2010 by the oceanographic buoys closest to the collecting sites. *Error bars* represent monthly standard deviation, and *interrupted lines* represent annual mean and range (minimum–maximum) in seawater temperature

further details see Gaspar et al. 1995, 2002, 2004; Moura et al. 2009). Based on previous studies with sympatric bivalve species from the Portuguese coast, such as *Callista chione* (Moura et al. 2009) and *Chamelea gallina* (Gaspar et al. 2004), it was assumed that the growth marks in the shells of *D. exoleta* are annual, being deposited in late autumn–early winter when shell growth is slower. Each growth ring observed in the acetate peel was marked on the glass slide. After digitising the entire acetate peel and respective marks, the distance between the umbo and each growth ring was measured to the nearest 0.1 mm using the digital image analysis software ImageJ (version 1.43). In both techniques (shell surface and acetate peels), counting and measuring of growth rings were made by two independent observers and a second reading was performed whenever numbers did not coincide. Since the measurements in acetate peels are relative to shell height (SH), data

were converted into SL using the following morphometric relationship ($n = 259$, $r = 0.990$; Gaspar et al. 2002):

$$\mathrm{Log\,SH} = -0.040 + 1.012\,\mathrm{Log\,SL}$$

Von Bertalanffy growth functions (VBGF) were fitted separately to the age–length data obtained using the two ageing methods (shell surface rings and internal growth marks). An iterative curve fitting procedure employing nonlinear least-squares regression (Gauss–Newton method) provides estimates of the growth coefficient (K), asymptotic SL (L_∞) and theoretical age at SL (zero (t_0)), through the following equation (von Bertalanffy 1938):

$$L_t = L_\infty\left[1 - e^{-K(t-t_0)}\right]$$

Linear methods commonly used in the statistical comparison of growth data (ANCOVA or ANOVA)

cannot be employed on the VBGF because of its nonlinear formulation and high degree of correlation between its three parameters (K, L_∞ and t_0) (Chen et al. 1992). Comparisons of VBGF can be performed using two general approaches, either by testing individual parameters or by using likelihood ratio statistics. In the present case, *D. exoleta* growth equations were compared between populations (Aveiro, Setúbal and Faro) using likelihood ratio tests (Kimura 1980; Cerrato 1990). This method allows testing several hypotheses to compare two growth equations, by analysing each growth parameter separately or all growth parameters simultaneously. Fitting and comparison of VBGF were performed using the packages "nlstools" (Baty and Delignette-Muller 2011), "car" (Fox and Weisberg 2011) and "fishmethods" (Nelson 2011) of the free software R (version 2.14.1) (R Development Core Team 2011).

Individual growth is a nonlinear process that must be described by multiparameter nonlinear models (such as the VBGF), making it difficult to compare growth among different *taxa* in a definite and statistically proper way (Brey 1999). To overcome this difficulty, several growth performance indices have been developed. In the present study, OGP (P) (Pauly 1979) was employed to compare the growth parameters estimated for *D. exoleta* in the present study with those available in the literature for other venerid species, using the following equation:

$$P = \text{Log}(K \times L_\infty^3)$$

Results

Mean annual seawater temperature (Fig. 1) was significantly different ($H = 4292.159$, $P < 0.001$) between collecting sites: Aveiro $= 15.4 \pm 1.8$ °C (11.4–20.4 °C), Setúbal $= 17.3 \pm 1.2$ °C (15.1–21.2 °C) and Faro $= 20.2 \pm 3.1$ °C (14.6–26.6 °C). There was a remarkable thermal range between the northernmost site (minimum of 11.4 °C in December 2010 in Aveiro) and the southernmost site (maximum of 26.6 °C in August 2010 in Faro). As expected, seawater temperature displayed a clear northward decreasing trend: Aveiro < Setúbal ($Q = 30.519$, $P < 0.05$) and Setúbal < Faro ($Q = 31.826$, $P < 0.05$).

Shell surface rings and acetate peel replicas of *D. exoleta* shell sections are presented in Fig. 2. Observation of the outer prismatic layer revealed distinct growth patterns deposited parallel to the ventral edge of the shell, but defined lines were not found in the umbonal region. The growth marks formed a growth ring in the outer shell surface that was associated with a cleft, and occasionally, two clefts were associated with an annual growth ring (Fig. 2a). In the acetate peels, the gradual decrease in the growth increment zone was the key to distinguish annual growth rings from false rings (caused by stress or shell

damage). The former were characterised by the progressive narrowing of growth bands (Fig. 2b), whereas the latter were characterised by the sudden interruption of the natural growth pattern. In false rings, it is also possible to observe a cleft in the shell surface, but the acetate peel does not display narrowing in the microgrowth increments (Fig. 2c).

The mean length-at-age and respective VBGF of *D. exoleta* populations from Aveiro, Setúbal and Faro, estimated using both ageing techniques (surface rings and acetate peels), are compiled in Table 1. The VBG parameters obtained from surface rings (Fig. 2d) displayed unrealistically high asymptotic SL's (Aveiro: $L_\infty = 76.6$ mm; Setúbal: $L_\infty = 65.8$ mm; Faro: $L_\infty = 53.3$ mm), and therefore, this ageing method was considered inappropriate for estimating *D. exoleta* age and growth. The comparison between shell surface rings and microgrowth patterns revealed by the acetate peel replica of the same individual (Fig. 2a, d) supports this conclusion. In contrast, the VBG parameters (K, L_∞ and t_0) estimated using the acetate peels were fairly realistic (Table 1). Accordingly, VBGF based on growth marks revealed in the acetate peels of the three populations of *D. exoleta* from the Portuguese coast (Aveiro, Setúbal and Faro) are presented in Fig. 3.

The likelihood ratio tests for comparison of VBG parameters between populations of *D. exoleta* are compiled in Table 2. When all VBG parameters (K, L_∞ and t_0) were analysed simultaneously (H_4:VBGF), all growth curves displayed highly significant differences ($P < 0.001$) between the populations from Aveiro, Setúbal and Faro. When each VBG parameter was analysed separately, it was possible to determine which parameter (K, L_∞ or t_0) was significantly different among populations. The growth coefficient (H_1: K) was significantly higher in *D. exoleta* from Faro ($K = 0.50$ year^{-1}) than in the populations from Aveiro ($K = 0.28$ year^{-1}) and Setúbal ($K = 0.30$ year^{-1}). The asymptotic SL (H_2:L_∞) was slightly higher in *D. exoleta* from Setúbal ($L_\infty = 47.1$ mm), although not statistically different from those in the populations from Faro ($L_\infty = 42.9$ mm) and Aveiro ($L_\infty = 43.9$ mm). Finally, the theoretical age at SL (zero (H_3:t_0), considered the VBG parameter with lower biological significance, only displayed significant differences between the populations from Faro ($t_0 = -0.07$ years) and Aveiro ($t_0 = 0.27$ years) (Table 2). Overall, growth rates of *D. exoleta* presented a latitudinal gradient along the Portuguese coast and were directly related to mean annual seawater temperature at the collecting sites. Indeed, the growth rate was highest in the southernmost and warmest site (Faro: $K = 0.50$ year^{-1}, temperature $= 20.2$ °C) and lowest in the northernmost and coldest site (Aveiro: $K = 0.28$ year^{-1}, temperature $= 15.4$ °C), with the transitional population at an intermediate position (Setúbal: $K = 0.30$ year^{-1}, temperature $= 17.3$ °C).
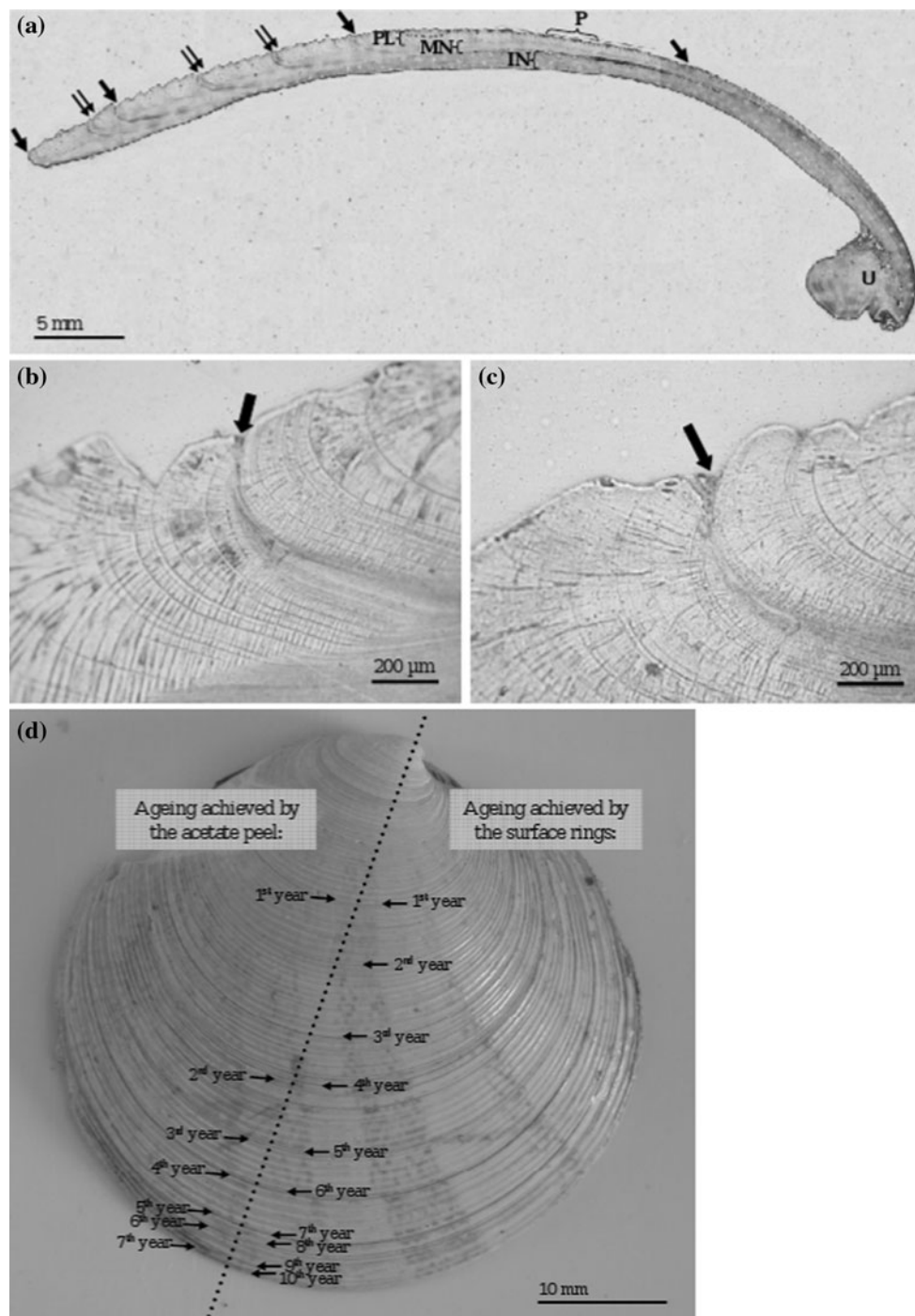
Fig. 2 Acetate peel replicas and surface growth rings in the shell of *Dosinia exoleta*: **a** Acetate peel of sectioned valve illustrating the sequential deposition of growth marks during ontogeny (from right to left). Annual growth rings are associated with one (*single arrow*) or two (*double arrows*) clefts on the shell surface. **b** Annual growth mark with the formation of one cleft (*arrow*), being possible to observe a slow-growth band where microgrowth increments become narrow. **c** False growth ring (*arrow*) without narrowing of microgrowth increments. **d** Comparison between growth rings observed on the shell surface and growth marks revealed by the acetate peel replica of the same shell (**a**). *PL* outer prismatic layer, *MN* middle nacreous layer, *IN* inner nacreous layer, *P* periostracum, *U* umbo

Two VBG parameters (K and L_∞) were applied to calculate the OGP of *D. exoleta* along the Portuguese coast. The OGP values obtained for the three studied populations were $P = 4.374$ in Aveiro, $P = 4.496$ in Setúbal and $P = 4.597$ in Faro. The VBG parameters and corresponding OGP values for *D. exoleta* and other venerid bivalve species are compiled in Table 3 and compared among different *taxa* in the auximetric grid presented in Fig. 4.

Table 1 Mean shell length-at-age (SL) and von Bertalanffy growth function (VBGF) of *D. exoleta* from three locations along the Portuguese coast (Aveiro, Setúbal and Faro) obtained using two ageing techniques (shell surface rings and acetate peels)

Location	Age (years)	Surface rings		Acetate peels	
		Number of observations	Mean SL (mm)	Number of observations	Mean SL (mm)
Aveiro (N)	1	50	11.2 ± 1.5 (7.5–13.5)	50	12.7 ± 1.6 (10.7–15.4)
	2	50	16.4 ± 1.0 (14.3–18.0)	50	21.8 ± 1.3 (19.5–23.6)
	3	50	20.7 ± 1.4 (18.1–23.4)	50	26.1 ± 0.9 (24.8–28.1)
	4	50	24.8 ± 1.0 (22.8–26.5)	50	30.7 ± 1.2 (28.7–32.7)
	5	50	28.3 ± 1.2 (27.0–30.7)	50	33.5 ± 1.3 (31.5–36.6)
	6	50	33.3 ± 1.0 (31.2–34.9)	50	36.2 ± 0.7 (34.7–37.1)
	7	50	36.6 ± 0.8 (35.2–38.0)	43	38.5 ± 0.9 (36.8–40.2)
	8	48	39.4 ± 0.8 (37.7–40.8)	18	40.1 ± 1.2 (38.1–41.7)
	9	21	41.3 ± 1.0 (40.0–43.0)		
	10	5	43.7 ± 1.3 (42.8–44.6)		
	VBGF		$L_t = 76.6\,[(1-e^{-0.08(t+0.97)}]$		$L_t = 43.9\,[(1-e^{-0.28(t+0.27)}]$
Setubal (SW)	1	50	9.5 ± 1.0 (8.1–11.4)	50	13.2 ± 1.1 (11.5–15.6)
	2	50	14.4 ± 1.4 (12.1-17.1)	50	19.8 ± 2.8 (14.3–23.5)
	3	50	19.5 ± 1.4 (17.4–22.1)	50	27.6 ± 2.7 (23.0–34.1)
	4	50	23.9 ± 1.8 (20.2–26.0)	50	33.6 ± 3.1 (28.3–40.9)
	5	50	29.1 ± 1.5 (27.2–31.6)	50	37.1 ± 3.6 (31.1–45.4)
	6	50	33.3 ± 1.4 (31.0–35.1)	46	39.2 ± 2.8 (34.1–44.3)
	7	50	36.4 ± 1.3 (34.2–37.9)	29	40.1 ± 2.7 (36.0–43.0)
	8	47	38.9 ± 1.4 (36.4–41.2)	25	42.3 ± 3.1 (37.5–45.8)
	9	43	41.4 ± 1.2 (38.1–43.0)	11	44.4 ± 4.9 (38.8–47.4)
	10	30	43.9 ± 0.5 (43.1–44.5)		
	11	13	46.1 ± 1.2 (44.6–47.3)		
	VBGF		$L_t = 65.8\,[(1-e^{-0.11(t+0.37)}]$		$L_t = 47.1\,[(1-e^{-0.30(t+0.2)}]$
Faro (S)	1	50	13.8 ± 1.8 (10.5–17.7)	50	16.0 ± 2.4 (12.2–19.3)
	2	50	20.4 ± 2.9 (15.6–28.0)	50	26.6 ± 2.6 (22.4–29.9)
	3	50	27.9 ± 3.5 (23.6–34.9)	50	33.1 ± 1.7 (30.0–35.8)
	4	50	34.4 ± 2.9 (29.8–38.9)	45	36.9 ± 1.4 (35.0–39.0)
	5	40	37.9 ± 2.6 (33.7–42.0)	17	39.2 ± 0.9 (38.1–40.9)
	6	27	39.5 ± 3.0 (35.1–43.2)	1	41.2 ± 0.0 (41.2–41.2)
	VBGF		$L_t = 53.3\,[(1-e^{-0.23(t+0.23)}]$		$L_t = 42.9\,[(1-e^{-0.50(t-0.07)}]$

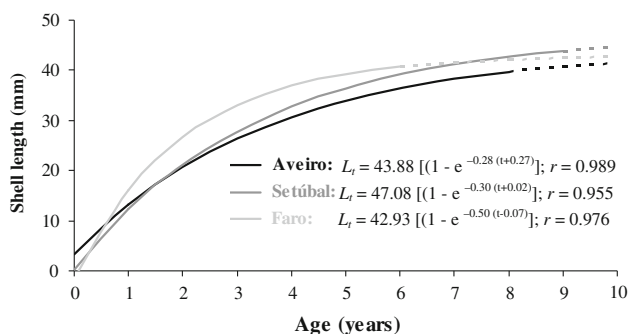Data presented as mean ± SD and size range

Fig. 3 Von Bertalanffy growth functions (VBGF) for the three populations of *D. exoleta* from the Portuguese coast (Aveiro, Setúbal and Faro), based on growth marks revealed in the acetate peels

Chart legend:
Aveiro: $L_t = 43.88\,[(1 - e^{-0.28\,(t+0.27)}]$; $r = 0.989$
Setúbal: $L_t = 47.08\,[(1 - e^{-0.30\,(t+0.02)}]$; $r = 0.955$
Faro: $L_t = 42.93\,[(1 - e^{-0.50\,(t-0.07)}]$; $r = 0.976$

Discussion

Age and growth of *D. exoleta* were more accurately estimated based on internal growth marks revealed in acetate peel replicas of sectioned shells than directly from surface growth rings. Although quick and economic, the examination of surface rings proved to be inadequate and unreliable for ageing *D. exoleta*. The unrealistic VBG parameters obtained from surface rings were already expected, because the growth rate is slower in older individuals making it difficult to distinguish and measure surface rings closer to the edge of the shell (Deval 2001; Gaspar et al. 2004; Moura et al. 2009). Differences

Table 2 Likelihood ratio tests for comparing the von Bertalanffy growth parameters of three populations of *Dosinia exoleta* from the Portuguese coast (Aveiro, Setúbal and Faro)

Locations	H_1:K	H_2:L_∞	H_3:t_0	H_4:VBGF
Aveiro versus. Setúbal	$\chi^2 = 0.12$	$\chi^2 = 2.11$	$\chi^2 = 1.99$	$\chi^2 = 39.77$
	$P = 0.729$ [ns]	$P = 0.146$ [ns]	$P = 0.158$ [ns]	$P < 0.001$
Aveiro versus. Faro	$\chi^2 = 18.97$	$\chi^2 = 0.37$	$\chi^2 = 7.05$	$\chi^2 = 198.91$
	$P < 0.001$	$P = 0.543$ [ns]	$P = 0.008$**	$P < 0.001$
Setúbal versus. Faro	$\chi^2 = 6.52$	$\chi^2 = 2.47$	$\chi^2 = 0.23$	$\chi^2 = 68.90$
	$P = 0.011$*	$P = 0.116$ [ns]	$P = 0.632$ [ns]	$P < 0.001$

ns not significant

* $P < 0.05$; ** $P < 0.01$

between surface and internal growth rings were also observed in *Macoma balthica*. In this case, the number of annual lines obtained from external rings was always higher compared to the internal rings determined from the acetate peel replicas (Cardoso et al. 2012).

Examination of acetate peel replicas of *D. exoleta* allowed identifying different phases of shell growth, namely narrow dark lines (slow growth) separated by wider microgrowth increments (rapid growth). Other bivalve species from the Portuguese coast showed the same growth pattern, which has been associated with annual shell growth, including *Donax trunculus* (Gaspar et al. 1999), *C. gallina* (Gaspar et al. 2004) and *C. chione* (Moura et al. 2009). Periods of shell slow growth might be caused by low metabolic rates related to low seawater temperature (Lomovasky et al. 2002), lack of food (Arneri et al. 1998) and/or by diversion of metabolic products into gamete production (Lomovasky et al. 2002). Narrow bands corresponding to shell slow growth are often followed by a reduction in the peripheral layer of the shell, thus forming a cleft (Leontarakis and Richardson 2005). Indeed, in *D. exoleta* the narrowing of microgrowth bands also appeared to always match with a cleft on the shell surface. Moreover, occasionally two narrow bands were deposited very close together (appearing like a double band) and were reflected by the occurrence of two clefts on the shell surface. This phenomenon has also been detected in *C. gallina* by Ramón and Richardson (1992) and Gaspar et al. (2004). The occurrence of double clefts on the shell surface further strengthens the acetate peel technique as the most adequate and accurate method for ageing *D. exoleta*. The examination of acetate peel replicas of sectioned shells also allowed detecting several clefts associated with a sudden interruption of the natural growth pattern and that were interpreted as false rings. On the shell surface, false rings induced by gonad development and spawning, diseases, extreme temperatures, storms, predation or dredging are in most cases indistinguishable from seasonal growth rings (Gaspar et al. 2004). In some bivalve species, age can be estimated by counting the number of growth rings deposited in the umbonal region of the shell (e.g. Anwar et al. 1990; Ridgway et al. 2011; Cardoso et al. 2012; Peharda et al. 2012). However, this was unfeasible with *D. exoleta*, since in most acetate peels the growth rings in the umbonal region were absent or very difficult to discern. Similarly, in *C. gallina*, the growth bands in the umbonal region were only observed in a limited number of individuals, making this method inappropriate for ageing this species (Dalgiç et al. 2010).

The VBGF of the population of *D. exoleta* from Setúbal displayed the highest shell asymptotic length (L_∞), followed by the population from Aveiro. The population from Faro presented the lowest L_∞, but in contrast, showed the highest growth rate (K). The populations from Setúbal and Aveiro showed lower and similar growth rates (K). These different growth features between populations of *D. exoleta* are probably a consequence of the fishing exploitation and certainly also reflect different environmental conditions between the collecting sites, namely in terms of seawater temperature.

Along the Portuguese coast, only the population of *D. exoleta* from Aveiro is exploited, whereas in Setúbal and Faro, it constitutes a by-catch species of the dredge fishery (sorted on-board and discarded alive in the fishing beds). Therefore, the fishery targeting *D. exoleta* in Aveiro certainly causes a decline in the proportion of larger individuals (decreasing L_∞). Studies on the fishing impact on bivalve growth were relatively scarce but have increased recently. For instance, fishery exploitation appears to have decreased L_∞ and L_{max} of *Anadara tuberculosa* from Bahía Magdalena, Mexico (Félix-Pico et al. 2009). Similarly, the decline in the abundance and sizes of *A. tuberculosa* over the years in Costa Rica suggest that the fishing pressure on this species is too high (Campos et al. 1990; Silva-Benavides and Bonilla-Carrion 2001).

The rayed artemis (or mature dosinia) is distributed along a widespread latitudinal range, from northern European coasts (probable northern limit in Finnmark)

Table 3 Comparison of the von Bertalanffy growth parameters and corresponding overall growth performance between *Dosinia exoleta* and other venerid species worldwide

Species	K (year^{-1})	L_∞ (mm)	P	Ageing method	Study area	Reference
D. exoleta (×, 1)	0.28	43.88	4.374	AP	Aveiro, Portugal (Atlantic Ocean)	Present study
D. exoleta (×, 2)	0.30	47.08	4.496	AP	Setúbal, Portugal (Atlantic Ocean)	Present study
D. exoleta (×, 3)	0.50	42.93	4.597	AP	Faro, Portugal (Atlantic Ocean)	Present study
D. exoleta (×, 4)	0.36	51.3	4.687	MR	Eggholmane, Norway (Atlantic Ocean)	Tunberg (1983a)
D. lupinus (×, 5)	0.36	36.0	4.225	SR	Eggholmane, Norway (Atlantic Ocean)	Tunberg (1983b)
D. nipponica (×, 6)	0.159	78.95	4.893	AP	Wakkanai Port, Japan (Pacific Ocean)	Tanabe and Oba (1988)
D. nipponica (×, 7)	0.203	74.46	4.923	AP	Hakodate Bay, Japan (Pacific Ocean)	Tanabe and Oba (1988)
D. nipponica (×, 8)	0.262	61.06	4.776	AP	Tokyo Bay, Japan (Pacific Ocean)	Tanabe and Oba (1988)
D. nipponica (×, 9)	0.295	55.46	4.702	AP	Seto Inland Sea, Japan (Pacific Ocean)	Tanabe and Oba (1988)
D. nipponica (×, 10)	0.403	76.44	5.255	AP	Ariake Bay, Japan (Pacific Ocean)	Tanabe and Oba (1988)
A. antiqua (●, 11)	0.183	80.00	4.972	MR	Chiloé, Chile (Pacific Ocean)	Clasing et al. (1994)
A. umbonella (○, 12)	0.28	58.0	4.737	LF	Park-e-Dolat, Iran (Persian Gulf)	Saeedi et al. (2010)
A. umbonella (○, 13)	0.29	62.0	4.840	LF	Park-e-Qadir, Iran (Persian Gulf)	Saeedi et al. (2010)
C. brevisiphonata (■, 14)	0.202	101.8	5.329	SR, CS	Ussuri Bay, Russia (Sea of Japan)	Selin and Selina (1988)
C. brevisiphonata (■, 15)	0.177	102.2	5.276	SR, CS	Putyatin Islands, Russia (Sea of Japan)	Selin and Selina (1988)
C. brevisiphonata (■, 16)	0.147	113.4	5.331	SR, CS	Vostok Bay, Russia (Sea of Japan)	Selin and Selina (1988)
C. chione (■, 17)	0.24	93.0	5.286	SR, TS	Gulf of Euboikos, Greece (Aegean Sea)	Metaxatos (2004)
C. chione (■, 18)	0.24	62.7	4.772	AP	Thassos Island, Greece (Thracian Sea)	Leontarakis and Richardson (2005)
C. chione (■, 19)	0.26	57.8	4.701	AP	Thassos Island, Greece (Thracian Sea)	Leontarakis and Richardson (2005)
C. chione (■, 20)	0.15	98.1	5.151	AP	Arrábida, Portugal (Atlantic Sea)	Moura et al. (2009)
C. chione (■, 21)	0.18	91.1	5.134	SR	Arrábida, Portugal (Atlantic Sea)	Moura et al. (2009)
C. chione (■, 22)	0.25	72.4	4.977	AP	Rab Island, Croatia (Adriatic Sea)	Ezgeta-Balić et al. (2011)
C. chione (■, 23)	0.15	74.5	4.793	AP	Pag Bay, Croatia (Adriatic Sea)	Ezgeta-Balić et al. (2011)
C. chione (■, 24)	0.11	82.8	4.795	AP	Kaštela Bay, Croatia (Adriatic Sea)	Ezgeta-Balić et al. (2011)
C. chione (■, 25)	0.34	79.3	5.229	AP	Cetina Estuary, Croatia (Adriatic Sea)	Ezgeta-Balić et al. (2011)
C. gallina (□, 26)	0.35	36.12	4.217	AP	Valencia, Spain (Mediterranean Sea)	Ramón and Richardson (1992)
C. gallina (□, 27)	0.40	40.05	4.410	LF	Valencia, Spain (Mediterranean Sea)	Ramón (1993)
C. gallina (□, 28)	0.21	52.20	4.475	TS	Ancona, Italy (Adriatic Sea)	Polenta (1993)
C. gallina (□, 29)	0.48	41.60	4.539	TS	Ancona, Italy (Adriatic Sea)	Arneri et al. (1995)
C. gallina (□, 30)	0.52	39.50	4.506	TS	Neretva Estuary, Croatia (Adriatic Sea)	Arneri et al. (1997)
C. gallina (□, 31)	0.429	34.17	4.233	SR	Turkey (Northern Marmara Sea)	Deval and Oray (1998)
C. gallina (□, 32)	0.37	33.46	4.142	TS	Turkey (Northern Marmara Sea)	Deval (2001)
C. gallina (□, 33)	0.609	27.25	4.091	TS	Russia (Northern Black Sea)	Boltachova and Mazlumyan (2001)
C. gallina (□, 34)	0.47	38.95	4.444	AP	Faro, Portugal (Atlantic Ocean)	Gaspar et al. (2004)
C. gallina (□, 35)	0.32	42.15	4.380	LF	Faro, Portugal (Atlantic Ocean)	Gaspar et al. (2004)
C. gallina (□, 36)	0.71	37.55	4.575	SR	Faro, Portugal (Atlantic Ocean)	Gaspar et al. (2004)
C. gallina (□, 37)	0.16	26.00	3.449	TS	Yakakent, Turkey (Black Sea)	Dalgiç et al. (2010)
C. gallina (□, 38)	0.21	28.88	3.704	TS	Inceburun, Turkey (Black Sea)	Dalgiç et al. (2010)
C. gallina (□, 39)	0.22	26.60	3.617	TS	Cide, Turkey (Black Sea)	Dalgiç et al. (2010)
C. striatula (□, 40)	0.23	32.90	3.913	SR	Millport, Scotland (Atlantic Ocean)	Ursin (1963)
C. striatula (□, 41)	0.25	38.75	4.163	SR	Bristol Channel, UK (Atlantic Ocean)	Warwick et al. (1978)

Table 3 continued

Species	K (year^{-1})	L_∞ (mm)	P	Ageing method	Study area	Reference
E. exalbida (◆, 42)	0.180	73.98	4.863	AP, IR	Beagle Channel, Argentina (Atlantic Ocean)	Lomovasky et al. (2002)
M. mercenaria (◇, 43)	0.182	94.31	5.184	SR	Southampton, UK (Atlantic Ocean)	Hibbert (1977)
M. mercenaria (◇, 44)	0.312	71.04	5.049	AP	Georgia, USA (Atlantic Ocean)	Walker and Tenore (1984)
M. mercenaria (◇, 45)	0.260	89.40	5.269	AP	Georgia, USA (Atlantic Ocean)	Walker and Tenore (1984)
M. mercenaria (◇, 46)	0.340	65.90	4.988	AP	Georgia, USA (Atlantic Ocean)	Walker and Tenore (1984)
M. mercenaria (◇, 47)	0.21	73.32	4.918	CS	Narragansett Bay, USA (Atlantic Ocean)	Jones et al. (1989)
Tawera gayi (+, 48)	0.288	28.03	3.802	AP, MR	Beagle Channel, Argentina (Atlantic Ocean)	Lomovasky et al. (2005)
V. corrugata (▲, 49)	0.31	49.98	4.588	SR	Mira Estuary, Portugal (Atlantic Ocean)	Guerreiro and Rafael (1995)
V. corrugata (▲, 50)	0.43	45.5	4.608	SR	Ria de Aveiro, Portugal (Atlantic Ocean)	Maia et al. (2006)
V. corrugata (▲, 51)	0.29	54.3	4.667	AP	Ria de Aveiro, Portugal (Atlantic Ocean)	Maia et al. (2006)
V. verrucosa (Δ, 52)	0.253	44.9	4.360	CS	Bari, Italy (Adriatic Sea)	Arneri et al. (1998)
V. verrucosa (Δ, 53)	0.352	54.1	4.746	CS	Gulf of Manfredonia, Italy (Adriatic Sea)	Arneri et al. (1998)
V. verrucosa (Δ, 54)	0.298	54.2	4.676	CS	Gulf of Maliakos, Greece (Aegean Sea)	Arneri et al. (1998)
V. verrucosa (Δ, 55)	0.324	52.1	4.661	CS	Bay of Thessaloniki, Greece (Aegean Sea)	Arneri et al. (1998)
V. verrucosa (Δ, 56)	0.360	43.4	4.469	CS	Alexandroupolis, Greece (Aegean Sea)	Arneri et al. (1998)

K growth coefficient, L_∞ asymptotic shell length, P overall growth performance, *AP* acetate peels, *MR* mark-recapture, *SR* surface rings, *LF* length-frequency, *CS* cross-sections, *TS* thin sections, *IR* isotope ratios

(Tunberg 1984) to western African coasts, not being found further south than Congo (Fischer-Piette 1968). This implies that Portugal is fairly within the middle of the latitudinal distribution of this species in the Atlantic Ocean. It is well known that physiological processes are influenced by the environmental conditions, namely temperature and food availability (e.g. Clarke 1987; Sprung 1991; Masilamoni et al. 2002), parameters that usually show an inverse trend with latitude (Barry and Carleton 2001; Jansen et al. 2007). With increasing latitude, it has been observed an increasing trend in reproductive effort, egg and larval size, whereas an opposite trend has been shown for age at first maturity, fecundity, reproductive output, growth rate and mortality (e.g. Clarke 1987; Contreras and Jaramillo 2003; Thatje et al. 2004; Ward and Hirst 2007; Petracco et al. 2010).

In the present study, it was also detected a latitudinal gradient in the growth of the three populations of *D. exoleta*, with growth rates (K) showing a southward increase (Faro > Setúbal ≈ Aveiro). Latitudinal trends in the physiological performance of marine invertebrates are commonly observed (Santos et al. 2011). Latitude has no environmental meaning by itself, being a proxy of annual solar energy input that translates mainly into average annual seawater temperature (Heilmayer et al. 2003), but also into primary production and related parameters. On a geographical scale, differences in growth rate of bivalves have been frequently associated with latitudinal gradients in seawater temperature. Examples of this phenomenon include *C. chione* (Hall et al. 1974), *M. balthica* (Beukema and Meehan 1985), *Mercenaria campechiensis* and *Mercenaria mercenaria* (Heck et al. 2002), *Mya arenaria* (Appeldoorn 1995), *Placopecten magellanicus* (MacDonald and Thompson 1988), *Tivela stultorum* (Hall et al. 1974) and *Zygochlamys patagonica* (Gutiérrez and Defeo 2003).

In the present study along the Portuguese coast, higher seawater temperatures were registered in the south, which may explain the higher growth rate displayed by the population of *D. exoleta* from Faro compared to the populations from the other two collecting sites. However, the abundance of this species in Faro is very low compared to Setúbal and Aveiro (Fig. 5) (Gaspar et al. 2010a, b, c). This north–south decreasing trend also supports that colder waters constitute a more suitable environment for this species. Indeed, although showing wide thermal range, the optimal environmental conditions for this eurythermal species appear to be shifted northwards. Tunberg (1983a) estimated a shell asymptotic length (L_∞) of 51.3 mm for *D. exoleta* from Eggholmen (western Norway), but this value was considered somewhat small compared to the maximum SL (reached in that area, where this species is abundant with a density of 9.9 ± 2.9 ind m^{-2} (Tunberg 1983a). Moreover, higher abundances were observed in Raunefjorden (western Norway), where *D. exoleta* reached an overall density of 17.1 ind m^{-2} (Tunberg 1984). The higher shell asymptotic length in northern (Norway:
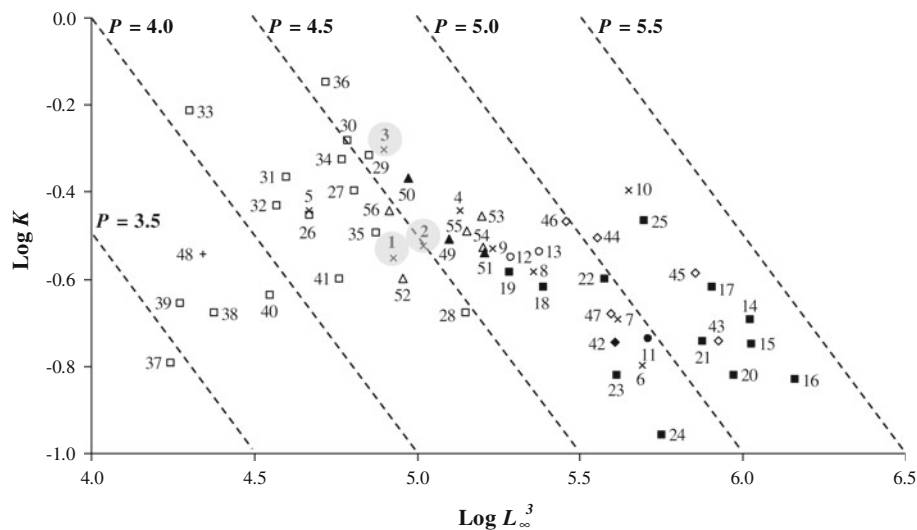
Fig. 4 Auximetric grid for comparison of OGP between *D. exoleta* and other venerid species worldwide. *Diagonal lines* denote OGP isolines, *symbols* and *numbers* refer to the species listed in Table 3 (multiplication symbol, *Dosinia* spp.; filled circle symbol, *Ameghinomya* sp.; open circle symbol, *Amiantis* sp.; filled square symbol, *Callista* spp.; open square symbol, *Chamelea* spp.; filled diamond symbol, *Eurhomalea* sp.; open diamond symbol, *Mercenaria* sp.; plus symbol, *Tawera* sp., filled triangle symbol, *Venerupis* sp.; open triangle symbol, *Venus* sp.). *Shadow circles* denote *D. exoleta* populations from the Portuguese coast (Aveiro, Setúbal and Faro)

$L_\infty = 51.3$ mm) than in southern populations (Portugal: $L_\infty = 42.9$–47.1 mm), further confirms that although this species grows faster in warmer waters, higher latitudes provide the most favourable environmental conditions for the development of population of *D. exoleta*.

Although with a few exceptions, the general consensus is that bivalves from low latitudes grow faster, attain a smaller maximum size and have a shorter lifespan than conspecifics from high latitudes (Newell 1964). In the present study, the calculation of the OGP allowed comparing growth among populations of *D. exoleta* and with other venerid bivalves. The values of OGP obtained for *D. exoleta* along the Portuguese coast corroborate the above-mentioned latitudinal gradient in growth and the influence of mean annual seawater temperature at the collecting sites Faro > Setúbal > Aveiro. In terms of intraspecific comparison, the only data available in the literature on the growth of *D. exoleta* lead to slightly higher OGP in Norway ($P = 4.687$) compared to the populations along the Portuguese coast ($P = 4.374$ in Aveiro to $P = 4.597$ in Faro). In general, worldwide comparisons highlight that OGP increases with decreasing latitude, in a general trend that is correlated with average annual seawater temperature (Heilmayer et al. 2003). However, this trend was not observed in the case of *D. exoleta* since a higher OGP was determined for Norway compared to that obtained for the Portuguese populations. This may be a consequence of the method used by Tunberg (1983a) to estimate growth. This author applied the mark-recapture method which may lead to bias in growth estimates whenever the data set is not representative of the full size range of the population

(Haddon 2001). The growth parameters estimated by Tunberg (1983a) were mainly based on large individuals, therefore are probably biased, which may have resulted in a higher OGP for the Norwegian population of *D. exoleta*.

Within the genus, *D. exoleta* both from Portugal and Norway has a slightly higher OGP than the sympatric *Dosinia lupinus* from western Norway ($P = 4.225$) (Tunberg 1983b), but lower than *D. nipponica* ($4.702 < P < 5.255$) from the Pacific Ocean (Tanabe and Oba 1988). In terms of inter-specific comparison, the auximetric grid revealed that *D. exoleta* has an average growth performance (within the family Veneridae). Indeed, *D. exoleta* is within the range of OGP values obtained for *Amiantis umbonella*, *Ameghinomya antiqua*, *Eurhomalea exalbida*, *Venerupis corrugata* and *Venus verrucosa* (mainly between $4.5 < P < 5.0$). In most cases, the sympatric *C. gallina* and *Chamelea striatula* exhibited lower OGP (mostly $P < 4.5$), whereas *Callista brevisiphonata* and *C. chione* (usually $P > 5.0$) and *M. mercenaria* (mostly $P > 5.0$) displayed the highest growth performances within the family Veneridae (Fig. 4).

The present study was the first to successfully estimate age and growth of *D. exoleta* by using the acetate peel technique, thus making available realistic growth parameters (K and L_∞) for this species. Furthermore, the present study showed some differences between the growth parameters of the three populations. Results suggest that growth is influenced by geographical distribution and probably also by fishing exploitation. In general, the latitudinal gradient in the growth features of the three populations revealed that, besides growing faster in warm
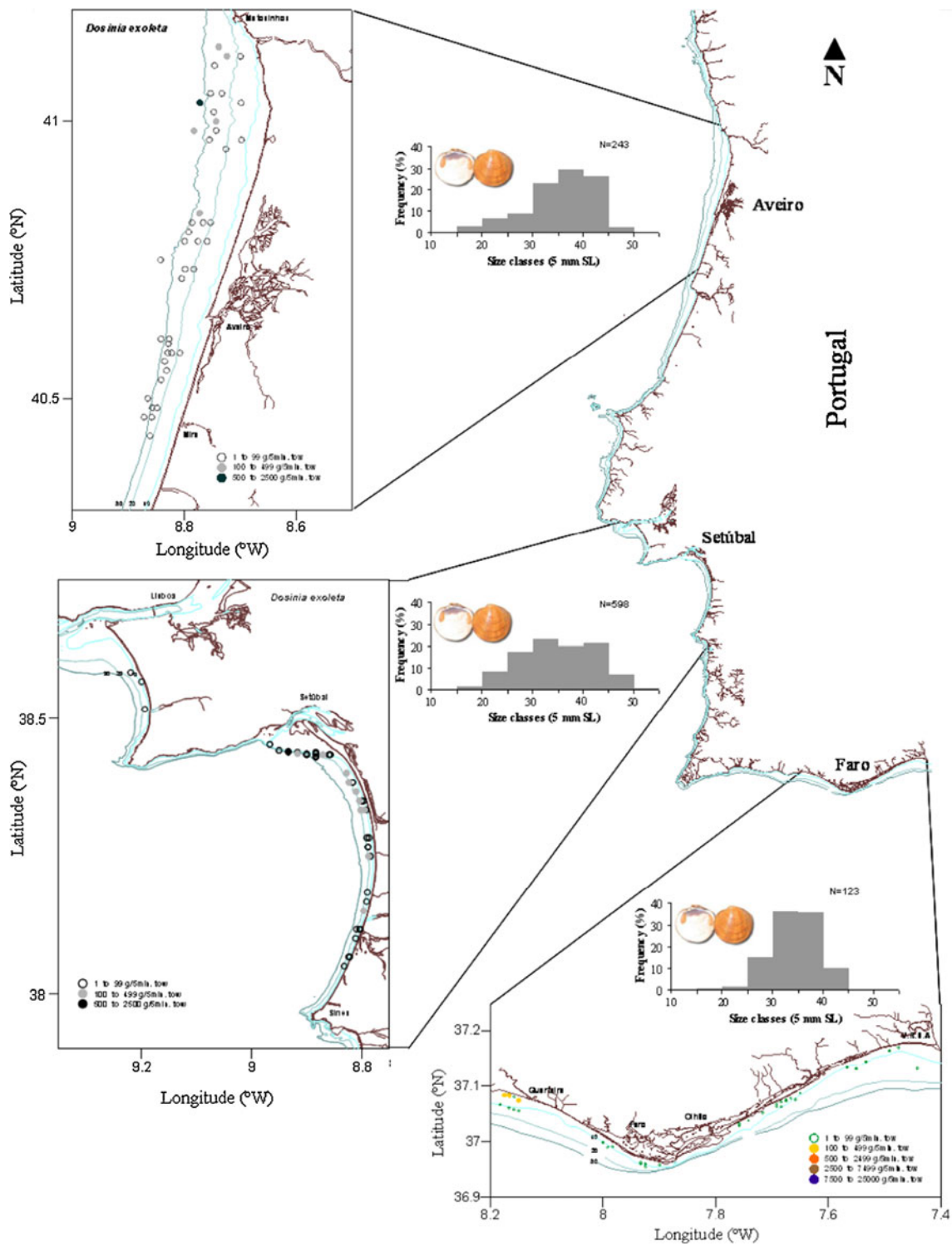
Fig. 5 Spatial distribution, abundance (g 5 min tow^{-1}) and size frequency distribution (grouped into 5 mm shell length classes) of *Dosinia exoleta* from Aveiro, Setúbal and Faro during the fishing surveys performed by IPIMAR along the Portuguese coast in 2010

waters, colder environments are beneficial for this species. It also seems that fishing exploitation affects the asymptotic SL of the populations of *D. exoleta* (decreasing L_∞),

but further investigation should be performed to confirm this hypothesis. Knowledge on the age and growth of exploited bivalve species is fundamental for the proposal of

fishery management measures. The present study provided the first data available on the growth parameters of *D. exoleta*, but further studies should be conducted, namely the estimation of the size at first sexual maturity, decisive for establishing a minimum landing size for the catches of this species by the bivalve dredging fleet that operates in northern Portugal.

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