



Population and production parameters of the wedge clam *Donax trunculus* (Linnaeus, 1758) in intertidal areas on the southwest Spanish coast: Considerations in relation to protected areas



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ABSTRACT

The main objectives of this study were (i) to provide an updated age-length key for *D. trunculus* from Atlantic waters, and (ii) to evaluate population dynamics, the timing of recruitment and production parameters of the wedge clam *Donax trunculus* in two moderately exposed sandy beaches (the protected area of Doñana National Park and the tourist destination of Isla Canela) along the littoral of Huelva (SW Spain). First an in-depth analysis of the shell and updated estimation of growth parameters of the intertidal *D. trunculus* population were performed between January 2014 and July 2015 using two different methods i) thin-layer cross section (TL) (ii) length-frequency distributions (LFD). Von Bertalanffy growth functions provided an asymptotic length of 46 mm (LFD) and 46.7 mm (TL) and growth constants of 0.48 (LFD) and 0.47 yr⁻¹ (TL) in Doñana beach. In addition, several deformities as well as signs of shell repair were observed. Population dynamics analyses through length-frequency distribution clarified the timing of recruitment (February–March and July). The mean annual biomass (\bar{B}) of intertidal populations of *D. trunculus* ranged between 3.03 (Doñana) and 3.31 g ash-free dry mass (AFDW) m⁻² yr⁻¹ (Isla Canela). Individual production showed the highest value at 27 mm length (0.117 g AFDW m⁻² yr⁻¹) and annual production (P) ranged between 3.40 (Doñana) and 4.91 g (Isla Canela), resulting in renewal rate (P/ \bar{B}) values between 1.03 and 1.61, respectively. The present results, together with information on environmental parameters, revealed clear differences in population dynamics and production between beaches related to the presence or absence of a protection figure.

1. Introduction

The wedge clam (*Donax trunculus* Linnaeus, 1758) is widely distributed along moderately exposed beaches at depths ranging between 0 and 6 m along the Mediterranean Sea, Black Sea and Atlantic Ocean, from France to Senegal (Tebble, 1966; Bayed and Guillou, 1985). According to Picard (1965) and Guillou and Bayed (1991), this species is exclusive of the superficial fine sand biocenosis, with beach characteristics such as beach profile, wave energy, tidal range and sand grain size being important drivers controlling the distribution of the populations. This species has high commercial importance. On the southwest coast of Spain, *D. trunculus* is harvested by licensed fishermen using hand-dredges in shallow waters throughout the littoral of Huelva (Fig. 1) (IDAPES, 2016). However, it is common to

observe unauthorised fishermen hand-dredging and tourists hand-gathering this valuable fishing resource from beaches, making official statistics unreliable and making difficult stock assessment and resource management. Indeed, an increasing fishing pressure over beach clams from recreational harvesters has been reported worldwide (McLachlan et al., 1996; Murray-Jones and Steffe, 2000). Additionally, this type of resource is generally subjected to strong episodic natural fluctuations in abundance, mainly due to marked recruitment variability and occasional mass mortalities (Defeo and de Alava, 1995). Consequently, the combination of environmental changes, uncontrolled fishing pressure and weak recruitment might lead to the overexploitation of this species.

Knowledge on growth parameters and production is essential to establish suitable management measures, and for understanding the ecology of bivalves. Several ageing techniques have been used to

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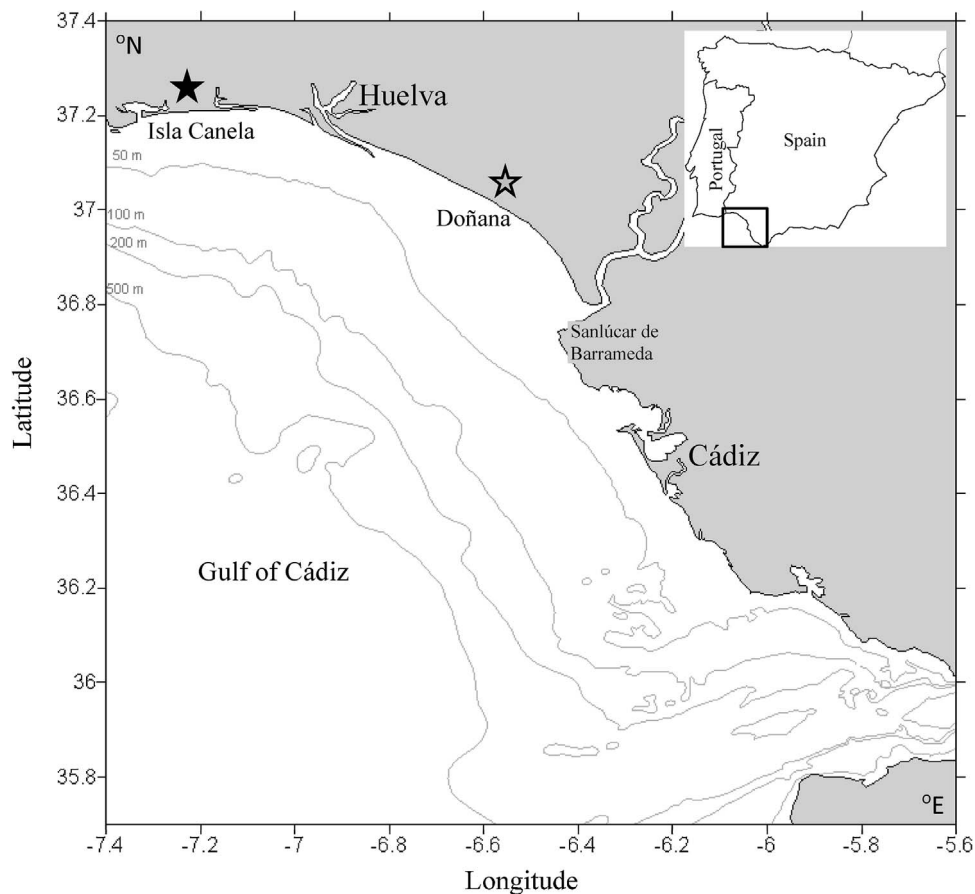


Fig. 1. Map illustrating the littoral of Huelva in the Gulf of Cadiz (SW Spain). ★ Isla Canela beach; ☆ Doñana beach.

estimate growth of bivalve populations, such as length-frequency distributions, surface growth rings, internal growth lines or mark-recapture experiments. In the case of *D. trunculus*, in the western Mediterranean Ramón et al. (1995) estimated the age from shell external surface ring readings, while Gaspar et al. (1999) made a detailed description of *D. trunculus* growth in southern Portugal using the acetate peel technique for reading internal lines. Additionally, Deval (2009) used thin shell sections to establish the length-age key for populations in the Marmara Sea.

Regarding the population structure and production, several species of the family Donacidae have been studied in Argentinean or Namibian beaches to promote sustainable exploitation activities and to clarify relationships between environmental conditions and species abundance (Laudien et al., 2003; Herrmann et al., 2009; Tenjing, 2016a,b). Ramón et al. (1995), Manca-Zeichen et al. (2002) and Çolakoglu (2014) analyzed growth and population structure of *D. trunculus* in the Mediterranean Sea and Marmara Sea, and some authors described depth segregation between juveniles and adults in *D. trunculus* populations (Ansell and Lagardère, 1980; Gaspar et al., 2002). However, until now, data on species production has only been reported for populations from the Atlantic coast of France (Ansell and Lagardère, 1980) and the Cantabrian Sea (Mazé, 1990). In fact, despite the intense fishing activity targeting *D. trunculus*, there is lack of information on growth parameters or production of populations of this species along the southwest Spanish coast.

In this context, the main objectives of this study were (i) to provide an updated age-length key for *D. trunculus* from Atlantic waters based in a modification of the thin-layer technique (embedding in poly-methyl methacrylate resin to avoid some misinterpretations resulting from the above-mentioned techniques) and length-frequency distributions, and (ii) to evaluate population dynamics, the timing of recruitment and

production parameters on two different beaches from the littoral of Huelva (the protected area of Doñana National Park and the tourist destination of Isla Canela).

2. Material and methods

2.1. Study sites and sampling

Two populations of *D. trunculus* in the littoral of Huelva (Fig. 1) were monitored during 18 months (February 2014–July 2015). Samples were collected monthly from the lower part of the intertidal area of the beaches of Doñana ($36^{\circ}54'37.44\text{ N}/6^{\circ}27'6.51\text{ W}$) and Isla Canela ($37^{\circ}10'44.4\text{ N}/7^{\circ}20'31\text{ W}$), where bivalve harvesters operate. Both beaches present similar morphological and hydrodynamic parameters: tidal range (0.7–3.7 m), wave period (7.75 s in summer and 9.07 s in winter) and wave height (0.51 m in summer and 1.66 m in winter), and have been classified as intermediate beaches close to the type “low tide terrace” (Almodovar et al., 2012; Benavente et al., 2015). However, these beaches represent different figures of protection and, consequently, are probably subject to different levels of anthropogenic pressure (fishing and tourism) (i) Doñana belongs to the protected area of Doñana national park (Site of Community Importance; MAGRAMA, 2016) where the affluence of tourists and authorised fishermen is strongly controlled by a team of forest rangers (ii) Isla Canela is a well-known tourist destination and fishing area (www.islacanela.es), where authorised and illegal fishermen operate (Delgado and Silva, 2015).

Sampling was conducted monthly during spring tides (semidiurnal tides) at the selected sites (Doñana and Isla Canela), at 0.5 m of water depth and under similar tidal coefficient. A methodology similar to that used by Juanes et al. (2012), La Valle et al. (2011) and Baeta et al. (2014) was used to estimate density (ind m^{-2}). Sampling was per-

formed using two hand-dredges similar to those used by local bivalve harvesters (experimental and commercial). These hand-dredges have an iron structure with a 44.5 cm wide opening that digs deeply into the sediment (upper 15 cm), using an experimental mesh size (3 × 3 mm) to allow for the collection of the smallest individuals and juveniles, and a commercial mesh size (7 × 7 mm). At each sampling site, hand-dredges were towed diagonally to the shoreline for 10 min, each transect being geo-referenced by means of a GPS (eTrex Legend HCx) in order to calculate the sampled area (m²). In the laboratory, the number of retained individuals was recorded to estimate population density (ind m⁻²) and biomass (g m⁻²) from experimental samples, and the yield (kg per 3 h of fishing trip) from commercial samples. The shell length (SL) was measured to the nearest 0.1 mm with a digital vernier caliper to produce monthly length-frequency distributions from experimental samples.

Data on surface seawater temperature (SST) was collected monthly in situ at the two sampling sites and adjacent areas using an YSI Professional probe. Surface sediment samples (0–10 cm depth) were collected seasonally through manual sampling in each sampling site in order to determine grain size distribution. Sediment samples were analysed by dry sieving to calculate granulometric parameters. Mean, sorting, skewness and kurtosis were calculated geometrically and logarithmically (in phi units) following the methodology proposed by Folk and Ward (1957) and using the statistical package Gradistat (Blott and Pye, 2001).

2.2. Shell microgrowth bands

According to Gaspar et al. (1999) and Deval (2009), the present study also assumes that *D. trunculus* annual growth rings are formed from alternating spring-summer active and autumn slow growth periods resulting in hyaline and opaque bands, respectively. However, to further confirm this annual periodicity in ring deposition, the ventral margin of valves from 360 clams (30 clams/month) was examined backlit using a strong light source (Ramón et al., 1995).

Additionally, a total of 150 *D. trunculus* (size range: 20–44 mm shell length) were collected to determine the species microgrowth pattern by means of the thin-layer cross section technique (TL). A modified protocol from Schenk et al. (1984) for calcified tissues was applied. The left valve of each clam was embedded in poly methyl methacrylate (PMMA) resin for two weeks. Thereafter, polymerized PMMA preparations were sequentially sectioned twice from the umbo to the ventral margin along the axis of maximum growth, using a low-speed diamond saw (ISOMET 4000) to obtain thin sections of 1 mm thickness that were glued with a cyanacrylate adhesive to a methacrylate slide. Subsequently sections were ground and polished with sequential grinders (sandpaper from 120 to 1 μm) to obtain approximately 100 μm thin sections. These preparations were examined under a light microscope (Nikon Eclipse 90i) and a stereomicroscope (Nikon DMZ 100), with images being taken and digitised using a digital camera (Nikon DXM 1200C).

After the identification of annual growth bands, the distance between the umbo and the annual ring was measured using the image analysis software NIS-Elements AR 3.2. Because these measurements are relative to shell height (SH), they were transformed into shell length (SL) using the following allometric relationship $SL = 1.077 SH^{1.191}$ (calculated from 1580 valves collected during the study period: size range = 5–36 mm SL, r^2 : 0.99, p -value < 0.01).

Von Bertalanffy growth (VBG) function was fitted using a non-linear least-squares regression (Gauss-Newton method) using the SPSS statistical software (16.0 version), in order to estimate the VBG parameters:

$$SL_t = SL_{\infty} [1 - e^{-K(t-t_0)}]$$

where SL_t = shell length at age t (mm), SL_{∞} = theoretical maximum shell length (mm), K = von Bertalanffy growth constant and

t_0 = theoretical age at shell length zero (years).

2.3. Length-frequency distribution

A total 8196 individuals with shell length ranging from 3 to 44.8 mm were measured during the study period. The modified version of the VBG function incorporating seasonal oscillation in growth was fitted using ELEFAN I routine of the FISAT II program package (Gayanilo et al., 2005) (Length-frequency distribution, LFD):

$$SL_t = SL_{\infty} \left[1 - e^{\left[-K(t-t_0) + \left(\frac{KC}{2\pi} \right) \sin 2\pi(t-t_s) - \left(\frac{KC}{2\pi} \right) \sin 2\pi(t_0-t_s) \right]} \right]$$

where SL_t = shell length at age t (mm), SL_{∞} = theoretical maximum shell length (mm) and K = von Bertalanffy growth constant. C is the constant that defines the degree of seasonal oscillation, ranging from 0 (continuous non oscillating growth) to 1 (growth ceases completely at the winter point – WP). t_0 is the theoretical age at shell length zero and t_s is the initial point of oscillation in relation to $t = 0$ and the WP. C and WP were estimated from the present data according to Pauly and Morgan (1987). Both parameters (C : 0.9 and WP: 0.8) were also consistent with those obtained in the study of *Penaeus kerathurus* growth in the same geographical area by Rodríguez (1977) and Pauly and Morgan (1987). K-scan and response surface analysis (Rn criterion of fit) subroutines were used to identify the best fit.

Growth performance indices (Overall growth performance (OGP) and Phi prime) were calculated using the following expressions (Pauly, 1979; Munro and Pauly, 1983):

$$OGP = \text{Log}(K[L_{\infty}]^3)$$

$$\text{Phi prime} = \text{Log}_{10}K + 2\text{Log}_{10}L_{\infty}$$

2.4. Production and biomass

Additional samples comprising 50 individuals (randomly taken) were collected in February, May, September and November 2014 for biomass analyses. The adductor muscles of each clam were cut and shells were placed on their ventral surface, allowing to drain for 5 min. The soft tissues and valves were separated and dried at 80 °C for 72 h (or until constant weight) and then weighed to obtain the soft-tissue and valves dry weights. Thereafter samples were ignited in a muffle furnace at 550 °C for 5 h to estimate the ash-free dry mass (AFDW) and the SL-AFDW relationship ($AFDW = a SL^b$).

Total annual production (February 2014–January 2015) in the intertidal area of both beaches was calculated using the mass-specific growth rate method (Brey, 2001). This method required data on the SL-AFDW relationship, shell length frequency distributions from pooled samples and VBGF parameters:

$$P = \sum N_i M_i G_i \text{ (g AFDW m}^{-2} \text{ yr}^{-1}\text{)}$$

where N_i is the average number of individuals (ind m⁻²), M_i is the mean individual AFDW in shell length class i , and G_i is the mass-specific growth rate:

$$G_i = bK \left[\left(\frac{L_{\infty}}{L_i} \right) - 1 \right] (\text{yr}^{-1})$$

where b is the exponent of the size-mass relation. K and L_{∞} are VBGF parameters and L_i is the mean shell length in class i .

Mean annual biomass was estimated by:

$$\bar{B} = \sum N_i M_i \text{ (g AFDW m}^{-2}\text{)}$$

The renewal rate (P/\bar{B} ratios) was calculated from P and \bar{B} .

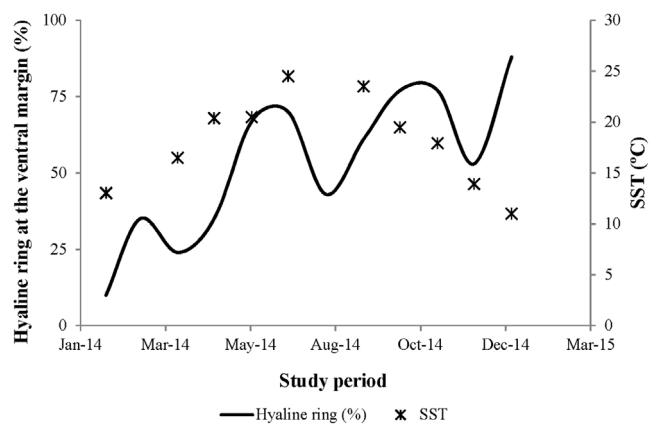


Fig. 2. Monthly frequency of individuals showing hyaline ring in the ventral margin of the shell, and monthly mean surface seawater temperature (SST) in the intertidal areas of the littoral of Huelva during the study period.

3. Results

Surface seawater temperature (SST) oscillated between minimum values in winter (11 °C in January 2015) and maximum values in summer (27 °C in July 2015) (Fig. 2). The sedimentary classification on both beaches (Doñana and Isla Canela) throughout the study period (Table 1) revealed surface sediments with similar mean grain sizes, ranging between 1.77 and 2.42 phi (i.e. from medium to fine sand). Sorting values varied between moderately sorted and well sorted sediments. Both beaches also displayed analogous and slight temporal variations, from medium sand in winter-spring to fine sand in summer-autumn, probably related to winter and summer beach profiles, respectively.

A total of 9864 individuals were collected and analysed during the study period. Mean population density ranged from $30.6 \pm 20.7 \text{ ind m}^{-2}$ on Doñana to $52.9 \pm 33.9 \text{ ind m}^{-2}$ on Isla Canela, while biomass varied between $54.5 \pm 39.6 \text{ g m}^{-2}$ on Doñana and $42.9 \pm 29.6 \text{ g m}^{-2}$ on Isla Canela. A seasonal trend was observed on both beaches (Fig. 3), with maximum density and biomass recorded in the spring-summer period (77.9 ind m^{-2} and 143.7 g m^{-2} on Doñana in May 2014; 111.9 ind m^{-2} and 109.6 g m^{-2} on Isla Canela in September 2014) and minimum values registered in winter (2.8 ind m^{-2} and 5.0 g m^{-2} on Doñana in February 2015; 1.9 ind m^{-2} and 1.3 g m^{-2} on Isla Canela in January 2015). Density was higher on Isla Canela throughout the study period, while Doñana presented higher biomass in most monthly samples. This opposite pattern was reflected in the biomass/density ratio, which was invariably higher in Doñana (Fig. 3). Yield estimates were also always higher on Doñana (Fig. 4), where two peaks were clear in May and October (65.2 and $40.2 \text{ kg } 3 \text{ h}^{-1}$). On Isla Canela a maximum was only observed in November ($14.2 \text{ kg } 3 \text{ h}^{-1}$).

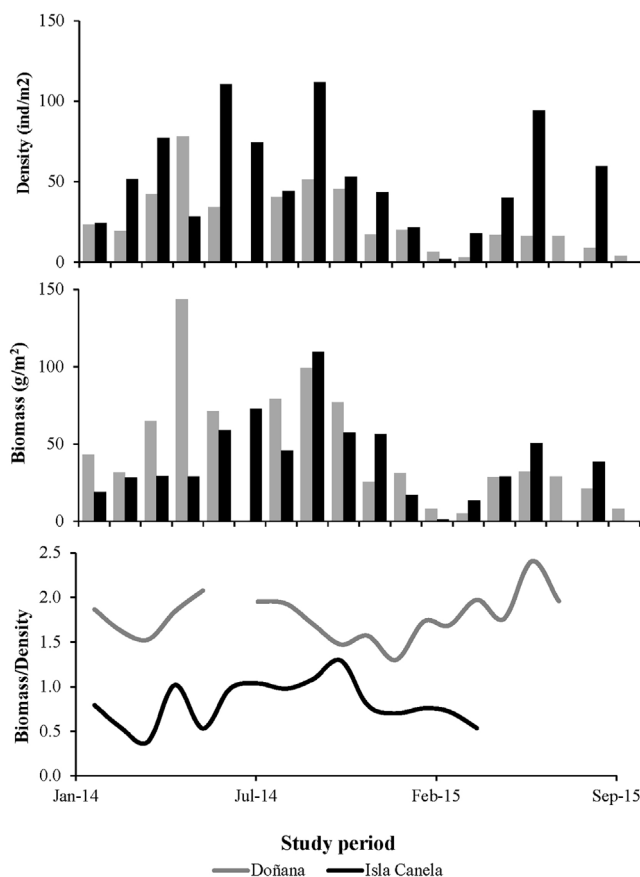


Fig. 3. Monthly mean density (ind m^{-2}), biomass (g m^{-2}) and ratio biomass/density of *Donax trunculus* in Doñana and Isla Canela beaches.

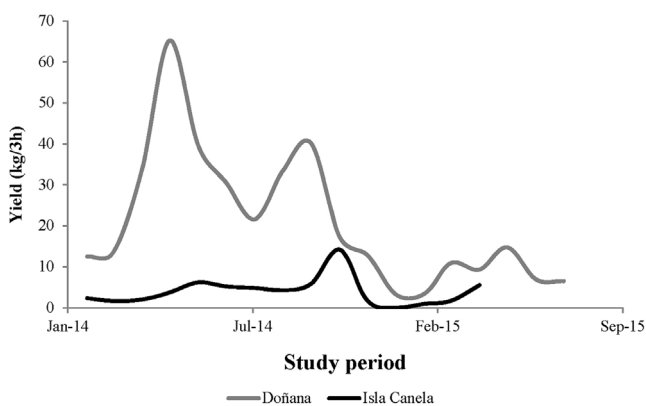


Fig. 4. Monthly variation of yield estimates (kg per 3h of fishing trip) in Doñana and Isla Canela beaches.

Table 1
Sand grain size parameters on Doñana and Isla Canela beaches throughout the study period.

Season	Beach	Mean		Sorting		Skewness		Kurtosis		Classification
		G	Φ	g	Φ	g	Φ	g	Φ	
Spring 2014	Doñana	275.7	1.859	1.653	0.725	-0.201	0.201	0.689	0.689	Medium sand
	Isla Canela	257.2	1.959	1.587	0.666	-0.210	0.210	0.702	0.702	Medium sand
Summer 2014	Doñana	186.6	2.422	1.424	0.510	0.554	-0.554	0.679	0.679	Fine sand
	Isla Canela	232.2	2.102	1.591	0.670	-0.106	0.106	0.876	0.876	Fine sand
Autumn 2014	Doñana	216.4	2.208	1.701	0.766	0.589	-0.589	0.782	0.782	Fine sand
	Isla Canela	238.5	2.068	1.572	0.652	-0.112	0.112	0.698	0.698	Fine sand
Winter 2014–2015	Doñana	293	1.771	1.528	0.612	-0.338	0.338	1.226	1.226	Medium sand
	Isla Canela	247.7	2.013	1.578	0.658	-0.162	0.162	0.691	0.691	Medium sand

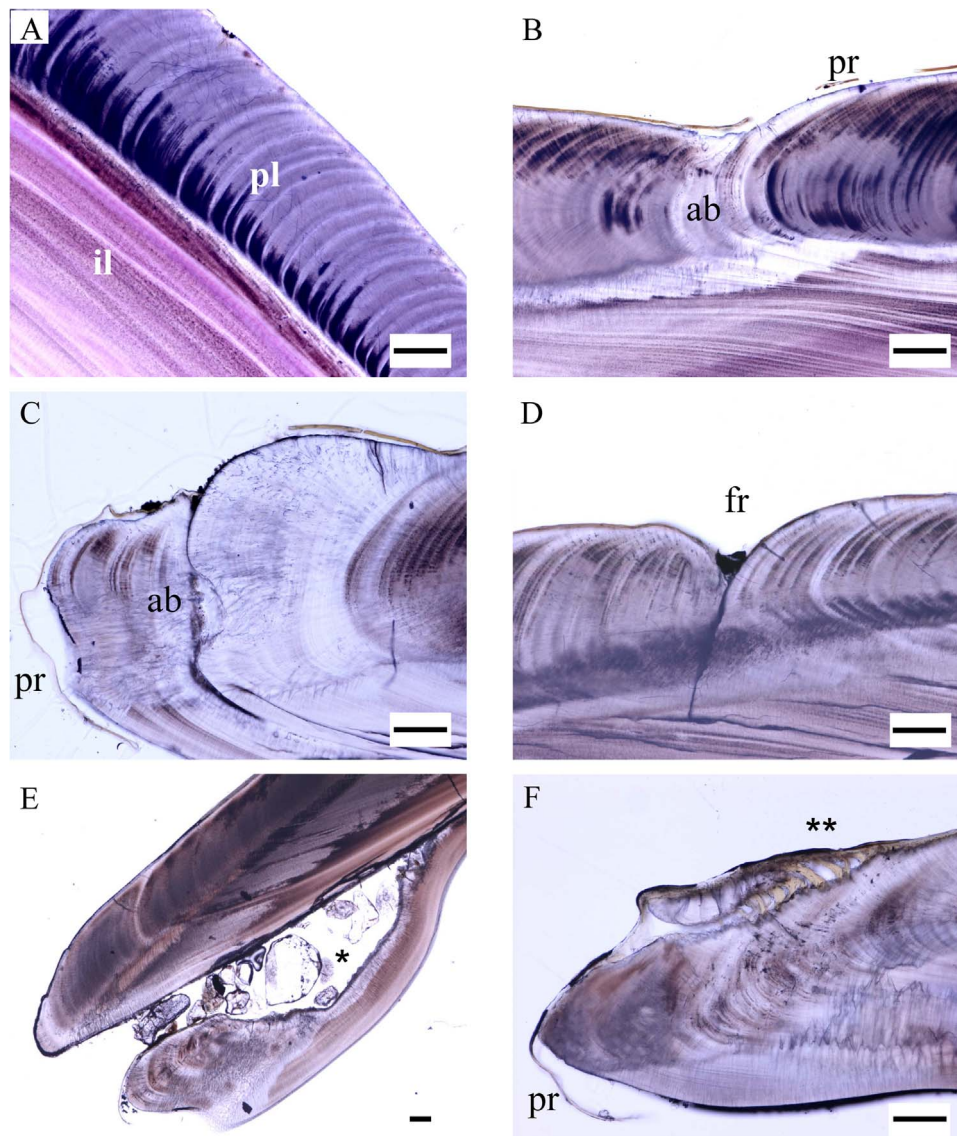


Fig. 5. Thin-layer micro-photographs of the valves of *D. trunculus*. A. Growth bands near the umbo. B. Aggregation of annual growth bands. C. Aggregation of annual growth bands in the ventral margin. D. False annual ring. E. Sand grain inclusion (*) and associated deformity in the ventral margin. F. Signs of shell repair after break in the ventral margin (**). Abbreviations: ab, annual growth bands; fr, false annual ring; il, inner layer; pl, prismatic layer; pr, periostracum. Scale bars: 100 μm .

3.1. Shell microgrowth bands

Annual growth bands were deposited especially in autumn when growth rate slows down coinciding with the declining SST (Fig. 2). Additionally, higher frequency of hyaline rings at the ventral margin was observed in late spring and summer. The embedding in poly methyl methacrylate and the subsequent procedures of sectioning, grinding and polishing until obtaining thin sections ($< 100 \mu\text{m}$ thick) allowed for highly detailed direct observations and an in-depth analysis of the inner structure of the valves (Fig. 5A). The analysis of microgrowth in the outer composite prismatic layer revealed an alternation of aggregated and widely spaced growth bands parallel to the ventral margin. Aggregation of bands occurred during shell slow growth periods, while shell fast growth periods were associated with wider bands. Aggregated bands are characterized by a predominance of small crystals (with probably higher concentration of organic matter), while widely spaced bands presented larger crystals. Additionally, the annual growth bands frequently showed a progressive aggregation of growth bands together with a depression in the valve profile (Fig. 5B and C). Abrupt interruption of the natural pattern of microgrowth bands is reflected

in the presence of false growth rings (Fig. 5D). The anomalous inclusion of sand grains (Fig. 5E) and breaks (Fig. 5F) in the ventral margin of the valve were also clearly evident. The periostracum (organic cuticle structure secreted by the periostracal groove) was also easily observed and identified as being involved in the subsequent regeneration process of damaged shells (Fig. 5F).

The VBG equation estimated from data on microgrowth bands provided a L_{∞} of 46.7 mm, a growth rate of 0.47 yr^{-1} and $t_0 = -0.59$. The OGP and Phi-prime values calculated using this methodology were 4.680 and 3.011, respectively.

3.2. Length-frequency distribution

Monthly length-frequency distributions throughout the study period are presented in Fig. 6. On Doñana beach, two cohorts were identified in February 2014 (approximate modes: 22 and 30 mm SL), and a third and weaker mode was observed around 35 mm SL. The cohort of 22 mm SL at the beginning of the study period rapidly joined the population fraction potentially exploited by harvesting (minimum landing size of *D. trunculus* in the Gulf of Cadiz = 25 mm SL). The

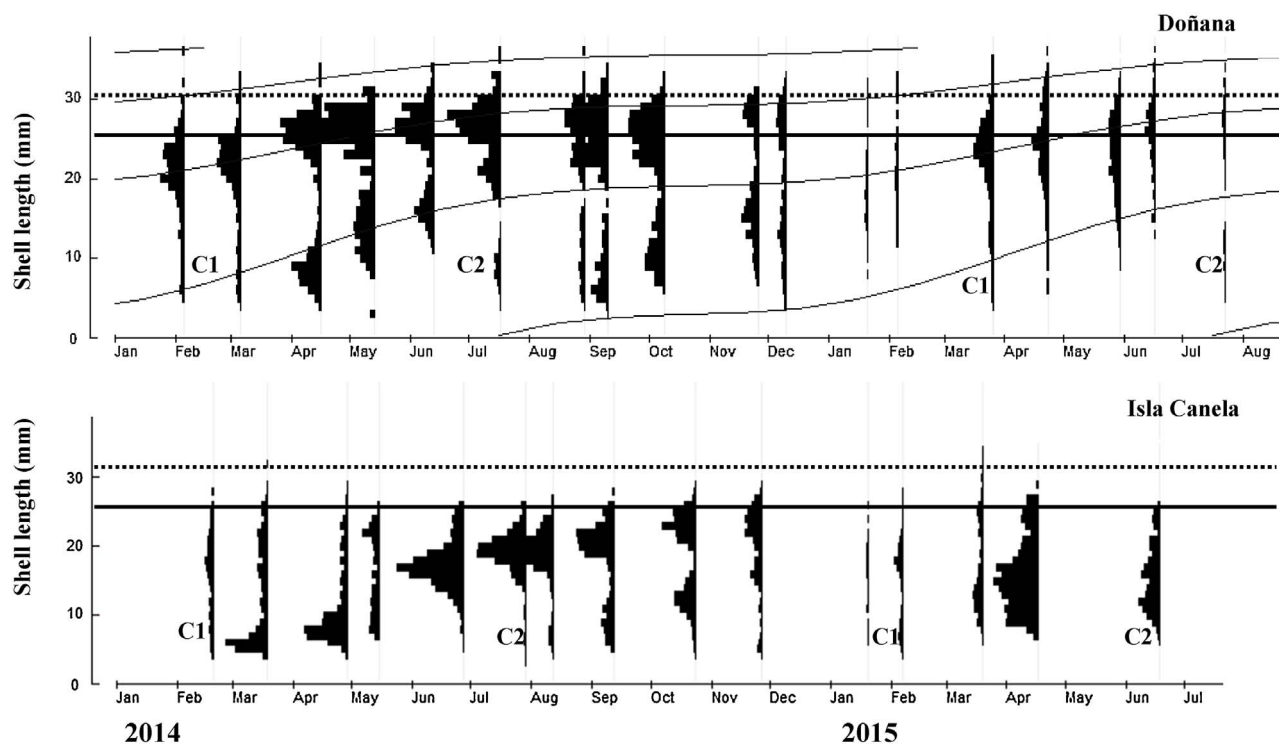


Fig. 6. Monthly shell length-frequency distributions and growth curves estimated for the period February 2014 to July 2015. Shell lengths of 25 mm and 30 mm are represented by solid and broken straight lines, respectively.

progression of the third cohort was difficult to follow possibly due to fishing effects (removal of larger individuals from the harvested population). Recruits within the size range of 3–10 mm SL and mode in 9 mm SL were incorporated in the population in two periods of the year: February–March (C1) and July (C2). These new cohorts beginning in 2014 were followed for 16 months and 13 months, respectively. At the end of the study period, their modes almost overlapped and were located between 25 and 30 mm SL. In 2015, both cohorts were observed again in the same periods. The von Bertalanffy growth parameters obtained were: $L_{\infty} = 46$ mm and $K = 0.48 \text{ yr}^{-1}$ ($R_n = 0.146$). OGP and Phi prime values obtained using length-frequency distributions were 4.669 and 3.006, respectively.

Similar recruitment dynamics were observed on Isla Canela beach and two new cohorts were identified in February and July (Fig. 6). However, individuals larger than 25 mm SL were scarce and clams over 30 mm SL were only registered in March. The scarcity of adult individuals in this beach did not allow adjusting the VBG function (Gayani et al., 2005).

3.3. Production and biomass

The following relationship between shell length and AFDW were used for estimating production: $\text{AFDW} = 4.03 \times 10^{-5} \text{ SL}^{2.48}$ ($r^2: 0.97$, $p < 0.001$).

The mean annual biomasses (\bar{B}) were 3.3 and 3.0 g AFDW m^{-2} in the intertidal zones of Doñana and Isla Canela beaches, respectively. Individual somatic production increased up to 27 mm SL ($0.12 \text{ g AFDW m}^{-2} \text{ yr}^{-1}$) and decreased after reaching this shell length (Fig. 7). The distribution of the total annual production (P) and mean density by size class is shown in Fig. 7. Annual production on Doñana and Isla Canela beaches were 3.4 g and 4.9 g AFDW $\text{m}^{-2} \text{ yr}^{-1}$, respectively. The annual P/\bar{B} ratio was 1.03 on Doñana and 1.61 on Isla Canela beach.

4. Discussion

4.1. Growth parameters and shell analysis

This study presents the first estimation of growth parameters for *D. trunculus* from the Spanish Atlantic coast from two techniques (thin-layer cross section, TL; length-frequency distribution, LFD). Acetate-peel and thin-layer techniques have been widely used to study the growth of *D. trunculus* (Ramón et al., 1995; Gaspar et al., 1999; Deval 2009). Here, we proposed a modification of the original methodology to protect the fragile valves of this species and allow higher quality observation and in-depth analysis of the valves inner structure (TL). The deposition periodicity and annual growth pattern coincided with the description made by Gaspar et al. (1999). Annual growth bands were deposited especially in autumn when growth rate slows down coinciding with the declining SST. Additionally, high frequency of hyaline rings at the ventral margin was observed in late spring and summer, coinciding with the species reproductive period (Delgado and Silva, 2016), a highly demanding energetic process according to Ramón et al. (1995).

This modified technique (TL) also allowed the detailed observation of anomalous inclusion of sand grains in valves (Fig. 5E), shell breaks or repaired shell damages. Damages and repairs around the shell margin are often also associated with the inclusion of sediment grains into the shell margin (Lomovasky et al., 2005), probably caused by impacts and damages inflicted during the hand-dredge fishery. In fact, Gaspar et al. (1998) attributed patterns of shell damage and consecutive repairs in the razor clam to bivalve dredging operations. Other authors associated shell damage to predator attacks or burrowing activity (Checa, 1993; Ramsay et al., 2001), but this does not seem to be the case of *D. trunculus*, which inhabits highly exposed beaches and exhibits a remarkable burrowing ability.

The von Bertalanffy growth constants (K) obtained from each technique (TL and LFD) were similar and slightly lower than those obtained using the acetate peel technique in *D. trunculus* from the

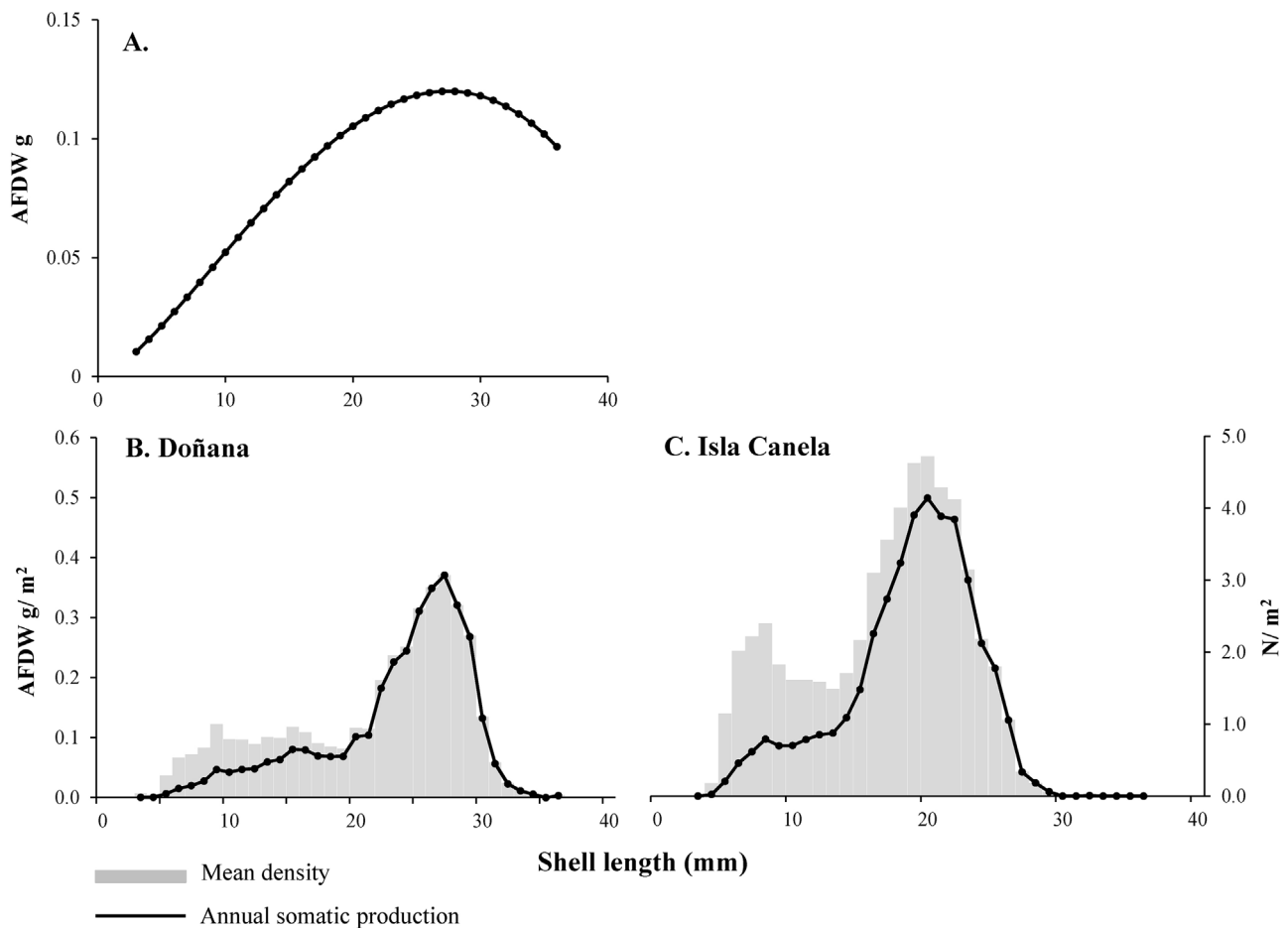


Fig. 7. Distribution of annual somatic production of *Donax trunculus* for the period February 2014 to January 2015 and mean density ($N\ m^{-2}$) for the different shell lengths. A. Individual production (g AFDW). B. Population production and mean density from Doñana beach (g AFDW m^{-2}). C. Population production and mean density from Isla Canela beach (g AFDW m^{-2}).

Algarve coast (southern Portugal) (Gaspar et al., 1999). Differences on prevailing hydrodynamics, beach geomorphology or sampling area between studies (infra-littoral in the Portuguese coast and intertidal in the Spanish littoral) might eventually explain these slight variations. In terms of growth performance indices, and according to the habitat-specific classification for Donacidae (Laudien et al., 2003), the population of *D. trunculus* from the littoral of Huelva fits into the temperate region group (OGP range: 4.17–4.91), as in the case of *D. vittatus* (Ansell and Lagardère, 1980) or *D. hanleyanus* (Herrmann et al., 2009).

4.2. Population dynamics

Regarding length-frequency distributions, several reproductive aspects should be taken into account to better understand the population dynamics of *D. trunculus* in the littoral of Huelva: (i) a resting period in the reproductive cycle occurs from August to November, without presence of ripe gonads until January-February; (ii) partial spawning events occur throughout the prolonged reproductive period (February to July) and intense emissions of gametes are evident at the end of this period (Delgado and Silva, 2016); (iii) larval development lasts approximately 21 days (Ruiz-Azcona et al., 1996). Considering these reproductive features it is possible to assume that C1 recruits on both beaches probably result from spawning events occurred at the end of the previous reproductive season, while C2 recruits originate from emissions of gametes at the beginning of the current reproductive period (Fig. 8). In this context, Lowere-Barbieri et al. (2014) suggested that species with extended spawning seasons have a wide range of birthdates that result in differing life history traits associated with early-born versus late-born individuals. Presumably C2 recruits grow

and settle under more favourable environmental conditions (spring) than C1 recruits (summer and autumn) (Gaspar et al., 1999; Prieto et al., 2009; Delgado et al., 2013), which results in predictable higher growth rates for C2. The present results confirmed this assumption, because C2 lasts 5 months to reach 9 mm SL, while C1 lasts at least 7 months to attain the same size. These differences in growth rates also promote the overlap of both cohorts after one year, shaping a yearly cohort easy to follow and to fit the growth curve through the two distinguishable modes generated by the wide spawning season (Pauly and Morgan, 1987).

4.3. Considerations in relation to protected areas

While recruitment events occur at the same time of year, overall frequency length-distributions differed markedly between beaches. Doñana beach exhibited a well-structured population with two clear cohorts and high proportion of individuals larger than 25 mm SL (minimum landing size). On the opposite, on Isla Canela beach the length-frequency distribution was shifted towards smaller sizes, with individuals above the minimum landing size being rarely collected, which also resulted in lower population biomass/density ratio compared to Doñana beach. Additionally, yield peaks coming from C1 and C2 cohorts, were clearly observed in Doñana but were almost absent in Isla Canela. Some authors reported the existence of depth segregation in this species in different geographic areas (Gaspar et al., 2002; Deval, 2009) and it could be assumed that these differences in demographic structure could result from bathymetric differences among sampling sites. However, in the present study, sampling was conducted in usual fishing zones of beaches with the same morphology, depth and tidal

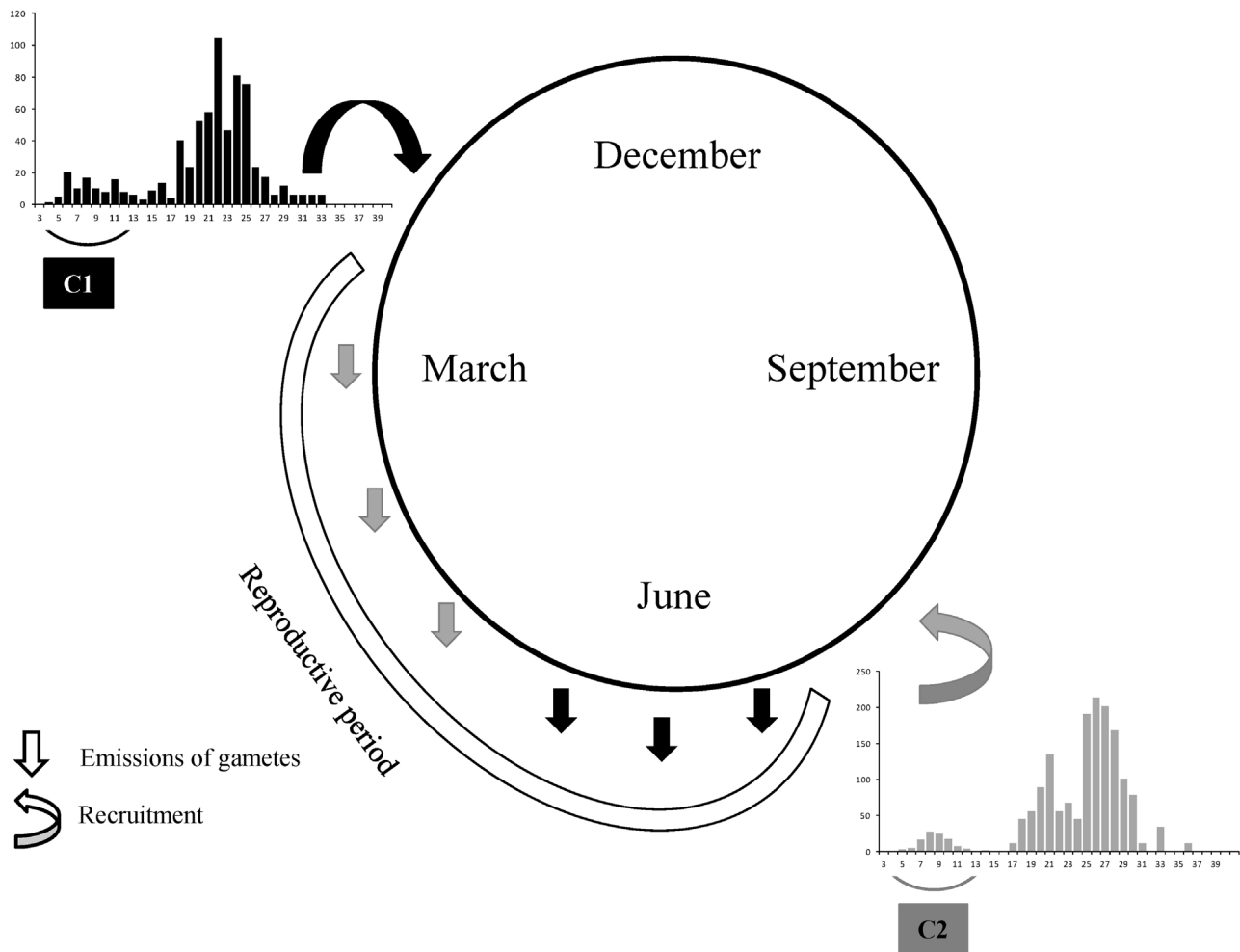


Fig. 8. Schematic representation of the reproductive cycle, periods of emission of gametes and related recruitment events in populations of *D. trunculus* from SW Spain. Black symbols represent the C1 cohort (from February–March) and grey symbols represent the C2 cohort (from July).

coefficient, therefore this situation probably reflects differences in the level of protection of each area. Doñana beach is integrated in the Natural Park of Doñana, one of the most important protected areas of Europe, where only authorised fishermen and few tourists have access. On the contrary, Isla Canela beach is a non-protected area intensively exploited by authorised and illegal fishermen and tourists from the nearby urbanisations (Delgado and Silva, 2015). In this sense, evidences of collapse of the fishery targeting *D. trunculus* due to excessive fishing effort have been recently reported in Mediterranean coasts (Escrivá et al., 2016).

With regard to the intertidal production of *D. trunculus* (P) in the littoral of Huelva, values oscillated between 3.4 and 4.9 g AFDW $m^{-2} yr^{-1}$, within the reported range for this species in the Cantabric Sea (1.8–3.7 g) (Mazé, 1990) and for other Donacidae species in tropical waters, namely *D. incarnatus* and *D. spiculum* (2.9 and 3.3 g, respectively) (Ansell et al., 1978). The present results are higher than the production of *D. hanleyanus* in Argentinean beaches (0.08–0.99 g), but considerably lower than that of *D. serra* in the continuous upwelling system of Namibia (167–637 g) (Laudien et al., 2003; Herrmann et al., 2009). Similarly, biomasses \bar{B} are consistent with data reported for donacids from tropical or temperate areas (0.15–3.7 g AFDW m^{-2} ; Ansell et al., 1978; McLachlan, 1979; Herrmann et al., 2009), but are comparatively lower than those from l'île d'Oléron (18.9–39.9 g) (France) (Ansell and Lagardère, 1980). Concerning P/\bar{B} , Isla Canela beach showed similar values (1.61 yr^{-1}) to the same species in the Cantabrian Sea (1.37–2.26 yr^{-1} ; Mazé, 1990), to *D. serra* (1.17–1.59 yr^{-1} ; Laudien et al., 2003) or *D. sordidus*

(1.3–1.78 yr^{-1} ; McLachlan, 1979), whereas Doñana beach (1.03 yr^{-1}) displayed comparatively lower values. These differences on P or P/\bar{B} ratio between Doñana and Isla Canela beaches might reflect different environmental conditions. Several authors highlighted the importance of beach morphodynamics, and particularly, the sediment grain-size as main factor controlling the distribution of *D. trunculus* populations (de la Huz et al., 2002; La Valle et al., 2011). However, from a morphological perspective, beach profiles along the littoral of Huelva belong to the intermediate types proposed by Wright and Short (1984), and particularly, both beaches (Doñana and Isla Canela) show morphologies close to the type “low tide terrace” (Benavente et al., 2015). This similarity, confirmed by the present results on sand grain distribution, dismisses this factor as explanatory variable for differences in wedge clam population between beaches. However, the effects of other hydrodynamic or environmental variables not included in our study cannot be ruled out.

Some authors revealed how fishing pressure shifted population demographic structure towards younger individuals with higher somatic production and P/\bar{B} ratio. Hall et al. (1970) demonstrated that increasing predation by fishes produced a rising benthonic production whilst biomass kept constant. In this case, fishes only consumed bigger individuals and, consequently, P/\bar{B} ratio increased. Bivalve fishing pressure acts in a similar way because (at least theoretically) the size-selectivity characteristics of the fishing gear targets mostly individuals above the minimum landing size. Similarly, Clasing et al. (1984) referred the same problematic and effects in a *Venus antiqua* population in Chiloé. As already mentioned, fishing pressure in Doñana beach is

under control, while this activity quite uncontrolled on Isla Canela beach, where illegal fishermen also act. In addition, Isla Canela is an important touristic destination and tourists not only impact by illegal hand-harvesting this living resource but also through the disturbance of intertidal areas by trampling. In agreement with the present findings, the urbanisation of coastal areas and the influence of human activities on the occurrence and abundance of diverse bivalve populations have been reported (Marcomini et al., 2002; Dadon, 2005). For instance, Herrmann et al. (2009) described intensive trampling as the primary cause for the decreasing abundance of *D. hanleyanus* in Argentinean beaches. Consequently, the protection and sustainability of this type of ecosystem and associated fishing resources require adequate control measures of tourism affluence and preventing illegal fishing.

As a conclusion, length-frequency distributions, population density, biomass and production revealed clear differences in population status between beaches. It seems clear that protection measures play an important role on the population conservation and dynamics. These findings also provide the basis for implementing a long-term monitoring system of: (i) fishing activity (gathering data on fishing effort, yields and discards), (ii) data collection on population structure, biomass and abundance, and (iii) on a wide range of environmental variables. Finally, further investigations should be performed to ascertain how environmental factors influence growth, reproduction, larval drift and settlement, recruitment and population dynamics of this commercially important bivalve species.

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