

Depth segregation phenomenon in *Donax trunculus* (Bivalvia: Donacidae) populations of the Algarve coast (southern Portugal)*

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SUMMARY: A study was undertaken to evaluate the existence of depth segregation between size classes of *Donax trunculus* populations that occur along the Algarve coast (southern Portugal). Five collecting areas were sampled in the Ria Formosa barrier islands, namely in the Culatra, Barreta and Armona Islands, between March and June 1998. The study was based on size frequency distribution analysis and shell biometric relationships. The size frequency distribution showed the predominance of smaller individuals (<25 mm) in the renewal area (0.5-1.0 m depth) and the prevalence of larger individuals (≥25 mm) at greater depths (4.0-6.0 m depth). The biometric study revealed the existence of significant differences in the type of growth between size classes in relation to depth distribution and burrowing activity. On the basis of these results, some specific management measures were proposed for this important bivalve fishery, taking into account the distinct fishing strategies and operations (manual and boat-operated dredging) performed at different depths.

Key words: Bivalvia, Donacidae, *Donax trunculus*, wedge clam, depth segregation, relative growth, management measures, Portugal.

INTRODUCTION

Bivalve fisheries play a very important role in the social-economical context of the Algarve coast, mainly due to the size of the fleet and number of fishermen involved in this activity. Among several bivalve species caught, *Donax trunculus* constitutes a very important fishing resource due to its high economical value. For this reason, this species has been subjected to intense exploitation involving two different types of fishing gears: hand-operated dredges, used only in shallow waters, and boat-operated

dredges, used both by the local fleet (<9 m length boats) and by the coastal fleet (>9 m length boats).

Bivalves of the genus *Donax* are widespread on the exposed sandy beaches of tropical and temperate coasts (Ansell, 1983). *Donax trunculus* is an Atlantic-Mediterranean warm-temperate species that has been recorded from Senegal to the French coast (Tebble, 1966). This species is preferentially distributed between 0 and 2 metres depth in the Mediterranean, and between 0 and 6 metres depth on the Atlantic coast. In Portuguese waters, *Donax trunculus* is the most inshore wedge clam species, occurring up to a depth of 6 metres, with higher densities between 0 and 3 metres depth (Gaspar *et al.*, 1999).

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This species can inhabit highly energetic environments on sandy beaches, where it is exposed to the tidal rhythm, intense wave action and sediment instability (Ansell, 1983; Brown and McLachlan, 1990). In these environments, *Donax trunculus* populations are capable of reaching very high densities, forming extensive and dense beds (Gaspar *et al.*, 1999), and often being the dominant macrobenthic organism in communities characterised by a low specific diversity (Donn *et al.*, 1986; Ramón *et al.*, 1995). This dominance is due to its adaptation to actively exploiting these severe conditions rather than passively surviving their effects (Ansell, 1983).

Several authors refer to the existence of an age gradient with depth for *Donax trunculus* and suggest that bathymetry is the determinant factor in the spatial distribution of this species. In some cases, the juveniles are located in shallower depths at the mid-tide level, while the adults are situated at greater depths down to their bathymetric limit (Wade, 1967; Guillou and Le Moal, 1978; Ansell and Lagardère, 1980; Guillou and Bayed, 1991; Le Moal, 1993).

However, this distribution can diverge with latitude, and some authors have found the inverse distribution phenomenon (Amouroux, 1972; Bayed and Guillou, 1985). Furthermore, some studies have not observed any type of spatial segregation in this bivalve species (Mouëza, 1975; Mazé and Laborda, 1988). In some cases this phenomenon was attributed to local hydrodynamics, with water column turbulence provoking the dislodgement of benthic fauna and inducing modifications in both juvenile and adult spatial distributions, mixing individuals from different depths (Nybakken, 1988; Turner *et al.*, 1995). Such a perturbation of depth segregation has already been described for *Donax trunculus*, both on the Roussillion coast (France) (Amouroux, 1974) and on the Rabat coast (Morocco) (Bayed, 1982).

The main objectives of the present study were to detect the existence of a depth segregation phenomenon between size classes of *Donax trunculus* populations from the Algarve coast, and to evaluate the depth effect on the relative growth of individuals.

Correct stock management suggests the adoption of a set of measures adjusted to the biological and ecological characteristics of this species. This type of resource is generally subjected to strong episodic natural fluctuations in abundance, mainly due to high recruitment variability and occasional mass mortalities (Le Moal, 1993; Defeo and Alava, 1995),

and has a rapid growth and short longevity (Gaspar, 1996). In this context, in order to prevent over-exploitation, it may be necessary to implement a management strategy directed towards the effective protection of areas inhabited by juveniles and smaller individuals, and the improvement of dredge efficiency and selectivity.

MATERIALS AND METHODS

Sampling operations

The sampling operations were carried out between March and June 1998 at five sampling stations situated in the Ria Formosa lagoon barrier islands, namely in the Barreta, Culatra and Armona Islands (Algarve coast - southern Portugal) (Fig. 1).

The sampling was undertaken using the commercial fishing boat “Caldeirão”, with an artisanal dredge adapted for the *Donax* fishery. The basic design of the Portuguese *Donax* dredge is a small, semicircular iron structure, with a net bag and a toothed lower bar at the mouth. Welded to this iron structure are three metal shafts forming a kind of “hen’s foot”, onto which the towing cable is attached (Fig. 2).

Samples were collected from the infra-littoral zone between 0.5 metres and 6.0 metres depth, where tow depth was recorded at the time of sampling with a multiparameter sounder (Yellow Spring Incorporated®). The tows were performed parallel to the shoreline and during low tide, with a duration of 3 minutes.

Sampling was undertaken at increasing depths (one tow per depth) and terminated only when catches ceased to contain target species, i.e. the

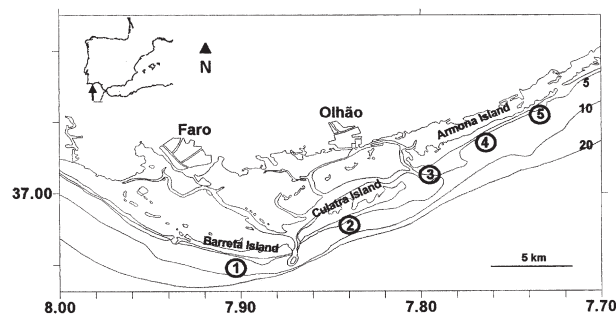


FIG. 1. – Geographical location of the sampling stations along the Algarve coast (southern Portugal). Ria Formosa lagoon barrier islands: 1, Barreta Island; 2, Culatra Island; 3, 4 and 5 Armona Island. Latitude and longitude scales are represented in centesimal degrees.

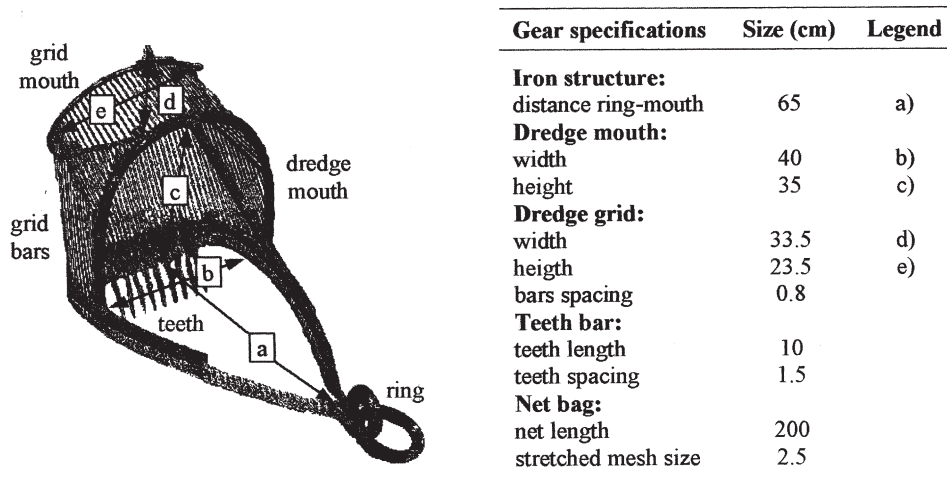


FIG. 2. – Schematic representation of the Portuguese *Donax* dredge and respective specifications.

number of depths towed per sampling station varied according to the respective fishing yield. At Culatra Island, due to particular local hydrodynamics that provoke irregular bottom topography, sampling only began at 2.5 metres depth (Table 1).

Length frequency distribution

After sorting samples, individual bivalve shell lengths (maximum distance along the anterior-posterior axis) were measured with a digital vernier caliper to the nearest 0.01mm (MITUTOYO® Digimatic: CD-15D). These measurements were performed separately for each depth, allowing the estimation of mean length and the length frequency distribution for set depths at each sampling station.

For the purpose of calculating the length frequency distribution, the individuals were initially divided into size classes of 2 mm, and later into two

broader size classes (individuals with a shell length greater or smaller than 25 mm). The selection of these broader size classes was made on the basis of the minimum landing size for this species (25 mm).

In order to evaluate the differences between size frequency distributions against depth, the Kolmogorov-Smirnov goodness of fit test (*K-S*) for two samples [$H_0: F_A(x) = F_B(x)$] was applied, with a significance level of $\pm 95\%$ ($\alpha=0.05$) (Zar, 1996):

$$D' = \max_{(x)} | S_A(x) - S_B(x) |$$

where, D' is the *K-S* test value; $S_A(x)$ the distribution function of the sample *A*; and $S_B(x)$ the distribution function of the sample *B*

Subsequently, the comparison between the obtained values of the *K-S* test and the tabled critical values of the *K-S* test allowed the null hypothesis (H_0) to be accepted or rejected.

TABLE 1. – Tow depths (recorded at the time of sampling) and number of individuals collected at each depth and sampling station along the Algarve coast (Ria Formosa lagoon barrier islands: Barreta, Culatra and Armona Islands).

Depth (meters)	Number of individuals				
	Barreta Island (1)	Culatra Island (2)	Armona Island (3)	Armona Island (4)	Armona Island (5)
0.5	-	-	-	433	33
1.0	270	-	715	524	-
1.5	-	-	-	-	331
2.0	247	-	133	237	219
2.5	-	170	-	-	-
3.0	269	-	157	418	290
3.5	-	210	-	-	-
4.0	290	-	255	222	337
5.0	-	179	140	-	235
6.0	-	215	-	-	304
Total	1076	774	1400	1834	1749

Note: - depths not sampled.

Relative growth

The study of the bivalves' relative growth was made by the biometric analysis of the three shell axes, namely the length (maximum distance along the anterior-posterior axis), height (maximum distance on the dorsal-ventral axis, across the shell middle axis), and width (maximum distance on the lateral axis, between the two valves of the closed shell).

For the establishment of the weight-length relationships the individuals were measured to the nearest 0.01 mm with a digital vernier calliper and weighed (wet weight, including intra-valves water) on a top-loading digital balance with a precision of ± 0.01 g (AND®: HF-2000G).

The establishment of these morphometric relationships was made by the adjustment of an exponential curve to the data:

$$Y = aX^b$$

This equation can also be expressed in its linearised logarithmic form:

$$\log Y = \log a + b \log X$$

where, Y - length (L-mm) (biometric relationship)

or weight (W-g) (weight/length relationship)

X - height (H-mm) or width (w-mm) (biometric relationship)

or length (L-mm) (weight/length relationship)

a - intercept (initial growth coefficient)

b - slope (growth coefficient, i.e., relative growth rates of the variables)

The allometry coefficient is expressed by the exponent b of the linear regression equations. In these equations, whenever both measurements are linear variables and are expressed in the same unit, when $b=1$ the biometric relationship describes an isometric growth. In relations between different types of variables and/or between different measuring units, when the exponent $b=3$ the weight-length relationship reflects an isometric growth.

The relationship parameters (a and b) were estimated by linear regression analysis (least squares method) on log-transformed data and the association degree between the variables was calculated by the determination coefficient (r^2). Additionally, the 95% confidence limits of the parameter b and the significance level of the linear regression determination coefficient (r^2) were also estimated.

In order to confirm whether the values of b obtained in the linear regressions were significantly different from the isometric value ($b=1$ or $b=3$) and described a negative ($b<1$ or $b<3$) or positive ($b>1$ or $b>3$) allometric relationship, a t -test ($H_0: b=1$ or $H_0: b=3$) was applied with a confidence level of $\pm 95\%$ ($\alpha=0.05$) (Sokal and Rohlf, 1987).

RESULTS

Length frequency distribution

The length frequency distribution and mean length variation against depth for *Donax trunculus* populations at five sampling areas on the Algarve coast are represented in Figure 3.

With the exception of the sampling stations at Culatra Island (Fig. 3b), a decrease in the number of smaller individuals and an increase in the number of larger individuals was observed with increasing depth. The mean length variation with depth confirmed previous results, revealing an increasing length gradient with depth (Figs. 3a, c, d and e). Again, the only exception occurred with data from the sampling carried out at Culatra Island, where mean lengths were approximately constant with depth (Fig. 3b).

Due to the differences between data obtained from Culatra Island and other sampling stations, the results from Culatra Island were not used for further calculations. Furthermore, since the same general pattern was observed at all other sampling stations, their results were pooled together for further calculations, in order to apply the segregation phenomenon to the whole study area.

The K - S test (Table 2) revealed the existence of significant statistical differences between depths ($p<0.05$ or $p<0.01$), confirming the existence of a differential distribution between size classes with depth. The only exception occurred with the samples from 1.0 m and 1.5 m depth, which did not display statistically significant differences in their length frequency distributions ($D'<D_0$; $p>0.05$).

The relative proportion and mean abundance (number of individuals/3 minutes tow) of smaller (<25 mm) and larger individuals (≥ 25 mm) of *Donax trunculus* in depth are illustrated in Figure 4.

The Figure 4 showed the predominance of smaller individuals at shallower depths, with a higher proportion distributed within the first metre of depth (0.5 m: 59% and 1.0 m: 62%). Between 1.5 m and

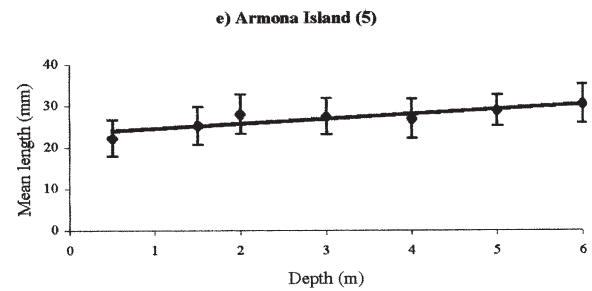
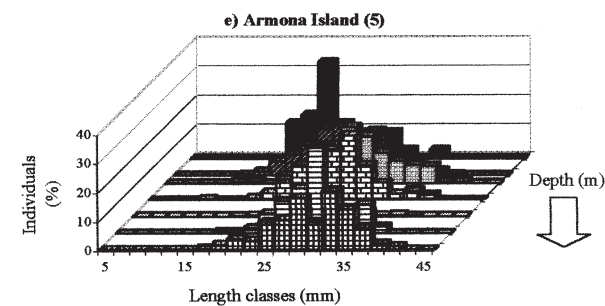
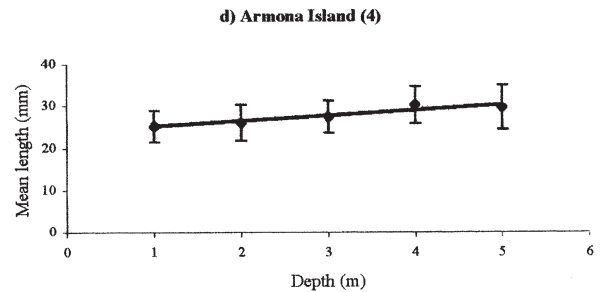
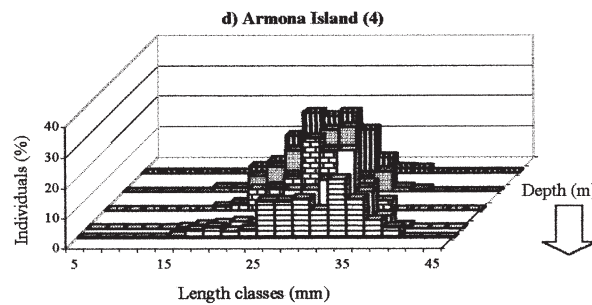
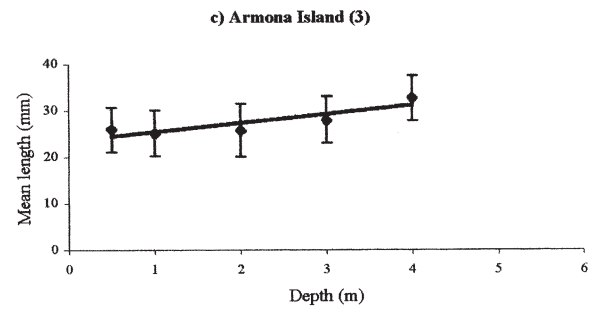
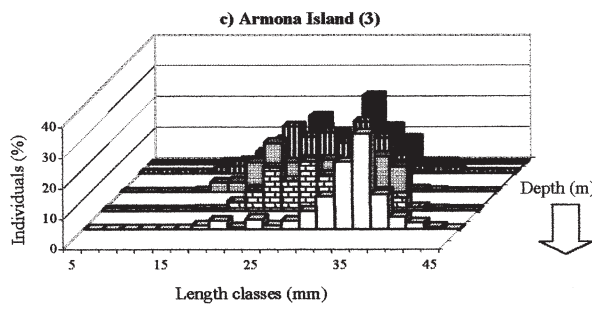
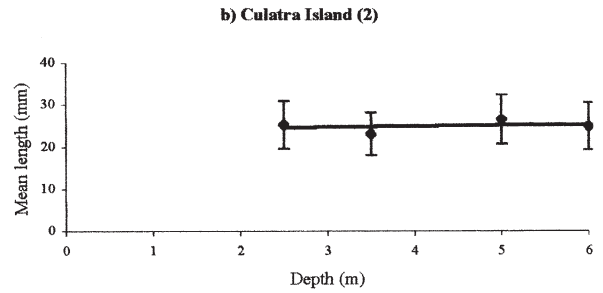
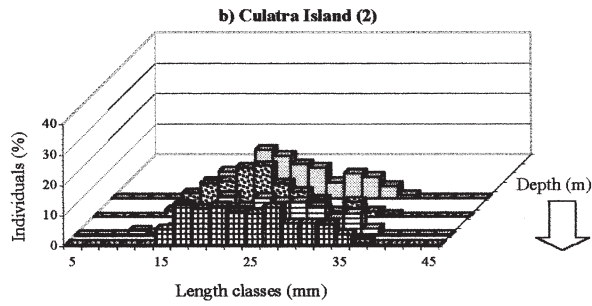
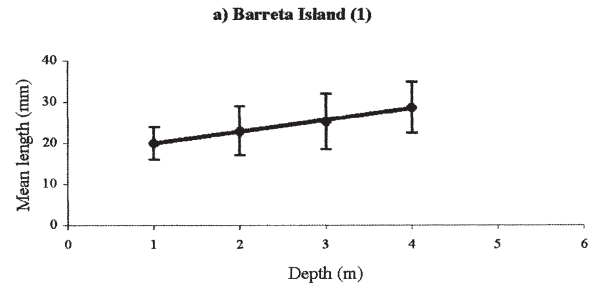
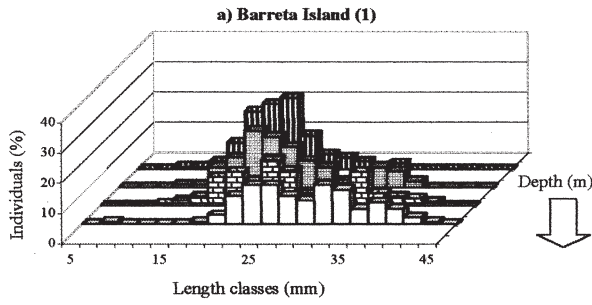


Fig. 3. – Length frequency distribution and mean length variation with depth for *Donax trunculus* populations at five sampling areas on the Algarve coast: a, Barreta Island; b, Culatra Island; c, d and e, Armona Island.

TABLE 2. – Results of the Kolmogorov-Smirnov test applied to size frequency distributions with depth of *Donax trunculus* populations from the Algarve coast.

Depths (m)	1.0	1.5	2.0	3.0	4.0	5.0	6.0
0.5	0.138*	0.117*	0.090**	0.119*	0.266*	0.282*	0.358*
1.0		0.058 ^{NS}	0.116*	0.198*	0.334*	0.396*	0.447*
1.5			0.109*	0.192*	0.321*	0.396*	0.432*
2.0				0.138*	0.247*	0.315*	0.354*
3.0					0.152*	0.204*	0.254*
4.0						0.108*	0.144*
5.0							0.170*

Notes: * = p<0.01; ** = p<0.05; NS = not significant

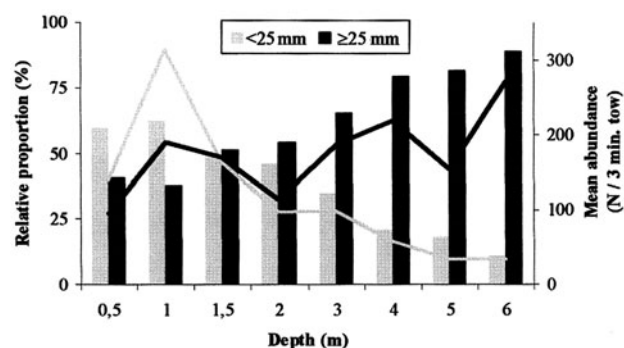


FIG. 4. – Relative proportion and mean abundance (number of individuals/3 minutes tow) of size classes with depth for *Donax trunculus* populations from the Algarve coast.

2.0 m depth an overlapping was observed, despite the slight increase in predominance by larger bivalves. However, at deeper bathymetrics (between 3.0 m and 6.0 m depth) an increasing prevalence of larger (3.0 m: 65%, 4.0 m: 79%, 5.0 m: 82% and 6.0 m: 89%) over smaller individuals was detected.

Relative growth

Due to the general tendency observed in Figure 4, i.e. predominance of smaller individuals at shallower depths (0.5-1.0 m), equilibrium/overlapping at intermediate depths (1.5-2.0 m), and prevalence of larger individuals at deeper bathymetrics (3.0-6.0 m), the data from these depth intervals were pooled together for the morphometric analysis. The results obtained for the biometric relationships of *Donax trunculus* caught at different depths on the Algarve coast are presented in Table 3.

The analysis of Table 3 showed a consistent type of growth in height/length (H/L) and weight/length (W/L) relationships, with the maintenance of a negative allometry with increasing depth. The H/L morphometric relationship obtained in the present study exhibited a consistent negative allometric growth with depth, between $b=0.882$ (0.5-1.0 m) and $b=0.897$ (3.0-6.0 m). The W/L morphometric relationship also displayed a consistent negative allometric growth with depth, varying between $b=2.698$ (0.5-1.0 m), $b=2.754$ (1.5-2.0 m), and $b=2.701$ (3.0-6.0 m).

On the other hand, in the relationship width/length (w/L) there occurred a slight modification in the growth pattern, with the transition from a positive allometry at shallower (0.5-1.0 m) and intermediate depths (1.5-2.0 m) ($b=1.120$ and $b=1.078$ respectively) to an isometric growth at deeper bathymetrics (3.0 m - 6.0 m) ($b=0.999$).

TABLE 3. – Descriptive sample statistics and biometric relationships of *Donax trunculus* from different depths on the Algarve coast.

Depth (meters)	N	L mean ± S.D. (min – max)	Biometric relationship	Biometric Equation	Determination coefficient (r^2)	S.E. of b (95% C.I.)	Relationship (t -test)
0.5+1.0	1975	25.08 ± 4.69 (8.91 – 40.03)	H/L	$H=0.822L^{0.882}$	0.964*	0.004 (0.874 - 0.889)	- allometry
			w/L	$w=0.221L^{1.120}$	0.912*	0.008 (1.104 - 1.135)	+ allometry
			W/L	$W=0.0003L^{2.698}$	0.963*	0.012 (2.675 - 2.722)	- allometry
1.5+2.0	1167	25.71 ± 5.28 (11.88 – 41.14)	H/L	$H=0.800L^{0.888}$	0.969*	0.005 (0.879 - 0.898)	- allometry
			w/L	$w=0.250L^{1.078}$	0.902*	0.011 (1.057 - 1.099)	+ allometry
			W/L	$W=0.0003L^{2.754}$	0.943*	0.020 (2.715 - 2.794)	- allometry
3.0 - 6.0	2917	28.55 ± 5.22 (10.40 – 44.27)	H/L	$H=0.780L^{0.897}$	0.970*	0.003 (0.892 - 0.903)	- allometry
			w/L	$w=0.326L^{0.999}$	0.911*	0.006 (0.987 - 1.010)	isometric
			W/L	$W=0.0004L^{2.701}$	0.956*	0.011 (2.680 - 2.722)	- allometry

Note: * = p<0.01

DISCUSSION

Length frequency distribution

The length frequency distribution results obtained in this study for the *Donax trunculus* populations revealed the existence of a depth segregation phenomenon at almost all sampling stations, with an increase in the proportion of larger individuals and their respective mean length with depth. The only exception to this general tendency was detected at the Culatra Island sampling station, which displayed a uniform distribution of both smaller and larger bivalves with increasing bathymetrics.

The homogenisation found at Culatra Island might have been due to the peculiar characteristics of this area, located between two inlets (barrier islands channels), which induce the formation of sand piles (“eddies”) and consequently an irregular bottom topography. Since sampling tows were executed parallel to the shore, these bottom irregularities did not allow for a clear separation of catches at different depths, possibly masking the depth segregation phenomenon.

The spatial distribution pattern found at the remaining sampling stations, with marked depth segregation, was also found in several other studies performed in different geographical areas. Depth segregation between size classes or age groups was also reported for *Donax trunculus* and *Donax vittatus* on the French Atlantic coast (Guillou and Le Moal, 1978; Ansell and Lagardère, 1980; Le Moal, 1993), for *Donax serra* in South Africa (de Villiers, 1975; Stenton-Dozey and Brown, 1994), and for *Donax denticulatus* in the West Indies (Wade, 1967). All these studies detected the predominance of smaller individuals at shallower depths, while the larger individuals were mainly distributed at increasingly deeper bathymetrics.

According to Ansell and Lagardère (1980), marked differences in the relative proportions between juveniles and adults with depth fluctuate seasonally. It was found that before the recruitment period the population structure was composed mostly of adults and only after this period did spatial segregation phenomena with depth become more evident due to the presence of juvenile specimens.

A study by Stenton-Dozey and Brown (1994) revealed an intimate correlation between temperature and depth segregation in *Donax serra*, where juveniles are positioned higher in the mid-tide zone

and exposed to higher temperatures than in the “surf zone” occupied by the adults, this behaviour pattern being used by the juveniles to enhance burrowing speed and avoid dislodgement and predation. The opposite phenomenon was detected in a separate study on *Donax trunculus* from the Moroccan coast, where juveniles were situated at greater depths than the adult specimens (Bayed and Guillou, 1985). Nevertheless, in this case the depth segregation phenomenon was also attributed to the temperature effect, being justified by the fact that juveniles have lower tolerance and resistance to the higher temperatures registered in the surface sediments (30–40°C).

In some cases, the depth segregation phenomenon has been attributed to interspecific competition. In this context, Guillou and Le Moal (1980) referred to the existence of interspecific competition between *Donax vittatus* juveniles and *Donax trunculus* adults on the French coast. However, since the genus *Donax* includes species with distinct ecological requisites that determine their separated positioning, namely of sediment size and depth distribution (Salas, 1987), the probability of interspecific competition among these *Donax* species is perhaps questionable.

This spatial segregation phenomenon can also be related to biological factors characteristic of the species *Donax trunculus*, namely the intraspecific competition among juveniles and adults (Guillou and Le Moal, 1978). Several studies refer to the existence of intraspecific competition, mostly between larvae and adults, in which larval settlement contributes to the different depth distribution of juveniles and adults (Ansell and Lagardère, 1980; Woodin, 1986; Wilson, 1991).

As it is known that in bivalves intraspecific competition is strongly related to the availability of space for settlement and food (Caddy, 1989), the segregation phenomenon detected among these *Donax trunculus* populations can be interpreted as a particular survival strategy of this bivalve species.

This phenomenon apparently results from larval fixation at shallower depths distant from the deeper bathymetrics occupied by larger individuals. Subsequently, during growth the juveniles and smaller individuals undergo depth migrations, moving downwards and allowing space to become available for further larval fixation. It may also be considered that the greater food availability in the “surf zone” might be responsible for the preferential colonisation by smaller bivalves of the shallower areas, where the environmental conditions

are advantageous for their development (Scheltema, 1971). These theoretical assumptions easily explain the dominance of smaller individuals at shallower depths, the size mixture/overlapping at intermediate bathymetrics and the prevalence of larger bivalves at deeper grounds, as observed in the present study.

Research into the depth distribution of other bivalve species, caught simultaneously by this multispecific dredge fishery, using the same fishing gear, in the same area and at overlapping depths, further reinforce that depth segregation is a natural characteristic of *Donax trunculus*. In fact, for the species *Spisula solida*, *Chamelea gallina*, *Ensis siliqua* and *Pharus legumen*, size frequency is always independent of depth distribution, not showing any tendency for spatial or depth segregation phenomenon (Gaspar, 1996).

Relative growth

Apparently, the negative allometry in the H/L relationship is frequent in *Donax trunculus*, as the same type of growth was found for this species in Malaga (Spain) ($b=0.490$) (Salas, 1987) and Valencia (Spain) ($b=0.851$) (Ramón, 1993). The only known exception to this general tendency was a positive allometry ($b=1.150$) detected by Fernández *et al.* (1984) in Galicia (Spain).

This negative allometry in the H/L relationship indicates that during ontogeny the individuals growth is expressed more in terms of their length than in terms of their height, which in practice means that bivalves become progressively thicker, more elongated and more streamlined. This gradual morphological adaptation could correspond to a strategy that increases burial depth on the bottom substrata (Lauzier *et al.*, 1998), allowing bivalves to accommodate a longer siphon extending to the sediment surface (Newell and Hidu, 1982; Zwarts *et al.*, 1994; Kamermans *et al.*, 1999).

Bivalve species with more elongated shells (lower ratio: shell height / shell length) burrow into the sediment with greater efficiency (“*deep burrowing type species*”), as their movements require much less energy (Urban, 1994). The species of the genus *Donax* are rapid burrowing bivalves (Thayer, 1975; Donn *et al.*, 1986; Ramón *et al.*, 1995; Gaspar *et al.*, 1999), whose compressed shape and regular shell surface facilitate burrowing into bottom sediments (Vermeij, 1978). These features can also contribute to deeper burrowing, which is particularly important

to avoid potential predators and to consequently reduce mortality (Zaklan and Ydenberg, 1997).

The negative allometry observed for the W/L relationship is in agreement with the findings of all other authors that have studied the growth of *Donax trunculus* in several different geographical areas, including south-western Europe, the Mediterranean and northern Africa. Negative allometries were found in Spain, both in Lugo ($2.709 \leq b \leq 3.247$) (Mazé and Laborda, 1990) and in Valencia ($b=2.700$) (Ramón, 1993), and also in France (Ile d’Oléron), with a value of $b=2.618$ (Ansell and Lagardère, 1980). In northern Africa, this tendency was detected both in Morocco ($2.076 \leq b \leq 2.972$) (Bayed, 1990) and on the Algerian coast ($b=2.667$ and $b=2.720$) (Ansell *et al.*, 1980).

It can therefore be seen that during ontogeny, the growth in length is proportionally higher than the respective growth in weight, i.e. length increases faster than weight, which in practice means that growth in weight assumes preponderance for smaller size classes. As the smaller individuals of *Donax trunculus* populations occupy shallower and more hydrodynamic areas than the adults, their weight enables a more efficient burrowing behaviour, preventing dislodgement and avoiding predation and exposure to unfavourable temperatures, with the consequent risk of desiccation (Neuberger-Cywiak *et al.*, 1990; Stenton-Dozey and Brown, 1994). This “*anchor effect*” has been related to the different life styles of the active burrowing juveniles and the more sedentary adults (Pohlo, 1964).

In the present study, only the w/L morphometric relationship displayed any variation with depth, evolving from positive allometries ($b=1.120$ and $b=1.078$) at shallower and intermediate depths (0.5-1.0 m and 1.5-2.0 m respectively) to an isometric growth ($b=0.999$) at deeper bathymetrics (3.0-6.0 m). In comparative terms, the only other known researches that have studied the w/L relationship for *Donax trunculus* also detected positive allometries, namely on the Galician coast (Spain) ($b=1.150$) (Fernández *et al.*, 1984) and in the Gulf of Valencia (Spain) ($b=1.060$) (Ramón, 1993).

The positive allometries found on shallower grounds (0.5-2.0 m) indicate that during ontogeny the growth in width is increasingly more important than the growth in length, which in practice means that during growth bivalves become progressively wider, i.e. smaller individuals are thinner than larger individuals. These gradual biometric modifications are generally associated with the maintenance of a

physiologically favourable area/volume ratio relatively to the environmental conditions (Thayer, 1975; Seed, 1980). Additionally, the shell volume enlargement during growth allows the individuals to generate more visceral mass, which increases considerably during the maturation and reproduction phases of the bivalve life cycle (Mouëza and Frenkiel-Renault, 1973; Bayed, 1990).

In the current study, this phenomenon is apparently an adaptation strategy of the smaller individuals that enhances burrowing efficiency and helps to oppose the intense hydrodynamics that they are exposed to in the swash zone. For some bivalve species a marked decrease in burrowing ability during growth has been reported (Lauzier *et al.*, 1998), namely for *Donax serra*, for which burrowing speed declines with increasing size (Stenton-Dozey and Brown, 1994).

The isometric w/L relationship detected on deeper grounds (3.0-6.0 m) showed a perfectly proportional increase in length and width. This might reflect a progressive decrease in the importance of the burrowing efficiency with increasing depth, explained by the smoother hydrodynamic conditions at deeper bathymetrics in terms of wave exposure, currents, tidal flow and turbulence.

Fishery management measures

The *Donax* fishery on the Algarve coast is characterised by the existence of three different types of fishing operations: manually-operated dredges and boat-operated dredges, used by both the local fleet (smaller boats) and by the coastal fleet (bigger boats). These three different types of fishing operations use distinct catching strategies in terms of the operating depth, which due to the segregation phenomenon obviously exert distinct impacts on the smaller and larger fractions of bivalve populations.

The shallower depths are only operated by manual dredges that frequently have illegal mesh sizes (<25 mm stretched mesh size), allowing the capture of smaller and commercially undersized individuals. It was estimated that approximately 400 fishermen are permanently involved in this activity, which increases markedly during summer months.

Since during manual dredging the smaller individuals are more susceptible to involuntary dislodgement and exposure to excessive turbulence, this factor is also particularly aggressive to the smaller fraction of the population. Furthermore, during dredging the net bag becomes full of bivalves,

shell fragments and other debris, all of which help to prevent the escape of smaller individuals through the mesh. Finally, bivalve catches are commonly sorted on the beach, where smaller and commercially undersized individuals are rejected and abandoned on the exposed substratum.

The recreational fishery status has not yet been quantified, but it is believed that its catches and fishing effort are considerable, due to the hand-gathering of bivalves typically practised by tourists, mainly during the summer season. In some cases all over the world, beach clam fisheries have been subjected to increasing pressure from the recreational sector (McLachlan *et al.*, 1996; Schoeman, 1996; Murray-Jones and Steffe, 2000). This type of manual harvesting is generally less efficient, but the catches are also much less selective, often retaining very small individuals (Murray-Jones and Steffe, 2000). Altogether, this represents an important fishing effort towards this resource, which due to depth segregation is particularly concentrated on the smaller bivalves that dominate these shallower depths.

On the basis of the present results and due to the high social-economic importance of this fishing activity on the Algarve coast, it would be advantageous to adopt and implement some management measures to regulate the fishery and protect this very important living resource.

In order to protect the smaller fraction that dominates at shallower depths, it would be prudent to limit the number of fishing licenses issued for manual dredging and enforce the adoption of a minimum mesh size (25 mm stretched mesh size). On the same basis, for the boat dredging activities, it would be necessary to restrict the upper bathymetric limit of operation of the fishing fleet to 2.5 m depth. In both cases, management measures can only be achieved by means of an effective surveillance of the fishery.

Additionally, and since it appears to have a marked effect on these bivalve populations during the summer season, an information programme should be implemented to inform both local inhabitants and tourists of the sensitive nature of this resource, and that if they collect bivalves, they should only take those adults greater than the legal minimum landing size (25 mm shell length).

Finally, specific studies should be implemented to characterise the recreational fishery and quantify its catches and fishing effort, which are fundamental parameters for the correct stock assessment and management of this shared fishing resource.

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