This article was downloaded by: [University of Bath]

On: 13 February 2014, At: 15:17

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK

Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

Along- and across-shore components of the spatial distribution of the clam *Tivela mactroides* (Born, 1778) (*Bivalvia*, *Veneridae*)

Márcia R. Denadai^a, A. Cecília Z. Amaral^a & Alexander Turra^b

^a Departamento de Zoologia, Campinas, Brazil

^b Laboratório de Biologia Aquática, Curso de Ciências Biológicas, São João da Boa Vista, Brazil

Published online: 21 Feb 2007.

To cite this article: Márcia R. Denadai, A. Cecília Z. Amaral & Alexander Turra (2005) Along- and across-shore components of the spatial distribution of the clam *Tivela mactroides* (Born, 1778) (*Bivalvia*, *Veneridae*), *Journal of Natural History*, 39:36, 3275-3295, DOI: [10.1080/00222930500126156](http://dx.doi.org/10.1080/00222930500126156)

To link to this article: <http://dx.doi.org/10.1080/00222930500126156>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms &

Along- and across-shore components of the spatial distribution of the clam *Tivela mactroides* (Born, 1778) (Bivalvia, Veneridae)

MÁRCIA R. DENADAI¹, A. CECÍLIA Z. AMARAL¹, &
ALEXANDER TURRA²

¹Departamento de Zoologia, Campinas, Brazil, and ²Laboratório de Biologia Aquática, Curso de Ciências Biológicas, São João da Boa Vista, Brazil

(Accepted 23 March 2005)

Abstract

Beach clam fisheries often provide an alternate income for traditional fishermen, but this activity is highly vulnerable to urbanization of coastal areas. *Tivela mactroides* is a beach clam commonly harvested in the Caribbean (Venezuela) and on the south-eastern Brazilian coast. Only localized records on its spatial structure in size and abundance are available to support management of this clam. The present study showed that the spatial distribution in abundance and size of *T. mactroides* in Caraguatatuba Bay, state of São Paulo, Brazil, has both along- and across-shore (intertidal and subtidal) components. The nature of this distribution should be taken into account in the design of further population or monitoring studies concerning this species. Clam density varied along-shore, with a tendency towards higher numbers of individuals in the stations near the northern side of river mouths of this bay. Lower densities were related to the occurrence of sea-stars and sand-dollars. The intertidal and subtidal across-shore distribution of clam abundance and size varied between and within areas (southern and northern). The individuals from the southern area were concentrated at intermediate tidal levels (0.2–0.6 m in relation to mean low water), whereas in the northern area the clams were more homogeneously distributed. The uppermost limit of their distribution was 0.8 m (southern) and 0.4 m (northern), and an upwards tendency towards increased size was more evident in the northern area. In the subtidal, abundance and individual size tended to increase from the deepest (4.5 m) to the shallowest (0.5 m) levels only in the southern area. Individual clams in the northern area tended to be smaller and more abundant than in the southern area. The species had an ontogenic distribution: small-sized individuals were recorded only in the subtidal. Possible causes for these patterns and for the differences between areas (human exploitation, organic pollution, beach morphodynamics, differential recruitment, and adult–larvae interactions) are discussed, and specific studies are suggested to evaluate formally the proposed hypotheses.

Keywords: across-shore, along-shore, beach fishery, sandy beach, spatial distribution, *Tivela mactroides*

Correspondence: Márcia R. Denadai, Departamento de Zoologia, IB, UNICAMP, C. P. 6109, 13.083-970, Campinas, SP, Brazil. Email: marciard@hotmail.com

Published 22 November 2005.

ISSN 0022-2933 print/ISSN 1464-5262 online © 2005 Taylor & Francis
DOI: 10.1080/00222930500126156

Introduction

Commercial, recreational or traditional fisheries of beach clams are common but vulnerable activities that may require special attention from managers because of their importance to local and traditional people (McLachlan et al. 1996). The lack of background population information for decision makers is one of the major problems that complicates the development and implementation of adequate conservation strategies for these resources.

The venerid clam *Tivela mactroides* (Born, 1778) is commonly harvested on beaches in the Caribbean (Venezuela) and on the south-eastern Brazilian coast (McLachlan et al. 1996). Its range extends from Venezuela to Brazil (states of Pará to Santa Catarina) and includes some Caribbean islands (Rios 1994). It is an important component of the macrofauna of sandy beaches in the state of São Paulo in south-eastern Brazil (Narchi 1972). *Tivela mactroides* inhabits sandy beaches exposed to wave action, and is especially abundant near river mouths (McLachlan et al. 1996). A latitudinal variation in its vertical distribution was suggested, but not formally evaluated, by McLachlan et al. (1996); populations at higher latitudes occupy the intertidal zone (Narchi 1972), and those in lower latitudes are predominantly subtidal (Etchevers 1976). Although ontogenic segregative distribution, in which the larvae tend to establish apart from the adults, commonly occurs in beach clams (McLachlan et al. 1996), it has never been described for *T. mactroides*.

In general, the description of the along-shore (Donn 1987; Defeo and de Alava 1995; James and Fairweather 1996; McLachlan 1996; Lercari and Defeo 1999) and across-shore (de Alava and Defeo 1991; Defeo et al. 1992; Jaramillo et al. 1993; James and Fairweather 1996) spatial structure of sandy beach populations or communities is fundamental to the identification of possible regulatory factors. This preliminary step allows the delimitation of specific hypotheses that may, for example, reveal that human impacts (Defeo and de Alava 1995; McLachlan 1996), freshwater discharges (Lercari and Defeo 1999), beach morphodynamics (Defeo et al. 1992; Jaramillo et al. 1993), drift conditions (Etchevers 1976; Donn 1987), as well as bivalve densities (Fitch 1965; Rhoads and Young 1970; Woodin 1976; Brenchley 1982; Peterson 1982; Hines et al. 1989) may regulate species abundance in sandy beaches.

Most beach clams, including *T. mactroides*, occur in intertidal and shallow subtidal habitats; however, population studies generally focus on only one of these habitats (see McLachlan et al. 1996 for a review). This bias is also common for other marine bivalves (Moore and Lopez 1969; Schaeffer-Novelli 1980; Arruda-Soares et al. 1982; Thompson 1982; Hanekom 1986; Monti et al. 1991; Castro-Ortiz and García-Domingues 1993; Clasing et al. 1994; de Montaudouin and Bachelet 1996) and is explainable by the difficulties in sampling in the surf zone and in standardizing collecting methods and effort, especially because of differences in the spatial scale of subtidal habitats in relation to intertidal ones.

Although certain studies have addressed specific aspects of the biology of *T. mactroides*, there is only limited and fragmented information on the spatial distribution, in size and abundance, of this species on both along- and across-shore scales. The present study aimed to describe the spatial distribution of *T. mactroides* in Caraguatatuba Bay, considering its entire living area, i.e. the intertidal and subtidal zones, by addressing the following questions:

1. Is the distribution of *T. mactroides* homogeneous along the beach (along-shore distribution)?

2. Is the distribution of *T. mactroides* (abundance and shell size) homogeneous at different intertidal levels (intertidal across-shore distribution)?
3. Is the distribution of *T. mactroides* (abundance and shell size) dependent on depth (subtidal across-shore distribution)?
4. Are the physical characters similar between and within beach areas at specific tidal levels?
5. Is the distribution of *T. mactroides* (abundance and shell size) similar between and within beach areas with different environmental conditions in relation to specific tidal levels?

Methods

Study area

Caraguatatuba Bay is located on the northern coast of the state of São Paulo, Brazil, from Arpoar Point ($23^{\circ}43'25.3''\text{S}$, $45^{\circ}24'07.1''\text{E}$) to Camaroeiro Point ($23^{\circ}37'41.1''\text{S}$, $45^{\circ}24'02.4''\text{E}$) (Figure 1). It is bordered by a large sandy beach (about 16 km long), with moderate wave energy because of the shadowing effect of São Sebastião Island. Three important rivers (Juqueriquerê, Lagoa and Santo Antônio) flow into different parts of Caraguatatuba Bay, constantly importing terrigenous sediment. Beach characteristics vary markedly in a north–south orientation. The southernmost part has a wide intertidal ultradissipative terrace (800 m). In the central part, the beach is still gently sloping but has a narrower intertidal zone. The northern part has a more heterogeneous slope with a low tide dissipative terrace subjacent to a steeply sloped reflective high intertidal and berm. In the bay, *T. mactroides* is harvested exclusively in the intertidal zone and mainly in the southern area.

Figure 1. Location of Caraguatatuba Bay in the state of São Paulo, Brazil, and of the study areas (southern and northern). The numbers (1–14) indicate the stations sampled only in the along-shore study.

All samples were taken in autumn 2002, from 2 to 5 April in the subtidal, and from 13 to 16 April in the intertidal. This concentrated sampling effort controlled for any temporal effect. A particular methodology was employed for each question, as follows.

Along-shore distribution—abundance patterns (Question 1)

Fourteen sampling stations were established in Caraguatatuba Bay, 1000 m apart from each other, from Arpoar to Camaroeiro points (see Figure 1). Three 30-m long dredgings (speed 2 knots) were conducted perpendicular to the water line in the shallow subtidal zone (about 1.5 m deep) at each station, at neap high tide periods. This precaution was taken to exclude interference from human exploitation (observed in the intertidal zone) on clam density, and to avoid the higher spring tide variation that would prevent the boat from approaching the shallowest areas. A rectangular dredge (80×25 cm) with 3-mm internal mesh size was used to collect the sediment, which was sieved in a 3-mm mesh. The individuals sampled in each transect were counted and returned alive to the sea. The mean number of individuals per transect (fourth-root transformed) was then compared among stations (fixed factor, 14 levels) through a one-way model I ANOVA, under the null hypothesis that the mean number of individuals was similar among the defined beach stations. The data were transformed after the heterogeneity of variances was verified through the Cochran test (Underwood 1997). A Student–Newman–Keuls test (SNK test) was employed a posteriori to identify a valid alternative hypothesis.

Intertidal across-shore distribution—abundance and size (Question 2)

Two structurally different intertidal areas (southern and northern, Figure 1) were selected to describe the vertical (across-shore) distribution of *T. mactroides*. These environments had characteristic slopes (see below), the flattest, widest and more homogeneous being located in the southern part of the bay, and the steepest, narrowest and more heterogeneous in the northern. One 50-m wide sampling sector perpendicular to the water line was then selected in each area, based on burrow marks in the sediment. Because the objective here was not to compare the two areas but rather to address the vertical distribution of the clams, the sectors were neither sorted nor replicated, but were selected taking into account areas with high densities of clams.

Because of differences between areas in slope and intertidal width, different numbers of intervals were established to describe the zonation of this species: 12 in the southern and 11 in the northern. In each sector, 8-m intervals were used in the flattest parts of the intertidal and 4 m in the steepest part, thus allowing a relatively homogeneous vertical screening of this population. Six random samples (quadrats of 0.50×0.50 m, sampled to a depth of 10 cm) were taken during spring low tides in each interval, totalling 72 and 66 samples in the southern and northern areas, respectively. The samples were washed in the field using a 3-mm mesh sieve. The individuals were counted and returned alive to the sea. The data (number of individuals) for each interval were then averaged ($n=6$) and plotted in relation to intertidal distance from water line.

Based on the topographic slope, the tidal levels corresponding to the heights -0.2 , 0.0 , 0.2 , 0.4 , 0.6 , and 0.8 m in relation to MLW (mean low water, based on the forecasts from tide tables, DHN 2002) were standardized in both sectors. These tidal levels coincided with some of the intervals cited above, and allowed direct comparisons of the vertical patterns of abundance and size of this species between areas. This methodology also

allowed comparisons based on tidal heights instead of distances from MLW, which may be highly variable depending on the beach slope. To reduce sampling effort, only the individuals collected at these levels were measured (total shell length, mm).

The mean number of individuals (fourth-root transformed only in the southern area) and the mean shell length were compared among tidal levels (fixed factor, southern—five levels: -0.2, 0.0, 0.2, 0.4, and 0.6 m, northern—four levels: -0.2, 0.0, 0.2, and 0.4 m; only tidal levels where *T. mactroides* occurred were considered in these analyses) using a one-way model I ANOVA for each area independently, under the null hypotheses that (1) mean number of individuals and (2) mean shell size are similar among the above-specified tidal levels. The SNK test was employed a posteriori to identify valid alternative hypotheses.

Subtidal across-shore distribution—abundance and size (Question 3)

Four depth intervals [0–1 m (mean depth class value 0.5 m), 2–3 m (2.5 m), 4–5 m (4.5 m), and 6–7 m (6.5 m)] were established in both areas (southern and northern) in relation to MLW. Five stations were then sorted in each area at each depth interval, totalling 20 sampling stations (replicates) in each area. One sample was taken at each station at neap high tide periods, dredging the sediment (at 2 knots) for a distance of 50 m parallel to the water line using a rectangular dredge (80 × 25 cm with 3-mm internal mesh size). The individuals collected were counted, measured (shell length, mm), and then returned alive to the sea. The number of individuals (fourth-root transformed) and the shell size were compared between areas (fixed factor, two levels) and among depth intervals (fixed factor, three levels: 0.5, 2.5, and 4.5 m; no individuals were recorded in the 6.5 m interval) through a two-way model I ANOVA under the null hypotheses that the depth gradient in (1) mean number of individuals and (2) mean shell size is the same between areas. If the interaction term (area × depth) was significant, the depth differences in abundance and size were tested with the a posteriori SNK test for each area independently.

Comparisons between the intertidal areas—physical variables (Question 4)

The two intertidal areas (southern and northern) were then compared in relation to physical variables (beach profile and sediment). For this purpose, four sub-areas were sorted in each study area and the beach profile was measured ($n=3$) in each one. The profiles were described by measuring the elevation (cm) in 4 m intervals, from the vegetation (southern) or berm (northern) to the 0.0 m tidal level. For each transect, three variables were recorded: mean elevation (cm), standard deviation of elevation (cm), and total height of the beach (cm). The mean elevation was obtained by averaging all the elevation values recorded. The standard deviation (SD) of elevation was calculated based on these values to represent the degree of heterogeneity in beach slope, i.e. if the profile is more (smaller values of SD) or less (larger values of SD) continuous. Total beach height was the vertical distance between the highest part of the beach (vegetation or berm) and MLW. These three variables were compared between areas (fixed factor, two levels) and sub-areas (random factor, four levels) through a nested two-way model III ANOVA under the null hypothesis that they do not differ between nor within (among sub-areas) areas. The a posteriori SNK test was employed to verify the degree of profile homogeneity within each area independently.

The calculated profiles enabled the identification of the position of 0.0 and 0.4 m tidal levels. These levels were chosen due to the evident variation in number of individuals and

in shell size within this interval (see below). Sediment samples ($n=3$) were taken at these two tidal levels. The granulometric analyses were employed through dry screening of the sediment (Suguio 1973) using the Wentworth (1922) scale. The values of mean grain diameter and sorting coefficient were calculated according to the Folk and Ward (1957) method. The mean grain size (phi units) and sorting coefficient (phi units) of the sediment were then compared between areas, sub-areas nested in areas, and tidal levels (fixed factor, two levels) using a nested three-way model III ANOVA under the null hypothesis that the intertidal variation in these variables is independent of sub-areas (interaction term: sub-area (area) $\times$ tidal level) or of areas (interaction term: area $\times$ tidal level). The a posteriori SNK test was employed to verify specific differences among sub-areas and between tidal levels and areas if interaction terms were significant.

Comparisons between the intertidal areas—abundance and size (Question 5)

The abundance and size of *T. mactroides* were also compared between areas. The individuals were collected using six samples (quadrats of 0.50×0.50 m) at each tidal level (0.0 and 0.4 m) and sub-area (the same as described above), totalling 48 sampling units in each area. The sediment was washed in a 3-mm mesh sieve. The individuals were then counted, measured (shell length, mm), and returned alive to the sea. The abundance (individuals/quadrat) and size of *T. mactroides* were then compared between areas, sub-areas nested in areas, and tidal levels using a nested three-way model III ANOVA. Specifically, this design was developed to test the null hypothesis that the intertidal patterns of distribution in clam size and abundance did not depend on the area or sub-area being sampled (interaction terms: area $\times$ tidal level and sub-area (area) $\times$ tidal level, respectively). The a posteriori SNK test was also employed to verify specific differences among sub-areas and between tidal levels and areas if the interaction terms were significant.

Results

Along-shore distribution—abundance patterns (Question 1)

A total of 5177 individuals of *Tivela mactroides* was obtained in the three 30-m long dredgings at each of the 14 sampling stations in the shallow subtidal of Caraguatatuba Bay. These clams showed an irregular along-shore distribution in this habitat (fourth-root transformation; ANOVA: $F_{(13, 28)}=22.13$, $P<0.001$; Figure 2). In general, the southern part (stations 2–7) of the bay had higher and more constant numbers of individuals than did the northern part (stations 8–14). Fewer clams were found at stations 1, 10, 11, and 13. At station 1, the sediment was very fine and the beach profile was characteristic of a tidal flat. Stations 8–13 yielded sea-stars (*Astropecten marginatus* Gray, 1840, 5–30 individuals per dredging), which generally had juvenile clams in their stomachs (visible externally by protuberances). A large number of sand-dollars (*Mellita quinquiesperforata* (Leske, 1778), 30–50 individuals per dredging) was also recorded at station 13. At station 14, where the number of clams was relatively high, there were many hermit crabs (*Isocheles sawayai* Forest and Saint Laurent, 1967, 20–30 individuals per dredging).

Intertidal across-shore distribution—abundance and size (Question 2)

For this purpose, 2532 individuals were sampled in Caraguatatuba Bay along intertidal levels in one 50-m wide perpendicular sector in each of the two areas studied: southern (72

Figure 2. Along-shore variation in the number of individuals ($\pm$ SE; $n=3$) of *Tivela mactroides* in the shallow subtidal in Caraguatatuba Bay. The labels indicate the significant differences obtained in the a posteriori SNK test. ANOVA (see text for results) and SNK tests were conducted on fourth-root transformed data. See Figure 1 for location of stations.

quadrats, 1377 individuals) and northern (66 quadrats, 1155 individuals). In the southern area, individuals were mainly found in the strip between tidal levels 0.2 and 0.6 m, whereas in the northern area, the clams were more homogeneously distributed across the intertidal area (Figure 3). The higher across-shore variation in abundance in the southern area was demonstrated by contrasting the abundance of *T. mactroides* in the five previously defined tidal levels (Figure 4; Table I). The size of the individuals also varied in relation to the tidal levels in both areas (Table I), with a tendency towards increased size from the lowest to the highest level (Figure 4). This tendency was more evident in the northern area.

Subtidal across-shore distribution—abundance and size (Question 3)

A total of 2317 individuals was sampled at the five depth intervals in both southern (1572 individuals) and northern (745 individuals) areas. The number of individuals in the subtidal showed higher variability among depths in the southern than in the northern area (Figure 5), and the two-way ANOVA showed that the way clam density varied among depths differed between areas (significant interaction term: area $\times$ depth, Table II). In the southern area, abundance increased from the deepest (4.5 m) to the shallowest (0.5 m) subtidal depth intervals, whereas no variation was evident in the northern area (Figure 5). No individuals were sampled in the 6–7 m depth interval, in either area.

The size distribution patterns for this species differed across depth intervals depending on the area sampled (significant interaction term: area $\times$ depth, Table II). The size of the individuals tended to increase from the deepest to the shallowest levels only in the southern area (Figure 5). No clear size tendency among depths was apparent in the subtidal of the northern area. The abundance and size of the individuals in the shallowest subtidal depth

Figure 3. Zonation (mean number of individuals per quadrat $\pm$ SE; $n=6$) of *Tivela mactroides* in the intertidal region of the southern and northern areas of Caraguatatuba Bay in relation to MLW. Tidal levels correspond to different distances from -0.2 m in the two areas.

(0.5 m) tended to be higher than at the same level in the northern area (Figure 5). For the other depth intervals, the abundance and size of *T. mactroides* was roughly similar.

Comparisons between the intertidal areas—physical variables (Question 4)

The intertidal areas (southern and northern) and levels (0.0 and 0.4 m) were compared in relation to physical variables (beach slope and sediment constitution). Marked differences in the beach slope were shown between and within (sub-areas) the study areas (southern and northern, Figure 6), emphasized by the mean elevation, standard deviation of

Figure 4. Mean number of individuals per quadrat ($\pm$ SE; $n=6$) and mean shell length (mm; $\pm$ SE; n is variable) in the two areas (southern and northern) and in the different tidal levels (in relation to MLW) in Caraguatatuba Bay. The comparisons (one-way ANOVA) among tidal levels within each area are presented in Table I. The letters (southern) and the numbers (northern) represent the results of the a posteriori SNK test. The horizontal bar indicates non-significant differences in the SNK test.

Table I. One-way model I ANOVA for the mean number of individuals per quadrat (fourth-root transformed only in the southern area, $n=6$) and mean shell length (mm, n is variable) among tidal levels (fixed factor, southern—five levels: -0.2 , 0.0 , 0.2 , 0.4 , and 0.6 m, northern—four levels: -0.2 , 0.0 , 0.2 , and 0.4 m).

Source of variation	MS	df	<i>F</i>	<i>P</i>
Number of individuals per quadrat				
Southern area				
Tidal level	0.8341	4	12.48	<0.001
Residual	0.0668	25		
Northern area				
Tidal level	5.6111	3	0.27	0.847
Residual	20.8549	20		
Shell length (mm)				
Southern area				
Tidal level	75.3116	4	9.13	<0.001
Residual	8.2528	653		
Northern area				
Tidal level	816.0616	3	49.03	<0.001
Residual	16.6425	411		

elevation, and total beach height (Figure 7; Table III). The slope profile was wider, flatter, and more homogeneous in the southern area. The profile in the northern area was steeper, narrower, and more heterogeneous, showing higher elevations and standard deviation of elevation. This heterogeneity was evidenced by a low-tide terrace subjacent to a steeply sloping high intertidal. The northern area also showed higher variation among sub-areas in mean elevation and standard deviation of elevation (non-significant values in the southern area). The opposite situation was observed for the total height of the beach, with higher variability in the southern area and non-significant differences in the northern area (Figure 7).

Comparison of the mean grain size and sorting coefficient of the sediment revealed a significant interaction between tidal levels and both areas and sub-areas (Table III). Data interpretation was only possible for each sub-area independently (Figure 8), but in general, the sand was coarser and more poorly sorted at the 0.4 m tidal level in comparison to the 0.0 m tidal level (for exceptions see Figure 8), and more marked variations in grain size and sorting coefficient between tidal levels were reported in the southern than in the northern area (note that the steeply sloping coarse sand of the northern area was not included in this analysis; this part of the intertidal was above the 0.4 m tidal level).

Comparisons between the intertidal areas—abundance and size (Question 5)

As with the physical variables, the intertidal areas (southern and northern) and levels (0.0 and 0.4 m) were also compared in relation to abundance and size of *T. mactroides*. The number of individuals, compared between the two tidal levels (0.0 and 0.4 m) of the southern and northern areas, did not show differences for any of the spatial scales tested (area, sub-area, and tidal level, Table IV). However, higher abundances tended to occur in the northern area than in the southern one and, when differences occurred, at the upper (0.4 m) tidal level than the lower one (0.0 m) (Figure 9). These differences between tidal levels were evident only when clam density was high (>20 individuals per quadrat).

The size of the individuals varied significantly between tidal levels only in the northern area (sub-areas analysed independently; Figure 9), with the larger individuals occurring at

Figure 5. Mean number of individuals (fourth-root transformed; $\pm$ SE; $n=5$) and mean shell length (mm; $\pm$ SE; n is variable) in the two areas (southern and northern) and at different subtidal depths in Caraguatatuba Bay. The comparisons (two-way ANOVA) between areas and among depths are presented in Table II. The letters (southern) and the numbers (northern) represent the results of the a posteriori SNK test, and the horizontal bar indicates non-significant differences in the SNK test.

Table II. Two-way model I ANOVA for the mean number of individuals per transect (fourth-root transformed, $n=5$) and mean shell length (mm, n is variable) between areas (fixed factor, two levels: southern and northern) and among subtidal depths (fixed factor, three levels: 0.5, 2.5, and 4.5 m).

Source of variation	MS	df	<i>F</i>	<i>P</i>
Number of individuals per transect				
Area	0.0940	1	0.09	0.761
Depth	8.6489	2	8.68	0.002
Area $\times$ depth	5.2745	2	5.29	0.013
Residual	0.9968	24		
Shell length (mm)				
Area	74.4245	1	10.35	0.001
Depth	2843.7661	2	395.46	<0.001
Area $\times$ depth	414.1612	2	57.60	<0.001
Residual	7.1915	24		

the upper tidal level. Despite the marked variation in shell size among sub-areas, individual clams tended to be larger in the southern than in the northern area (Figure 9).

These results showed a non-consistent zonation pattern in clam size and abundance among sub-areas (see Table IV, significant interaction factor: sub-area (area) $\times$ tidal level), although the over-all tendency of increase in number of individuals and shell size was equivalent in the two areas (see Table IV, non-significant interaction factor: area $\times$ tidal level).

Figure 6. Average profile of the southern and northern areas in Caraguatatuba Bay. The distance of 0 m (x -axis) corresponds to the beginning of the vegetation in the dry sand zone (southern) and at the berm (northern).

Table III. Results of the nested two-way model III ANOVA (sub-area nested in area, four levels) for the mean elevation (cm), mean standard deviation of elevation (cm, fourth-root transformed), and mean total beach height (cm) between areas (fixed factor, two levels: southern and northern; $n=3$); results of the nested three-way ANOVA (sub-area nested in area, four levels) for the mean grain size (phi) and mean sorting coefficient (phi, $n=6$) of the sediment between areas (fixed factor, two levels: southern and northern) and tidal levels (fixed factor, two levels: 0.0 and 0.4 m).

Source of variation	MS	df	F	P
Mean elevation (cm)				
Area	222.4068	1	51.62	<0.001
Sub-area (area)	4.3089	6	15.25	<0.001
Residual	0.2825	24		
Mean standard deviation of elevation (cm)				
Area	3.5380	1	421.76	<0.001
Sub-area (area)	0.0084	6	15.54	<0.001
Residual	0.0005	24		
Mean total beach height (cm)				
Area	37,604.1667	1	107.21	<0.001
Sub-area (area)	350.7500	6	3.62	0.018
Residual	96.8333	24		
Mean grain size (phi)				
Area	0.0037	1	0.28	0.618
Tidal level	0.3234	1	41.09	<0.001
Sub-area (area)	0.0133	6	10.01	<0.001
Area $\times$ tidal level	0.0588	1	7.47	0.034
Sub-area (area) $\times$ tidal level	0.0079	6	5.94	<0.001
Residual	0.0013	80		
Sorting coefficient (phi)				
Area	0.0001	1	0.01	0.938
Tidal level	0.1018	1	9.40	0.022
Sub-area (area)	0.0154	6	5.14	<0.001
Area $\times$ tidal level	0.0668	1	6.17	0.048
Sub-area (area) $\times$ tidal level	0.0108	6	3.62	0.008
Residual	0.0030	80		

Discussion

Along-shore distribution

Except for a few stations, *Tivela mactroides* was roughly homogeneously distributed along Caraguatatuba Bay. A relatively high number of individuals was recorded at almost all the sampling stations, especially on the northern sides of the mouths of important rivers in this area, in accordance with previous reports by McLachlan et al. (1996) for other populations of this species. According to these authors, the water in river mouths has a high organic-matter content, thus contributing to the suspension-feeding habit of *T. mactroides*.

Tivela mactroides dominated the benthic community of Caraguatatuba Bay, reaching densities of 388 individuals per m² (over-all mean 77 individuals per m²) in the intertidal. Although dredging did not allow density estimates, we suppose that the density of small-sized individuals in the subtidal may reach considerably higher values. Other studies

Figure 7. Mean elevation (cm; $\pm$ SE; $n=4$), standard deviation of elevation (cm; $\pm$ SE; $n=4$), and total height of the beach (cm; $\pm$ SE; $n=4$) in the southern and northern areas in Caraguatatuba Bay. Data are presented for each area and sub-area. The results of a nested two-way ANOVA are presented in Table III. The letters represent the results of the a posteriori SNK test, and the horizontal bars indicate non-significant differences in the SNK test.

Figure 8. Mean grain size (ϕ ;+SE; $n=4$) and sorting coefficient (ϕ ;+SE; $n=4$) in the four sub-areas in the southern and northern areas in Caraguatatuba Bay and in the 0.0 and 0.4 m tidal levels (in relation to MLW). Data are presented for each area and sub-area. The results of the nested three-way ANOVA are presented in Table III. The horizontal bars indicate non-significant differences in the SNK test.

revealed similar (220 individuals per m^2 ; Brito 1984) to higher (1024 individuals per m^2 ; Prieto 1983) densities in areas where *T. mactroides* was also harvested. High densities are common in populations of this species, and are attributed to its suspension-feeding habit

Table IV. Nested three-way model III ANOVA (sub-area nested in area, four levels) for the mean number of individuals per quadrat (fourth-root transformed, $n=6$) and mean shell length (mm, n is variable) between areas (fixed factor, two levels: southern and northern) and tidal levels (fixed factor, two levels: 0.0 and 0.4 m).

Source of variation	MS	df	F	P
Number of individuals per quadrat				
Area	2.7853	1	2.74	0.149
Tidal level	1.6026	1	3.49	0.111
Sub-area (area)	1.0157	6	19.01	<0.001
Area $\times$ tidal level	0.0014	1	<0.01	0.958
Sub-area (area) $\times$ tidal level	0.4587	6	8.58	<0.001
Residual	0.0534	80		
Shell length (mm)				
Area	18,022.6310	1	73.19	<0.001
Tidal level	1306.4200	1	21.70	0.003
Sub-area (area)	246.2460	6	27.55	<0.001
Area $\times$ tidal level	209.1516	1	3.47	0.112
Sub-area (area) $\times$ tidal level	60.2050	6	6.73	<0.001
Residual	8.9394	1833		

(Narchi 1972) and the wave action that constantly suspends the terrigenous sediments deposited on the bottom of the areas where this species occurs (McLachlan et al. 1996).

Other organisms co-occurred with *Tivela mactroides* in some parts of the subtidal region, and may at some level influence its abundance. The sea-star *Astropecten marginatus* was recorded (5–30 individuals per dredge) only between stations 8 and 12. Many individuals of this species had young (small) individuals of *T. mactroides* in their stomachs, which could be seen by external protuberances in the aboral surface of the sea-stars (personal observation). This finding may indicate that the predatory activity of *A. marginatus* on *T. mactroides* may be responsible for decreasing clam densities, at least at stations 10 and 11. The sand-dollar *Mellita quinquesperforata* (30–50 individuals per dredge) was recorded only at station 13, and may be competing for space with *T. mactroides*. The presence of the sand-dollar may prevent water circulation through the siphons of the clam and, as a consequence, cause clam mortality. Contrariwise, the density of *T. mactroides* was very high at the only station where the hermit crab *Isocheles sawayai* was recorded. This may suggest that this hermit crab species did not have any negative effect on the clam, although there are reports that the con-generic *I. wurdemanni* Stimpson, 1858 preys upon *T. mactroides* (Prieto 1987). Similarly, the hermit crab *Clibanarius vitattus* (Bosc, 1802) was considered by Prieto (1983) as the most important predator of this clam on a Venezuelan beach. Despite the indirect results found here, specific studies are necessary to demonstrate the importance of these co-occurring organisms (sea-stars, sand-dollars, hermit crabs, and even fish) in regulating the abundance of *T. mactroides*.

Across-shore distribution

Narchi (1972, 1974) reported *T. mactroides* to be intertidal, occurring in the swash zone, in Ubatuba Bay in south-eastern Brazil. Etchevers (1976) and Prieto (1983) recorded it only on shallow subtidal flats in the Caribbean. McLachlan et al. (1996) suggested that these differences represent a latitudinal change in the distribution of this species. The present study showed that *T. mactroides* occurs from the upper intertidal zone until about 5 m in the subtidal. Narchi (1972, 1974) probably sampled only in the intertidal or used a sampling

Figure 9. Mean number of individuals (fourth-root transformed; +SE; $n=4$) and mean shell length (mm; +SE; n =variable) in the four sub-areas in the southern and northern areas in Caraguatatuba Bay and in 0.0 and 0.4 m (in relation to MLW). The comparisons (two-way ANOVA) between areas and between tidal levels are presented in Table IV. The horizontal bars indicate non-significant differences in the SNK test.

method that was not adequate to sample the smaller individuals in the subtidal. On the other hand, the microtidal regime in the Caribbean probably does not allow the exposure of the shallow subtidal flats where *T. mactroides* occurs. Apart from tides, which have a maximum range of 2 m in south-eastern Brazil, the areas studied by Narchi (1972, 1974),

Etchevers (1976) and Prieto (1983) are physically similar to the northern area of Caraguatatuba Bay. They have a steep, coarse-sand, upper intertidal-supralittoral fringe and a subjacent low tide, or shallow subtidal, fine-sand terrace and are typical of morphodynamically tide-dominated environments (Short 1996).

The clams in the southern area preferentially occupied the strip encompassed between the 0.2 and 0.4 m intertidal levels, reaching a distribution limit at 0.8 m. In contrast, the clams in the northern area showed a homogeneous distribution in the intertidal zone and did not occur above the 0.4 m level. Vertical variations in the distribution of *T. mactroides* were also reported by Etchevers (1976). This author observed that *T. mactroides* occupied the deepest areas (up to 3 m) in the subtidal zone, where it co-occurred with two other bivalve species of the genus *Donax*. *Donax hanleyanus* Philippi, 1847 is a common species associated with intertidal coarse sediments of Brazilian reflective beaches (Cardoso and Veloso 2003), and was recorded in sympatry with *T. mactroides* by Narchi (1972, 1974), and in the present study in the northern area, where it occupied only the upper intertidal. *Tivela mactroides* never occupied this strip even when *D. hanleyanus* was absent. Therefore, these differences in shore-level distribution of *T. mactroides* are more likely attributable to morphodynamic along-shore changes rather than a competitive interaction with *D. hanleyanus*. The southern area is flatter, more homogeneous, and has finer sand than the northern area, thus allowing the water to reach higher levels and to drain more slowly. These differences in the intertidal distribution may also be a consequence of the larger size of the individuals in the southern than those in the northern area, i.e. the larger the individuals, the higher their tolerance to desiccation and the farther landwards their distribution.

In fact, individuals showed a tendency to increase in size along a gradient from the subtidal to the intertidal boundaries of their distribution. This peculiar distribution pattern has been observed in other high-density populations of beach clams around the world (McLachlan et al. 1996), but not for *T. mactroides*. Individuals seem to recruit in depths of about 2–5 m, ending their life cycle in the intertidal zone, thus leading to an ontogenic differential across-shore distribution. The vertical migratory process may be possible because of the passive drift of individuals generated by the environmental dynamics, such as waves and tides (see Etchevers 1976; Prieto 1983).

This distribution pattern, in which shell size tends to increase in an upshore direction, is similar to that of type 1 described by Vermeij (1972) for intertidal rocky shore species. According to this author, there are more pre-reproductive individuals in the zone of minimal mortality (subtidal) within the vertical range of the species because their survival is necessary to the maintenance of the population as a whole. The intertidal levels may be critical for *T. mactroides*, because of high mortality caused by natural disturbance, such as extended rainy periods and dry seasons, and extended low tide periods associated with high temperatures and sea storms. These stochastic events may be responsible for mass mortality of clams (McLachlan et al. 1996; Defeo 2003; personal observation), and consequently responsible for regulating their densities and for causing periodic renewal of individuals in the population.

Another hypothesis for the absence of small individuals in the vicinity of the adults, i.e. in the intertidal zone, may be involuntary cannibalism (passive filtering) of larvae by suspension-feeding conspecific individuals (Woodin 1976). Fitch (1965), studying populations of the pismo clam *T. stultorum* (Mawe, 1823) in California, verified the absence of recruits in a higher adult-density environment and hypothesized that the conspecific adults remove the larvae from the water column before their settlement.

The sustainable use of this species may be guaranteed by the resettlement of individuals in the capture zone (intertidal and shallow subtidal up to 1.0 m depth), through migration of smaller individuals from the subtidal. Nothing is yet known about resettlement rates in this population, but it may be under the control of subtidal predators (sea-stars, fish, blue crabs, and hermit crabs), larval cannibalism, or bottom disturbance by shrimp trawling, which is a common fishing practice in Caraguatatuba Bay. In contrast, the ontogenic segregative distribution in this population may reduce the risk of incidental mortality from harvesting of other species of clams (McLachlan et al. 1996).

Comparisons between areas

Despite the great environmental variability along the 16 km extent of Caraguatatuba Bay, *T. mactroides* was able to occupy the whole area. Based on the universal consensus for sandy beach ecology that environmental characteristics, such as sediment grain size and beach slope, are the principal factors structuring the macrofauna (McLachlan 1983), spatial distribution of *T. mactroides* was compared between two particular environment types in Caraguatatuba Bay. The southern area had a gentle continuous beach slope, while the northern area had a steeper slope in the high intertidal associated with a low intertidal terrace. Sediment grain size and sorting coefficient were roughly similar for the two areas at the tidal levels considered (0.0 and 0.4 m), and thus did not explain the differences in clam density and size between these areas.

Etchevers (1976) and Prieto (1983) hypothesized a transport of larvae and newly settled individuals by drift currents to explain differential along-shore distribution by size. This hypothesis cannot be applied to the situation in Caraguatatuba Bay, because it does not explain the absence of adults from the areas occupied by the juveniles in the across-shore gradient. Moreover, drift currents are a limited mode of transport for *T. mactroides*, which frequently remain buried instead of continuously migrating with the tides as observed for *Donax serra* (Röding, 1798) (Donn 1987). Passive migration in *T. mactroides* seems to be limited to the across-shore scale, and may continue during its entire life.

The higher density of *T. mactroides* in the northern area may be also caused by differential human exploitation of the clams between the two areas. In the northern area, fishermen collected small individuals (20–25 mm), while in the southern area the individuals were on average larger than 30 mm, a size generally selected by the fishermen in this region. Additional reasons for the smaller size of the clams in the northern area may be previous over-exploitation or mass mortality in this area, which could have provided space for new, small-sized migrating individuals. These arguments may suggest an important role of human exploitation in the abundance and size structure of this *T. mactroides* population, which merits further investigation.

Final considerations

This study showed that the structure of the population of *T. mactroides* in Caraguatatuba Bay varies over both along- and across-shore scales, and suggested that abundance and size of the individuals may be regulated by different factors. A complex and dynamic environment, with its intrinsic variability in biotic and abiotic factors, may be acting on populations of this species. Consequently, the spatial variability recorded here should be taken into account in the design of future population and monitoring studies on *T. mactroides*. Any study on the ecology of these clams should focus on both the intertidal

and subtidal environments in order to record the population as a whole. The along-shore distribution also needs to be taken into account at different scales and hierarchically replicated (quadrats, transects, sub-areas, areas; see Underwood 1991). In addition, as the along- and across-shore pattern in density and size of the individuals was suggested to be influenced by pulses of recruitment, as also recorded for *T. stultorum* (Fitch 1950), the importance of long-term temporal replication is reinforced.

Finally, to understand the factors that influence the spatial and temporal structure of this population, as well as the ontogenic segregation, a series of experimental studies is needed to investigate larval preferences and tolerances, density-dependent recruitment, and the effect of predation. A long-term monitoring study of the environmental factors and of the population growth, maximum sustainable yield, and reproductive cycle would certainly furnish a solid basis for the establishment of future policies for the sustainable use of this resource.

Acknowledgements

This study is part of the Biota/FAPESP Program, the Brazilian Virtual Institute of Biodiversity. We are grateful to the Fundação de Auxílio à Pesquisa do Estado de São Paulo (FAPESP) for research and fellowship grants, and to Project A.W.A.R.E. Foundation and PADI Foundation for research grants. Thanks also for the valuable comments from an anonymous referee of the *Journal of Natural History*, and to Janet W. Reid for English revision.

References

- Arruda-Soares H, Schaeffer-Novelli Y, Mandelli J Jr. 1982. "Berbigão" *Anomalocardia brasiliiana* (Gmelin, 1791), bivalve comestível da região da Ilha do Cardoso, Estado de São Paulo, Brasil: aspectos biológicos de interesse para a pesca comercial. *Boletim do Instituto de Pesca* 9:21–38.
- Brenchley GA. 1982. Mechanisms of spatial competition in marine soft-bottoms communities. *Journal of Experimental Marine Biology and Ecology* 60:17–34.
- Brito PJ. 1984. Algunos aspectos de la dinámica poblacional del guacuco (*Tivela mactroides* Born, 1778) em dos localidades de Barlovento [dissertation]. Caracas: Universidad Simón Bolívar, División de Ciencias Biológicas.
- Cardoso RS, Veloso VG. 2003. Population biology and secondary production of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) on a high-energy, subtropical beach of Brazil. *Marine Biology* 142:153–162.
- Castro-Ortiz JL, García-Domínguez F. 1993. Crecimiento de *Chione californiensis* (Broderip, 1983) (Veneridae) en la ensenada de la paz, Baja California Sur, México. *Investigaciones Marinas CICIMAR* 8:45–52.
- Clasing E, Brey T, Stead R, Navarro J, Asencio G. 1994. Population dynamics of *Venus antiqua* (Bivalvia: Veneracea) in the Bahía de Yaldad, Isla de Chiloé, Southern Chile. *Journal of Experimental Marine Biology and Ecology* 177:171–186.
- de Alava A, Defeo O. 1991. Distributional pattern and population dynamics of *Excirolana armata* (Isopoda: Cirolanidae) in a Uruguayan sandy beach. *Estuarine, Coastal and Shelf Science* 33:433–444.
- de Montaudouin X, Bachelet G. 1996. Experimental evidence of complex interactions between biotic and abiotic factors in the dynamics of an intertidal population of the bivalve *Cerastoderma edule*. *Oceanologica Acta* 19:449–463.
- Defeo O. 2003. Marine invertebrate fisheries in sandy beaches. *Journal of Coastal Research, Special Issue* 35:56–65.
- Defeo O, de Alava A. 1995. Effects of human activities on long-term trends in sandy beach populations: the wedge clam *Donax hanleyanus* in Uruguay. *Marine Ecology Progress Series* 123:73–82.
- Defeo O, Jaramillo E, Lyonnet A. 1992. Community structure and intertidal zonation of the macroinfauna on the Atlantic coast of Uruguay. *Journal of Coastal Research* 8:830–839.
- DHN (Diretoria de Hidrografia e Navegação). 2002. *Tabuas das Marés 2002*. São Paulo: Edições Náuticas. 18 p.
- Donn TE. 1987. Longshore distribution of *Donax serra* in two log-spiral bays in the eastern Cape, South Africa. *Marine Ecology Progress Series* 35:217–222.

- Etchevers SL. 1976. Notas ecológicas y cuantificación de la población de guacuco, *Tivela mactroides* (Born, 1778) (Bivalvia-Veneridae), en la Ensenada de la Guardia, Isla de Margarita, Venezuela. Boletim del Instituto Oceanográfico de la Universidad del Oriente 15:57–64.
- Fitch JE. 1950. The pismo-clam. California Fish and Game 36:285–312.
- Fitch JE. 1965. A relatively unexploited population of pismo clams, *Tivela stultorum* (Mawe, 1823) (Veneridae). Proceedings of the Malacological Society of London 36:309–312.
- Folk RL, Ward WC. 1957. Brasos river bar—a study in the significance of grain size parameter. Journal of Sedimentary and Petrology 27:3–27.
- Hanekom N. 1986. Growth and somatic production estimates of *Dosinia hepatica* (Lamarck) (Mollusca: Bivalvia) in the Swartkops estuary, South Africa. South African Journal of Zoology 21:325–330.
- Hines AH, Posey MH, Haddon PJ. 1989. Effects of adult suspension- and deposit-feeding bivalves on recruitment of estuarine infauna. The Veliger 32:109–119.
- James RJ, Fairweather PG. 1996. Spatial variation of intertidal macrofauna on a sandy ocean beach in Australia. Estuarine, Coastal and Shelf Science 43:81–107.
- Jaramillo E, McLachlan A, Coetzee P. 1993. Intertidal zonation patterns of macroinfauna over a range of exposed sandy beaches in south-central Chile. Marine Ecology Progress Series 101:105–118.
- Lercari D, Defeo O. 1999. Effects of freshwater discharge in sandy beaches populations: the mole crab *Emerita brasiliensis* in Uruguay. Estuarine, Coastal and Shelf Science 49:457–468.
- McLachlan A. 1983. Sandy beach ecology: a review. In: McLachlan A, Erasmus T, editors. Sandy beaches as ecosystems. The Hague: W. Junk Publishers. p 321–380.
- McLachlan A. 1996. Physical factors in benthic ecology: effects of changing sand particles size on beach fauna. Marine Ecology Progress Series 131:205–217.
- McLachlan A, Dugan JE, Defeo O, Ansell AD, Hubbard DM, Jaramillo E, Penchaszadeh PE. 1996. Beach clam fisheries. Oceanography and Marine Biology Annual Review 34:163–232.
- Monti D, Frenkiel L, Moueza M. 1991. Demography and growth of *Anomalocardia brasiliensis* (Gmelin) (Bivalvia: Veneridae) in a mangrove, in Guadalupe (French West Indies). Journal of Molluscan Studies 57:249–257.
- Moore HB, Lopez NN. 1969. The ecology of *Chione cancelata*. Bulletin of Marine Science 19:131–148.
- Narchi W. 1972. Comparative study of the functional morphology of *Anomalocardia brasiliensis* (Gmelin, 1791) and *Tivela mactroides* (Born, 1778) (Bivalvia, Veneridae). Bulletin of Marine Science 22:643–670.
- Narchi W. 1974. Aspectos ecológicos e adaptativos de alguns bivalves do litoral paulista. Papéis Avulsos de Zoologia, São Paulo 27:235–262.
- Peterson CH. 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension feeding bivalves, *Protothaca staminea* and *Chione undatella*. Ecological Monographs 52:437–475.
- Prieto AS. 1983. Ecología de *Tivela mactroides* Born, 1778 (Mollusca, Bivalvia) en Playa Güiria (Sucre, Venezuela). Boletim del Instituto Oceanográfico de la Universidad del Oriente 22:7–19.
- Prieto AS. 1987. Ecología de *Tivela mactroides* (Born, 1778) (Mollusca: Bivalvia), crecimiento, mortalidad numérica, eliminación y rendimiento en la localidad de Playa Guiria (Sucre, Venezuela) [dissertation].. Cumana (Venezuela): Universidad de Oriente, Departamento de Biología.
- Rhoads DC, Young DK. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. Journal of Marine Research 28:150–178.
- Rios EC. 1994. Seashells of Brazil. Rio Grande: Fundação Universidade do Rio Grande. 492 p.
- Shaeffer-Novelli Y. 1980. Análise populacional de *Anomalocardia brasiliensis* (Gmelin, 1791), na praia do Saco da Ribeira, Ubatuba, Estado de São Paulo. Boletim do Instituto Oceanográfico, São Paulo 29:351–355.
- Short AD. 1996. The role of wave height, period, slope, tide range and embaymentisation in beach classifications: a review. Revista Chilena de Historia Natural 69:589–604.
- Suguio K. 1973. Introdução a sedimentologia.. São Paulo: Edgard Bluche/EDUSP. 321 p.
- Thompson JK. 1982. Population structure of *Gemma gemma* (Bivalvia: Veneridae) in South San Francisco Bay, with a comparison to some Northeastern United States estuarine populations. The Veliger 24:281–290.
- Underwood AJ. 1991. Beyond BACI: experimental designs to detecting human environmental impacts on temporal variations in natural populations. Australian Journal of Marine and Freshwater Research 42:569–587.
- Underwood AJ. 1997. Experiments in ecology—their logical design and interpretation using analysis of variance. Cambridge: Cambridge University Press. 504 p.
- Vermeij GJ. 1972. Intraspecific shore-level size gradients in intertidal molluscs. Ecology 53:693–700.
- Wentworth CK. 1922. A scale of grade and terms for clastic sediments. Journal of Geology 30:377–392.
- Woodin SA. 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. Journal of Marine Research 34:25–41.