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ORIGINAL ARTICLE

The clam *Neilonella sulculata* in San Jorge Gulf (Argentina, Southwest Atlantic): spatial distribution pattern and inverse relationship between size and density

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ABSTRACT

Neilonella sulculata is a dominant bivalve on muddy bottoms of the continental shelf and gulfs off Argentina (Southwest Atlantic). Two benthic surveys performed in 2007 and 2009 in San Jorge Gulf, a depositional area characterized by silt/clay sediments, gave us the opportunity to test whether the population of this clam displays a significant spatial structure and to analyse if there is an inverse relationship between size and density. Density, biomass and size–frequency distribution displayed significant spatial structure, being positively autocorrelated at the smallest spatial scales (c. 1.7–14/17 km). Biomass also showed spatial contiguity at scales of 25–33 km. A substantial increase in density and biomass occurred between 2007 and 2009. Empty valves in the sediment showed that the maximum size attained by the species may exhibit considerable variation at relatively short temporal scales. Regardless of temporal changes in density and biomass, the spatial structure of these variables remained stable. In densely populated areas, shell size decreased with increasing density, suggesting a density-dependent control of growth. A clear north–south increase in density and biomass was detected, which might be related to a gradient in food availability caused by a thermohaline frontal system associated with wind-related upwelling.

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Introduction

Marine benthic invertebrates represent an important link in the recycling of sedimentary organic matter and in the energy flow from primary producers to fish (Bolam et al. 2010). Temporal fluctuations in fishery yields may be linked to changes in density and biomass of macrobenthic communities (Salen-Picard et al. 2002). The estimation of benthic biomass and production is thus of basic importance to the rational management of natural resources (Tumbiolo & Downing 1994).

The scale of analysis chosen for a given study may have profound effects on the spatial patterns found (Wiens 1989; Bellehumeur & Legendre 1998), and the information gathered from these patterns becomes essential for understanding ecological processes (Thrush et al. 1989; Legendre & Legendre 1998; Orensanz et al. 1998). In the marine environment, the spatial distribution pattern of benthic biomass is not random. As a rule, populations of infaunal bivalves are not randomly distributed on the sea bottom, but usually show different degrees of spatial structure (David et al. 1997; Legendre et al. 1997; Morsan 2003; Kraan et al. 2009; Santos et al. 2011; Boldina & Beninger 2013; among others). Spatial autocorrelation may be

induced by a causal relationship with another spatially autocorrelated variable (Fortin et al. 2002). Spatial distribution patterns in infaunal bivalves have been analysed with regard to a range of environmental factors such as depth, sediment characteristics, hydrodynamics, and availability of food to deposit feeders (Legendre et al. 1997; Morsan 2003; Santos et al. 2011, 2012).

Body size or mass of bivalves may be affected by the density of the adult population (Alunno-Bruscia et al. 2000). At low densities, competition is unlikely to be important, and therefore body mass is usually independent of density. At intermediate densities, however, competition begins to have an effect on individuals, and thus body mass tends to decrease with density (Guiñez et al. 2005). Observational (Jensen 1993; Craig 1994; Vincent et al. 1994; Weinberg 1998; Morsan et al. 2011) and experimental (Peterson & Andre 1980; Peterson 1982; Peterson & Black 1987; Vincent et al. 1989) studies dealing with infaunal bivalves have provided evidence about the density-dependent regulation of growth rate due to intra- and interspecific competition for food.

San Jorge Gulf (Argentina, Southwest Atlantic, Figure 1) is an important fishing ground that shelters

fishery resources of high economic value (Góngora et al. 2012). Its central, deeper area is characterized by a uniform prevalence of fine silt to very fine clay (4 to 5 phi units, Fernández et al. 2003). Several demersal fish species occurring in this gulf feed upon benthic organisms, including bivalves (Sánchez & Prenski 1996). Juveniles of the clam *Neilonella sulculata* (Gould, 1852) have also been found among the food items consumed by the red shrimp, *Pleoticus muelleri* (Spence Bate, 1888) (Roux et al. 2009). Due to the great ecological and economic importance of this gulf, a detailed cartography of its sediments (Fernández et al. 2003), an oceanographic synopsis (Glebocki et al. 2015), and a physico-chemical characterization of its benthic environment have been published (Fernández et al. 2005, 2007, 2008).

The present study focused on *N. sulculata*, one of the dominant bivalves on muddy bottoms of the continental shelf and gulfs off Argentina (Roux et al. 1995; Leonardi et al. 1996 as *Nuculana sulculata*). This diatom-feeding species (Leonardi et al. 1996) is not exploited commercially due to its small size. It has a Magellanic distribution spanning the southern tip of South America, from off the Río de la Plata estuary (36°S) in the Southwest Atlantic, up to the Chilean fjord region in the Southeast Pacific, where it has been found in depths ranging from 58 to 237 m (Leonardi et al. 1996; Osorio & Reid 2004 as *Tindariopsis sulculata* Couthouy in Gould, 1852).

Benthic surveys performed on muddy bottoms of San Jorge Gulf gave us the opportunity to address the following questions: (1) Can spatial patterns be recognized in the distribution of density, biomass and size structure of *N. sulculata*? (2) Are these patterns stable over time? (3) Is there a relationship between density and size in the areas most densely populated by this clam?

Materials and methods

Sampling design

Two benthic surveys were performed during austral spring on board supply vessels chartered to carry out baseline studies in three depositional areas of San Jorge Gulf: *Martes Santo* (13–15 December 2007, 48 samples) and *Mr. Big* (6–10 October 2009, 48 samples). The minimum sampling interval and the extent of the study area (*sensu* Legendre & Legendre 1998) were c. 1.7 km and 95 km, respectively. Samples were arranged in three different zones of uniform topography and granulometry (see Results), hereafter called areas N, Z and S. The fact that area Z

was larger than areas N and S (Figure 1) and that its samples were not arranged in a regular grid allowed us to test whether spatial patterns were present along a more complete range of intermediate scales.

Benthic samples were collected with a 13.49 dm² Van Veen grab. Samples were washed with seawater through a 1 mm mesh sieve. The material retained in the sieve was then fixed in a 5% formaldehyde solution in seawater and preserved in 70% ethanol. All infaunal bivalves present in the samples were identified to species level.

Data analysis

All individuals of *Neilonella sulculata* were separated, counted and their length measured with a micrometer eyepiece under a Zeiss stereoscopic microscope. Measurement error was 0.133 mm. Size–frequency distributions were constructed after grouping the clams in 1 mm size classes. Presence and maximum size of empty valves in the sediment were also recorded.

A length–weight regression was calculated on a subsample of 109 clams by measuring the shells and weighing the dry flesh individually to the nearest mg on a Chyo JK-180 analytical balance. A logarithmic transformation was applied to both variables to make the relationship linear. The flesh dry weight (g) of each individual was then estimated by the following exponential model:

$$\text{dry weight} = (3.27 \times 10^{-6}) \times \text{length}^{3.3407}; R^2 = 0.75.$$

Data normality was tested with the Lilliefors test (Sokal & Rohlf 1995). When data were normal, the bivariate correlations were calculated using the Pearson moment–product coefficient (*r*). If the assumption of normality was not met after trying different transformations, the Spearman rank correlation (*r_s*) was applied instead (Zar 2010). The correlation between median size and density was calculated separately for each survey and area (2007: areas Z and S; 2009: areas N, Z and S).

To assess whether the spatial distribution of *N. sulcata* was significantly different from random, spatial autocorrelation in density (ind. m⁻²) and biomass (g m⁻²) was evaluated using the Moran's *I* statistic (Cliff & Ord 1981), the most commonly used coefficient in univariate autocorrelation analyses of continuous variables (Diniz-Filho et al. 2003). Spatial autocorrelation in size structure was assessed through multivariate Mantel tests (Oden & Sokal 1986; Legendre & Legendre 1998), using the relative frequencies of 1 mm size classes in each sample. Samples without *N. sulculata* were not included in this

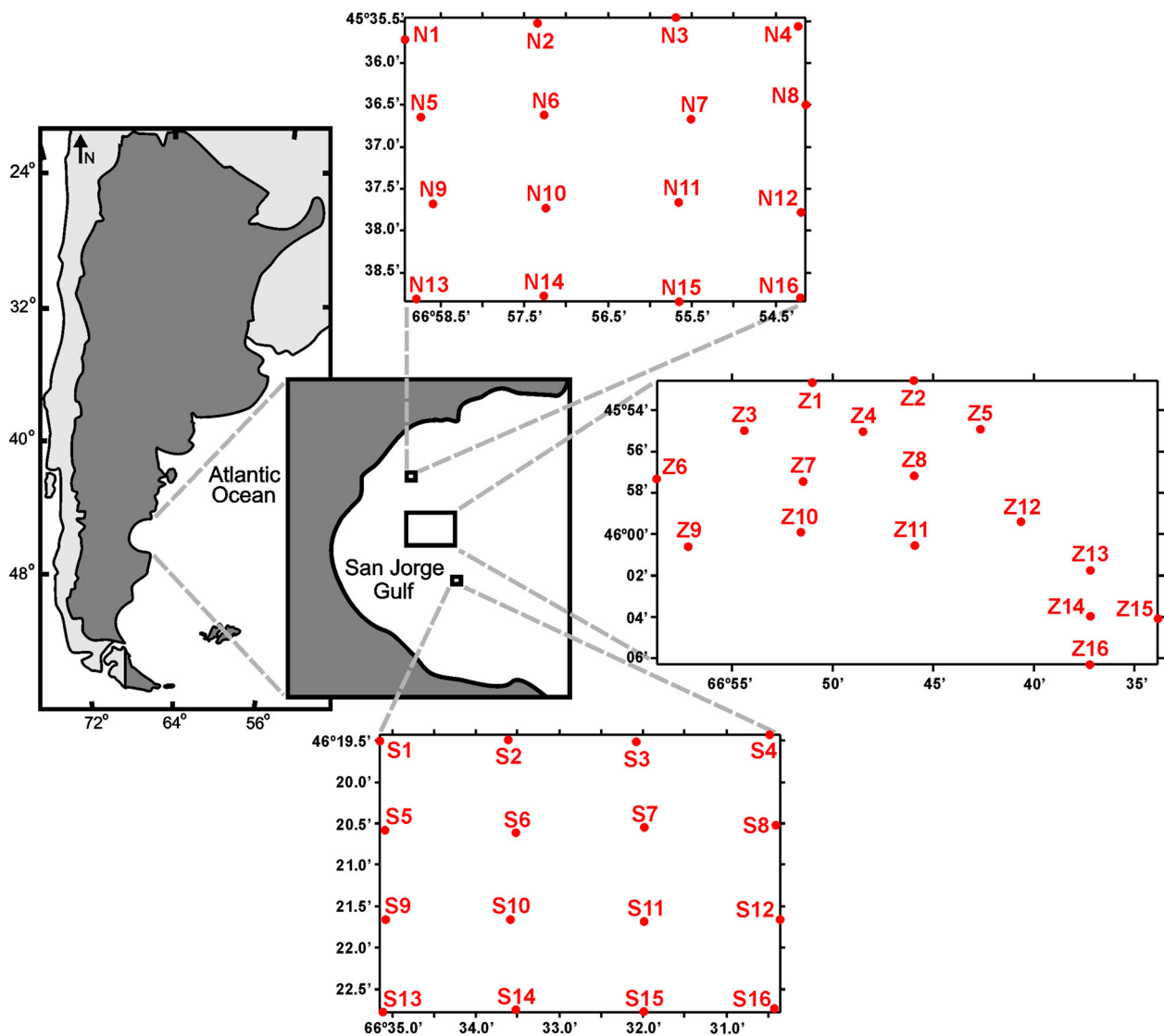


Figure 1. Location of samples in areas N, Z and S, San Jorge Gulf.

analysis. The optimal number of distance classes in an autocorrelogram was obtained by applying the Sturge's rule (Legendre & Legendre 1998). In order to control for the overall Type I error rate in multiple tests, *P*-values were adjusted using Holm's sequential Bonferroni procedure (Abdi 2010).

Data analyses were performed using the statistical programming language and computing environment R (R Development Core Team 2011).

Results

The bottom topography was fairly uniform, with a depth range of only 12 m (N: 88–92 m, mean: 89 m; Z: 87–99 m, mean: 93 m; S: 96–100 m, mean: 98 m).

Neilonella sulculata was the dominant clam in the study area, which was dominated by silt/clay sediments of uniform characteristics. Other infaunal bivalves, such

as *Ennucula puelcha* (d'Orbigny, 1842), *Malletia cumingii* (Hanley, 1860), *Pandora cistula* Gould, 1850 and *Thyasira patagonica* Zelaya, 2010 were found in very low densities.

A total of 5136 live *N. sulculata* ranging from 1.9 to 15.1 mm were found in the 96 samples. A maximum density of 3921 ind. m⁻² was observed in sample S5 in 2009. Empty valves were found in all samples, even in those without living clams. The maximum size of dead clams observed in the sediment was 18.8 mm, i.e. almost 25% greater than the maximum size of living clams collected in the present study.

Clam density was higher in 2009 than in 2007 in all areas (Figure 2). In area N, no clams were found in 2007, while a few individuals (0–15 ind. m⁻²) were found in 2009. In area Z, the abundance of *N. sulculata* was more than 2.5 times higher in 2009 than in 2007, but the trend of increasing densities towards the southeast

of this area remained unchanged. Area S always showed the highest densities, which increased by almost 50% from 2007 to 2009.

A positive autocorrelation in density was observed both in 2007 and 2009 (Figure 3). Densities tended to be similar at the two smallest distance classes (2007: $P < 1.1 \times 10^{-6}$; 2009: $P < 1.3 \times 10^{-7}$), i.e. at scales of 1.7–17.2 km, thus encompassing all the pairwise distances separating samples within the same area in areas N and S, and also the distances between the closest samples within area Z. Moran's I values were non-significant for distances greater than 17.2 km, i.e. for pairwise distances between samples belonging to different areas, and for the longest distances between samples belonging to area Z. This spatial pattern remained unchanged between 2007 and 2009, regardless of the increase in density observed between both surveys.

Biomass showed a similar pattern as that observed for abundance, i.e. it was higher in 2009 than in 2007, and attained the highest values in area S (Figure 2). Although clams reached a larger size in area Z than in area S (Figure 4), biomass variation per unit area mainly depended on the abundance of *N. sulculata*. Biomass spatial structure also displayed a positive autocorrelation both in 2007 and 2009 (2007: $P < 4.0 \times 10^{-4}$; 2009: $P < 1.4 \times 10^{-4}$). The two smallest distance classes (1.7–17.2 km) showed more similar biomass than those involving longer distances (Figure 3). The smallest spatial scales comprise all the distances separating samples belonging to the same area in areas N and S, and the smallest distances between samples belonging to area Z. Moran's I index was also significant (2007: $P < 7.1 \times 10^{-4}$; 2009: $P < 1.3 \times 10^{-4}$) at a scale of 25.0–32.7 km, which mainly includes distances between the closest samples belonging to contiguous areas (N–Z, Z–S). This spatial pattern remained unchanged between 2007 and 2009, regardless of the increase in biomass observed between both surveys.

The population at area Z showed a markedly bimodal size structure in 2007 (modal sizes: 5 and 12 mm) and three modes (3, 8 and 13 mm) in 2009 (Figure 4). At area S, however, the population was dominated by only one cohort with modal sizes of 8 and 9 mm in 2007 and 2009, respectively (Figure 4). Only eight clams were obtained in the 16 samples from area N during the 2009 survey.

Size structure displayed significant autocorrelation both in 2007 and 2009, with neighbouring samples tending to show more similar size structures than those separated by longer distances. In 2007, the Mantel autocorrelogram (Figure 3) showed positive values at the two smallest distance classes ($P < 1 \times$

10^{-4} and $P = 0.0013$, respectively), i.e. at scales of 1.8–14.0 km. These scales included all pairwise distances separating the 16 samples within area S and also distances between the closest samples within area Z. The size structures of areas Z and S were so clearly contrasting (Figure 4) that the Mantel test for the fifth distance class (i.e. 26.2–32.4 km, mostly including Z–S distances) was negative ($P = 0.0063$). In 2009, the Mantel autocorrelogram (Figure 3) showed positive autocorrelation ($P < 1 \times 10^{-4}$) only at the smallest distance class (1.6–10.1 km, i.e. encompassing most distances separating samples from the same area), but no significant size structure contrasts at higher scales.

Median clam size decreased with increasing density in samples from area S (2007: $r = -0.619$, $P = 0.011$, $n = 16$; 2009: $r = -0.664$, $P = 0.005$, $n = 16$), but no correlation between size and density was detected in low-density samples from areas N and Z (2007, area Z: $r_s = 0.141$, $P = 0.645$, $n = 13$; 2009, area N: $r_s = 0.621$, $P = 0.188$, $n = 6$, area Z: $r = 0.533$, $P = 0.074$, $n = 12$).

Discussion

The surveys performed in the present study show that *Neilonella sulculata* is the dominant bivalve on muddy bottoms occupying most of the central part of San Jorge Gulf. We found a clear north–south increase in density and biomass of *N. sulculata*, with minimum and maximum values in areas N and S, respectively. This may be related to the availability of food, since Fernández et al. (2008) found that the horizontal distribution of chlorophyll-*a* in bottom water was characterized by minimum values towards the central area and maximum concentrations in the southern sector of San Jorge Gulf, which may be caused by a thermohaline frontal system associated with wind-related upwelling recently detected near its southern coastal area (Glembocki et al. 2015). The role of upwelling may be crucial for the recruitment and larval dispersion of benthic invertebrate populations (e.g. Poulin et al. 2002; Lagos et al. 2007; Tapia et al. 2009; Pfaff et al. 2011; and references therein). For instance, an upwelling system in the Cantabrian Sea may not only define the spatial scale and direction of the dispersal of a gooseneck barnacle, but also the genetic structure of its metapopulation (Rivera et al. 2013).

As has been previously documented for other infaunal bivalves (David et al. 1997; Legendre et al. 1997; Kraan et al. 2009), the population of *N. sulculata* exhibited significant spatial structure. In general terms, the density, biomass and size structure tended to be similar at the smallest scales, i.e. in samples belonging to the same area, but showed no spatial contagion

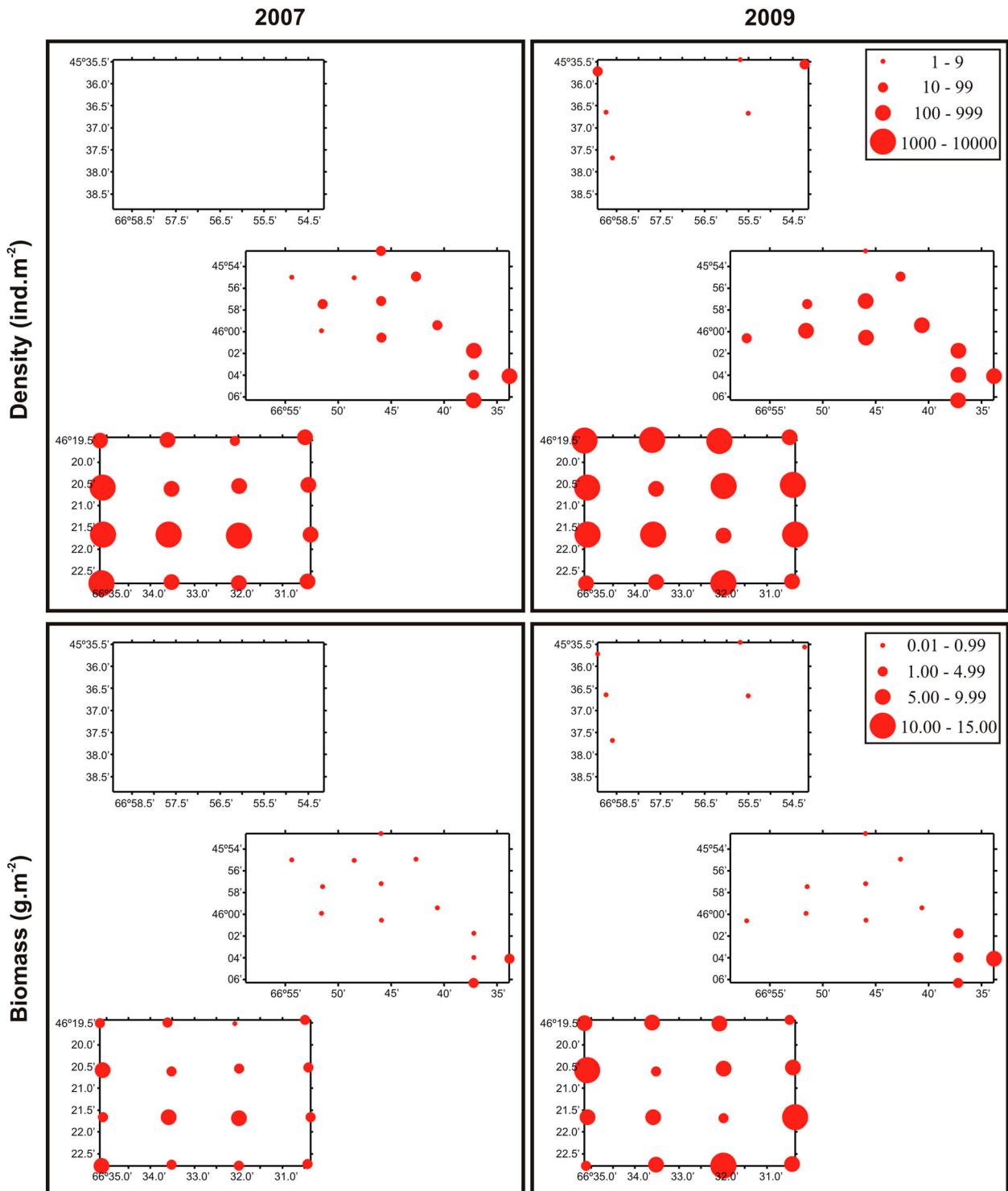


Figure 2. Spatial distribution patterns of density (ind. m⁻²) and biomass (g m⁻²) of *Neilonella sulculata* in areas N (top), Z (middle) and S (bottom) in 2007 and 2009. No living clams were found in area N during the 2007 survey.

among different areas. The exception to this pattern was total biomass, that was also autocorrelated for distances separating the closest samples belonging to contiguous areas. The positive autocorrelation displayed at scales ranging from the smallest sampling interval (~ 1.7 km) up to 14–17 km is related with the

clear-cut north–south gradient observed in this population. Food availability might be regarded as the most likely environmental factor generating this pattern, as *N. sulculata* density and biomass increase with decreasing distances to the thermohaline frontal system having its maximum expression during the

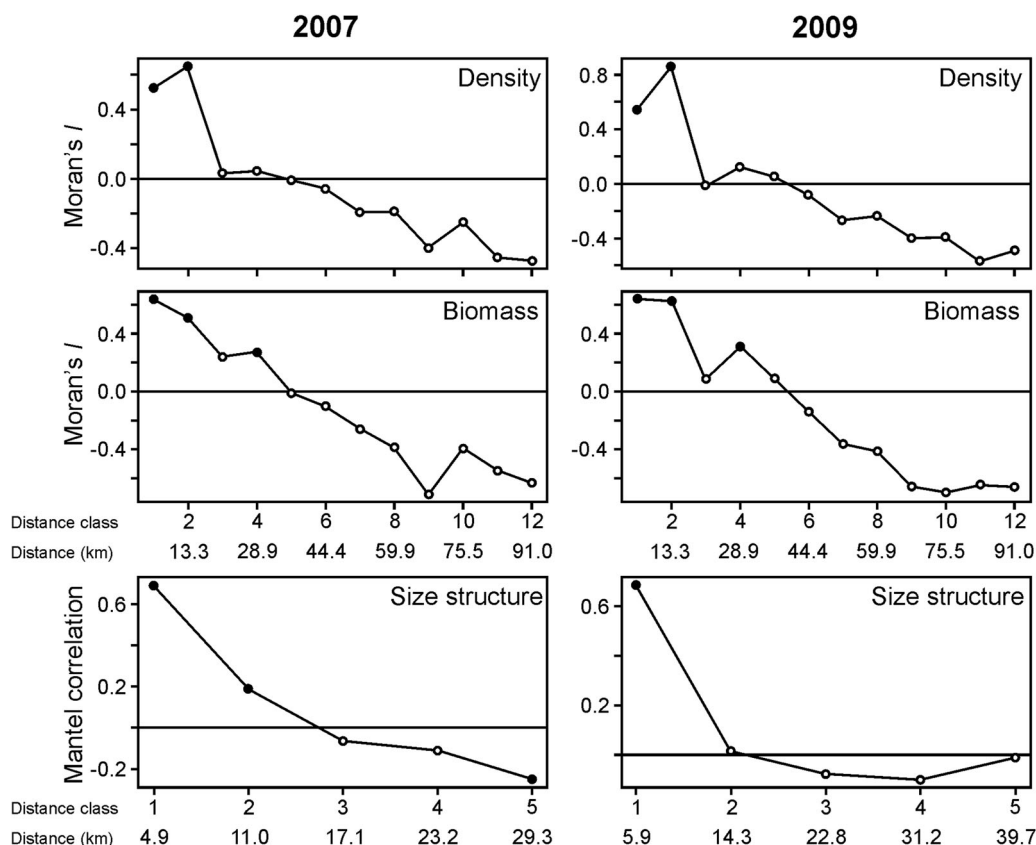


Figure 3. Autocorrelograms of density, biomass and size structure in 2007 and 2009. Horizontal scales show the mid-point of each distance class. Solid circles: $P < 0.05$.

winter near the southern coast of San Jorge Gulf (Glembocki et al. 2015).

This study shows that the population of *N. sulculata* experienced substantial changes in density and biomass between 2007 and 2009. Previous research has demonstrated that the major cause of temporal variation in abundance and production of infaunal bivalves is the inter-annual variation in recruitment (e.g. van der Meer et al. 2001), although post-settlement processes in marine soft sediments may also play a significant role in population regulation (reviewed in Ólafsson et al. 1994). Despite these changes, the spatial pattern of *N. sulculata* remained relatively stable over time. Population density and biomass exhibited substantial differences among sampling areas separated by c. 25 km, but their spatial structure remained constant during the two years elapsed between surveys. Length–frequency distributions, that were strikingly different among sampling areas, remained relatively unchanged between surveys in area S, but not in area Z. Since *N. sulculata* is a fast-growing species (Leonardi et al. 1996), a seasonal or monthly sampling scheme will be necessary to analyse in detail the population dynamics of this clam.

The size range observed in San Jorge Gulf (1.9–15.1 mm) is similar to that found in *N. sulculata* populations on the continental shelf off Buenos Aires province (Leonardi et al. 1996; 2–15.7 mm). Empty shells in the sediment, however, showed that this species may occasionally reach a maximum size of 18.8 mm, i.e. up to 20% larger than the largest size ever measured in a living specimen (see Leonardi et al. 1996). This may be explained by time-averaging of naturally variable populations, a phenomenon by which death assemblages accumulate and preserve specimens over several seasons and years, thus lengthening the window of observation on local composition (Fürsich & Aberhan 1990; Albano & Sabelli 2011). In this case, the presence of larger individuals in the sediment than in the living population indicates that the maximum size attained by this species at a given site may exhibit considerable variation over relatively short temporal scales.

The negative correlation between clam size and population density found in our study may be brought about by different processes. A density-dependent control of growth due to intraspecific competition for food, as observed in other bivalves (Peterson & Andre 1980; Peterson 1982; Peterson & Black 1987; Vincent

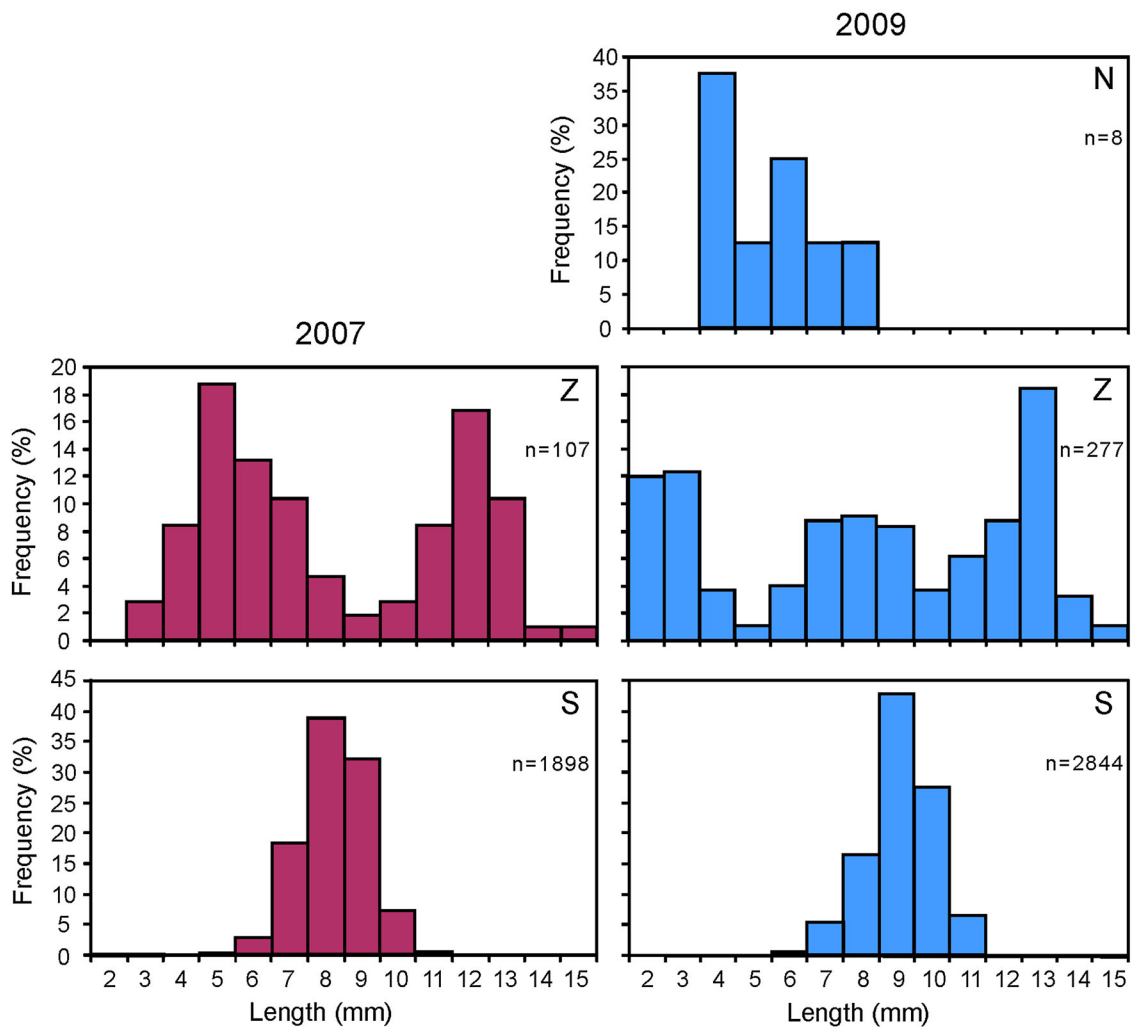


Figure 4. Size–frequency distributions of living *Neilonella sulculata* in areas N, Z and S in 2007 and 2009. Each graph was constructed by pooling data from the 16 samples collected in the same area and survey. No living clams were found in area N during the 2007 survey. It should be noted that due to the fast growth rate of this species (Leonardi et al. 1996), clams found in 2009 almost certainly belong to a cohort that had not yet recruited in 2007.

et al. 1989, 1994; Jensen 1993; Craig 1994; Weinberg 1998; Morsan et al. 2011), appears as the most likely explanation for this pattern. Passive movement of juveniles due to hydrodynamic resuspension into the water column or to bedload transport causing local increases in clam density has been documented in small infaunal bivalves (Emerson & Grant 1991; Commito et al. 1995). Selective loss of smaller (Andresen et al. 2013) or larger (Boldina & Beninger 2013) individuals by predation pressure, patchy recruitment patterns due to density-independent effects (David et al. 1997), and feeding on settling larvae by conspecific adults (André & Rosenberg 1991) might also conceivably produce spatial heterogeneity in clam size. On the other hand, variation in larval supply (i.e. recruitment limitation) has not been regarded as a determinant

process in the generation of spatial pattern in marine soft sediments (Ólafsson et al. 1994).

Conclusions

Neilonella sulculata was the dominant bivalve on muddy bottoms of San Jorge Gulf. Its density, biomass and size-frequency distribution displayed significant spatial structure, being positively autocorrelated at the two smallest distance classes analysed in this study (1.7–14/17 km). Biomass also showed spatial contagion at scales of 25–33 km. The population of this clam experienced a substantial increase in density and biomass between 2007 and 2009. Empty valves in the sediment showed that the maximum size attained by the species may exhibit considerable

variation over relatively short temporal scales. Regardless of temporal changes in density and biomass, the spatial structure of these variables remained stable. At densely populated areas, shell size decreased with increasing density, suggesting a density-dependent control of growth. A clear north–south increase in density and biomass was detected, which might be related to a gradient in food availability caused by a thermohaline frontal system associated with wind-related upwelling.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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