

Growth compensation as a regulatory mechanism of purple clam *Amiantis purpurata* population dynamics in Patagonia

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ABSTRACT: Density-dependent processes may drive the population dynamics in marine species through intraspecific competition for food or space. We examined processes controlling population dynamics in the purple clam *Amiantis purpurata* population of Playa Villarino (north of San Matias Gulf, Argentina) at the southernmost limits of its distribution. Population structure at this location has been dominated for more than 2 decades by 3 consecutive cohorts settled in 1978–1980. We used data on mean size and mass, growth rate, area covered by residents, density and biomass collected at 2 sites between 1982 and 2003, and a survey performed in 1995 over the whole population, to explore density dependence. The spatial pattern showed that: (1) whereas density was heterogeneous with highest values at the western side of the ground, biomass was more uniform, and the relationship between biomass and density was non-linear, becoming asymptotic at a density of 200 clams m⁻²; (2) body size and density decreased over time; and (3) the substrate area used by clams was less than 35% of the available substrate. Temporal patterns showed that (1) density decreased with time but biomass was almost constant, and (2) growth curves were indicative of a density-dependent effect: individuals at low-density sites grew faster than individuals at high-density sites. Differences were strong between sites and slight (or absent) between cohorts. Natural mortality, which did not differ between cohorts, was estimated by the decrease in density over time as $M = 0.126$. We propose that the purple clam population is regulated by a compensatory effect whereby losses due to mortality are compensated by increased growth rate, and therefore enhancement of local biomass.

KEY WORDS: Compensatory growth · Survivorship · Growth rate · Biomass trend · *Amiantis purpurata*

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INTRODUCTION

The fate of natural populations is controlled by the 3 processes of individual growth, mortality and recruitment, and the variability of these in time and space (Brey & Gage 1997). In the case of marine bivalves, which have a complex life cycle that involves an early planktonic phase strongly exposed

to environmental stochasticity and an adult sedentary phase, these processes have additional sources of variability derived from the nature of 'space-related' species (sensu Hall 1983). Local density, population structure and spatial distribution of adults are relevant to settlement processes (Roegner 1991, Defeo 1996), reproductive output (Levitan 1991) and individual growth patterns (Orensanz et al. 2006).

Thus, the population of adult residents has a dual role in the interaction with settlers: (1) supplying larvae by reproduction (pre-dispersal effect) and (2) limiting the available space (post-dispersal effect). At the local scale, residents interact with neighboring individuals, essentially by competing for resources such as food or space (Fréchette et al. 1992). At high density, these pre-dispersal density-dependent processes could affect either fertilization success or growth rate. Post-dispersal processes could operate as inhibition of larval settlement by resident adults (compensation effect) (Orensanz et al. 2004). Evidence of density-dependent regulation of growth rate due to space or food has mainly been obtained from experiments (Peterson & Andre 1980, Fréchette & Lefaiivre 1990). Evidence from the field is difficult to obtain due to the superposition of several year classes and temporal modifications of density due to recruitment, and several years of observations are also required (Weinberg 1998). Some field studies have explored the relationships between body size or individual mass (m_i) with density (N) in mussels (Guiñez & Castilla 1999, Guiñez et al. 2005), which are usually modeled as $m_i = \alpha N^\beta$, to describe self-thinning processes in crowded animals. The parameter β is the exponent of the power function and can be interpreted as the result of metabolic or spatial constraints acting on size, and the parameter α is expected to vary according to the metabolic efficiency of the animals and to site quality (Fréchette & Lefaiivre 1990). Whereas at low density, when competition is unlikely to be important, values of β are approximately 0, at high population density negative values of β are expected (Guiñez et al. 2005). Theory suggests that the degree of self-thinning should vary if competition is driven by food or space (Fréchette & Lefaiivre 1990). Usual assumptions in space-driven self-thinning are that individuals have isometric growth, and that they are arranged as a monolayer covering 100% of the available space. The value of β can be altered by departures from this assumption (Guiñez et al. 2005). Layering implies 3-dimensional use of the habitat, as described in mussels (Guiñez & Castilla 1999), but it could be valid for other benthic organisms such as clams.

The present study focused on the southernmost population of the purple clam *Amiantis purpurata* (Lamarck, 1856) (Bivalvia: Veneridae) because 20 yr of information on this population allowed us to explore density-dependent process at different spatial scales. This population is located at Playa Villarino (San Matías Gulf, Argentina); it is relatively isolated from populations located outside the gulf, and

it is an uncommon case of a population dominated by 2 year classes for more than 15 yr. *A. purpurata* is a warm-temperate water species, distributed from Espirito Santo, Brazil (26° S), to San Matías Gulf, Argentina (41° S) (Scarabino 1977). The purple clam is a gonochoric species that spawns during the summer (Morsan & Kroeck 2005). Growth rings are evident on the valve surface, and its periodicity is annual (Morsan & Orensanz 2004). A survey conducted in 1995 revealed that (1) there was a conspicuous absence of juveniles, (2) demographic composition was restricted to 2 annual classes recruited between 1979 and 1980 (Morsan & Orensanz 2004), (3) spatial distribution was highly contagious—half of the population lives at densities up to 240 clams m^{-2} (Morsan 2003), and (4) maximum density reached unusually high levels for populations without juveniles, 632 clams m^{-2} (10 270 g m^{-2}) (Morsan 2007).

In this paper we analyze spatial patterns of individual size, mass and density from survey data collected in 1994–1995. Also, we analyze data of the purple clam population at Playa Villarino collected between 1982 and 2003. To describe density-dependent processes affecting population dynamics, we explore the temporal patterns of size, cover, growth rate, survivorship and biomass. These processes are proposed to explain the comparatively slow growth of the 1979–1980 year classes. The hypothesis we test in this study is that growth rate is regulated by local biomass.

MATERIALS AND METHODS

Study area

Playa Villarino (Fig. 1) is a 9 km long dissipative sandy beach located in the proximity of San Antonio Bay (NW of San Matías Gulf). Average tidal amplitude is 7.6 m (maximum 9.2 m); at low tide the beach is 450 m wide. Sediment is predominantly fine sand, with patches of shell hash. Water temperature ranges, on average, from 6°C in August (winter) to 22.5°C in January (summer) (Morsan & Kroeck 2005). Water circulation in the NW of San Matías Gulf was described by N. W. Lanfredi & J. L. Pousa (unpubl. data) as a clockwise coastal eddy predominantly influenced by tidal currents, with limited interaction with the general circulation in the gulf. The population under study is distributed in the intertidal and subtidal zones, down to 10 m depth at low tide.

Data set for assessment of spatial pattern

Between March 1994 and February 1995, a survey was conducted over the whole purple clam ground of Villarino using a geostatistical approach (detailed in Morsan 2003). The sampling design was systematic with 15 transects perpendicular to the coast line and separated by 500 m, and 10 sampling stations per transect separated by 250 m, for a total of 150 samples (Fig. 1). The samples were obtained using a metal frame of 0.25 m²; all clams within that area and to a depth of 20 cm inside the sediment were collected using an air-lift. In the laboratory, clams were counted, measured (shell height, length and width) and weighed to calculate density and biomass (clams m⁻² and g m⁻², respectively).

Data set for assessment of temporal pattern

Studies over time (individual size–mass variation, growth rate, survivorship and local biomass) were conducted at a small scale at 2 different sites: (1) El Molino (EM), located near the eastern end of the beach, and (2) La Conchilla (LC), located at the opposite end of the bed (Fig. 1). The distance between the 2 sites is 7 km. We defined a rectangular plot (500 × 1000 m) at each site, where periodic samples were randomly obtained by divers between 1980 and 2003 (Table 1):

(1) Recovered samples (1980–1983): these samples were obtained at EM before this study, recovered in 1994, and used in an ageing study (Morsan & Orensanz 2004). The data include date, position, number of individuals per area and individual sizes.

(2) Periodic samples (1987–1990): random samples obtained inside EM and LC.

(3) Survey (1994–1995): comprehensive survey over the whole ground (EM and LC), as detailed above.

(4) Periodic samples (2003): random samples obtained inside EM and LC.

Between 1980 and 1983, clams were dug manually; an air-lift was used starting in 1987. Samples were obtained by divers and processed in the same way as described above to estimate density and biomass.

Response variables

Spatial variation in individual mass and size

The first analysis was of the relationship between size, mass, local biomass and density over the whole population in 1995. Given that the age structure was dominated by 2 consecutive year classes (Morsan & Orensanz 2004), we analyzed these variables using bidimensional self-thinning relationships between size and density (Weller 1987, Fréchet et al. 1995). We analyzed 2 different self-thinning relationships:

(1) $B = kN^\beta$, which is termed a B – N diagram (Westoby 1984, Fréchet et al. 2005), where B is biomass per area and N is density. Usually this relationship is represented using logarithmically transformed data: $\log B = \log k + \beta \log N$, where β is the slope (which in this snapshot case, and with the population structure simplified to 2 year classes, is expected to equal 1 in the absence of competition) and $\log k$ is the intercept (Fréchet et al. 1992);

(2) Individual mass (whole body mass, m_i) and size (shell height, H_i) as a function of density. Given that age structure could be assumed to be composed of a unique cohort, it is expected that both variables vary with density if food or space is limiting. Conversely, mass and size could also be limited by factors other than density, such as sediment, depth or currents. In this case, some data points would fall below an upper limit and, in

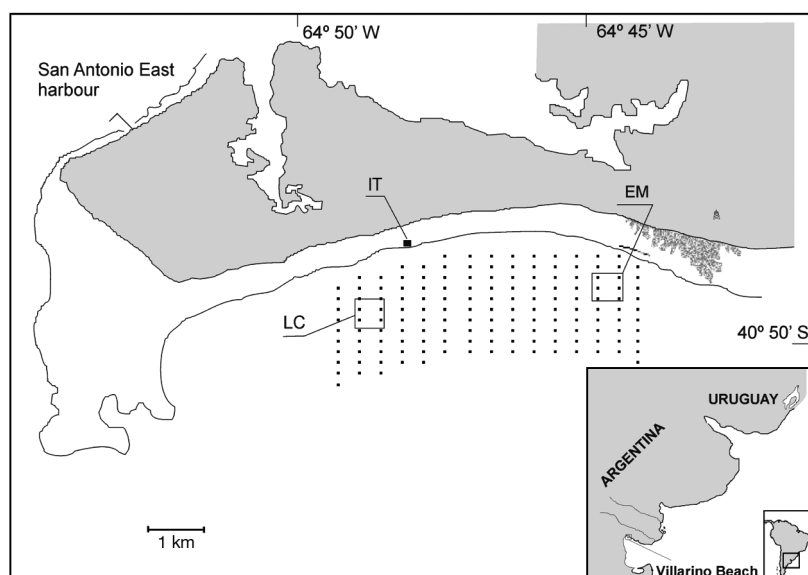


Fig. 1. *Amiantis purpurata*. Position of the El Molino (EM) and La Conchilla (LC) sites inside the Villarino purple clam bed. IT: position of the intertidal sampling site. Sampling sites of the survey carried out in 1994 are represented by black dots

Table 1. *Amiantis purpurata*. Purple clam samples collected between 1982 and 2003. EM: El Molino; LC: La Conchilla

Date (dd/mm/yyyy)	Site	No. quadrats	No. of ind. collected
Recovered samples			
19/01/1982	EM	2	298
01/02/1982	EM	2	386
19/03/1982	EM	2	831
27/08/1982	EM	3	609
08/10/1982	EM	2	661
22/02/1983	EM	2	202
22/02/1983	EM	1	202
19/03/1983	EM	1	547
21/03/1983	EM	1	223
22/04/1983	EM	1	200
08/07/1983	EM	2	593
15/09/1983	EM	1	382
26/10/1983	EM	2	728
11/11/1983	EM	2	245
02/12/1983	EM	2	891
22/12/1983	EM	3	683
Periodic samples			
05/10/1987	EM	5	137
09/01/1988	EM	2	167
23/03/1988	LC	2	396
08/09/1988	EM	4	352
16/02/1989	EM	1	261
09/01/1990	EM	3	260
23/03/1990	EM	8	1400
09/08/1990	LC	1	168
Survey			
21/02/1994	LC	4	304
02/03/1994	LC	4	393
01/11/1994	EM	2	37
10/03/1995	EM	8	211
15/03/1995	EM	4	151
27/05/1995	EM	8	257
1994	Rest of sites	120	1746
Periodic samples			
29/01/2003	LC	17	399
26/02/2003	EM	19	386

some cases, the correlations between individual mass or size and density would be variable. To locate the upper limit we adopted the following procedure. First, mass data were grouped into regular classes of density. Second, maximum values within each class were chosen to fit the model $m_i = \alpha_m N^{\beta_m}$. The parameters were estimated by linear regression after log-transformation ($\log m_i = \log \alpha_m + \beta_m \log N$). The procedure was repeated for size data, replacing the sub-index by 's' ($\log H_i = \log \alpha_s + \beta_s \log N$).

Temporal variation in individual size at small scale

To examine the hypothesis of space limitation, we estimated the average area projected by the

clams onto the substrate (S) using size data (shell height, length and width). We assumed that clams are buried with the anterior–posterior axis perpendicular to the seafloor, and the shape of projected area is an ellipse whose surface can be estimated as $S_i = \pi(H_i/2)(A_i/2)$, where A_i is shell width. The degree of clam crowding in each sample was inferred from the number of layers (L), which is equivalent to percentage of the sampling area covered by clams ($L = NS/a$), where \bar{S} is the average of individual projected area and a is sampled area. We reduced the spatial scale of observations to 2 sites (LC and EM) and extended the temporal series to include 3 periods: 1982–1983 (recovered samples), 1994–1995 (survey) and 2003 (periodic samples).

Growth rate over time

We compared growth rates of clams between EM, LC and a fixed location in the intertidal (IT) using growth increments from external bands on the shell; 100 clams were collected at each site. The external banding pattern of purple clam shells is conspicuous, with an annual alternation of thick dark-purple and thin pink bands (Morsan & Orensanz 2004). Bands were measured (distance from the umbo to the distal border of the band) along the same axis used to measure total height. The beginning of the well-defined pink band was defined as the boundary between 2 consecutive bands. Purple clams spawn during early summer. Recruitment occurs during this season and the narrow pink band is deposited during the winter. Thus, the first band marks approximately a half year and was not included in the previous analysis of growth rate.

Growth of clams at EM was modeled with the von Bertalanffy function by Morsan & Orensanz (2004), who compared parameters discriminating between sites and cohorts: 1979, 1980 and old clams collected in 1982 whose ages varied from 9 to 18, indicating that they settled during the period 1965–1974 and vanished in 1994. Growth parameters estimated on the basis of size-at-age for the multi-cohort group ($L_\infty = 57.23$ mm; $k = 0.154$ yr⁻¹; $t_0 = -0.246$ yr; Morsan & Orensanz 2004) were higher than those of the 1979–1980 cohorts.

Growth increment trends from EM, LC and IT sites were used to reconstruct growth rate by back-calculation and were contrasted with those predicted by a von Bertalanffy growth model estimated for the multi-cohort group.

Survivorship

Survivorship was inferred from direct observation of density (N_t) changes in periodic samplings at EM and LC (Table 1) between 1981 and 2003. In both cases, survivorship was modelled by a negative exponential function:

$$N_t = N_0 e^{(-Mt)} \quad (1)$$

where t is time, and density at recruitment time (N_0) and instantaneous natural mortality rate (M) were estimated by a linear regression of the logarithmic form:

$$\ln(N_t) = \ln(N_0) - Mt \quad (2)$$

The hypothesis of equal M between sites was tested by slope comparison of the 2 regressions (Kleinbaum & Kupper 1978).

Temporal changes in biomass

Temporal changes in local biomass were evaluated in 2 ways. First, the temporal trend of theoretical local biomass was back-calculated using growth parameters from the von Bertalanffy model (cohort 1979: $H_\infty = 43.545$ mm, $k = 0.1329$ yr⁻¹, $t_0 = -1.412$ yr; cohort 1980: $H_\infty = 42.025$ mm, $k = 0.1333$ yr⁻¹, $t_0 = -1.199$) (Morsan & Orensanz 2004), natural mortality estimation and allometry coefficients ($\hat{a} = 7.06$ g mm⁻¹, $\hat{b} = 2.944$; Morsan 2000):

$$B_t = N_t m_t = N_t a(H_t)^b \quad (3)$$

where B_t is local biomass (g m⁻²) at time t , N_t is density at time t and m_t is individual mass (g) at time t .

Second, we used direct observation of local biomass changes from samples at EM and LC.

RESULTS

Spatial variation in individual mass and size

During the extended period analyzed, the density range decreased through time because of the absence of recruitment and mortality of clams that settled in 1979 and 1980. In 1995, maximum density reached unusually

high levels for populations without juveniles: 632 clams m⁻² and 10270 g m⁻². There were some discrepancies between local biomass and density patterns. Whereas density was heterogeneous with the highest values at the western side of the ground, biomass was more uniform (Fig. 2a,b). The relationship between these variables was non-linear, reaching an asymptote at 200 clams m⁻² and an estimated slope ($\beta = 0.82$, 95% CI = 0.75, 0.89) that differed significantly from 1.

Mean size and mass were lowest, coincident with high density and biomass, suggesting an inverse correlation (Fig. 2c,d). For log-transformed data ($N = 2676$), the estimated slopes were $\beta_m = -0.312$ (mass–density relationship, $R^2 = 0.35$; 95% CI = -0.328, -0.296) and $\beta_s = -0.107$ (height–density relationship, $R^2 = 0.37$; 95% CI = -0.112, -0.102). However, the bivariate scatterplots of mass and size–density seem to be clouds of points placed in a region of the graph, suggesting an upper limit rather than a simple correlation (Fig. 3a,b). Size and mass were lower with low variation at high densities, whereas at low densities they were higher and more variable.

Density range was divided into 22 classes of 20 clams m⁻² and only the maximum values of individual size and mass within each density class were log-transformed. Estimated slopes of the regression equation were $\beta_m = -0.40$ (maximum mass–density

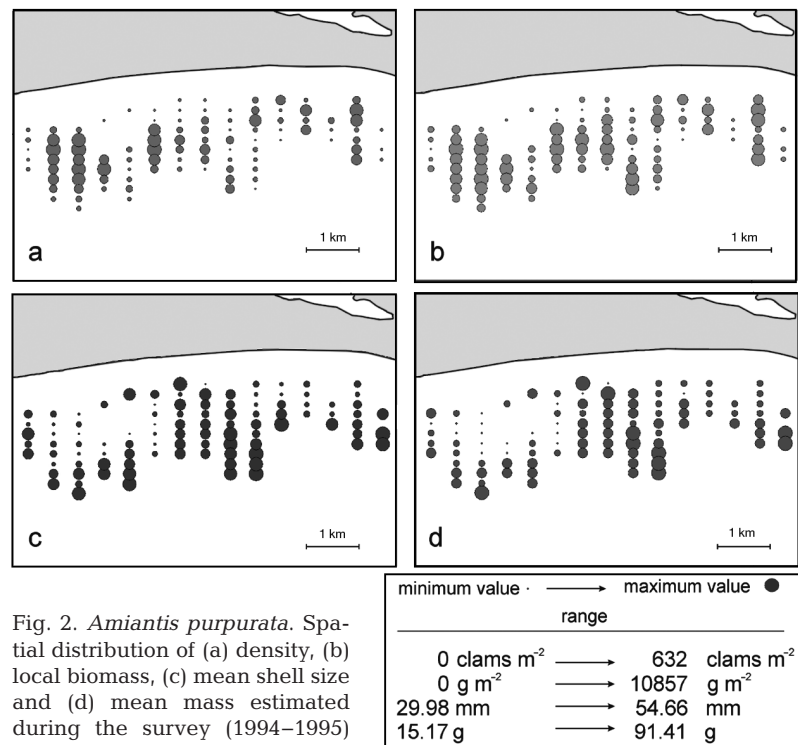


Fig. 2. *Amiantis purpurata*. Spatial distribution of (a) density, (b) local biomass, (c) mean shell size and (d) mean mass estimated during the survey (1994–1995)

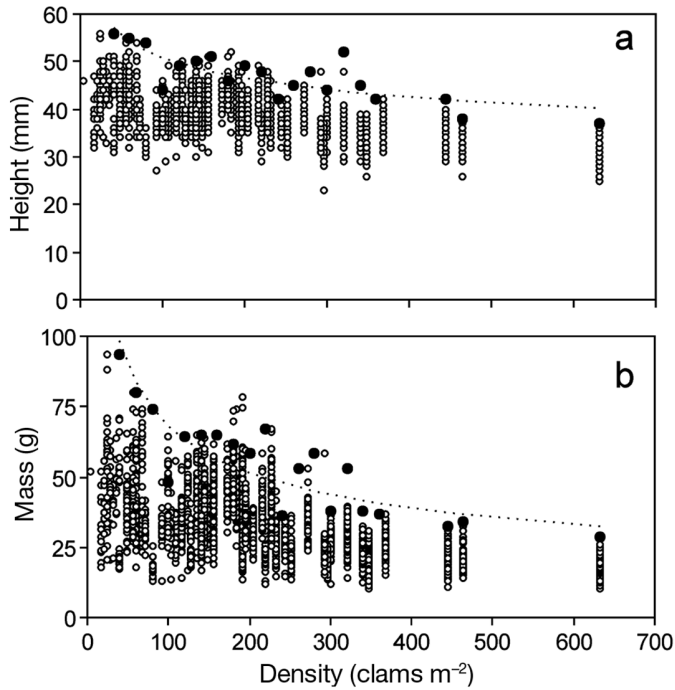


Fig. 3. *Amiantis purpurata*. Relationship between surrounding density and (a) shell size (height) and (b) dry mass of *A. purpurata* individuals. Density range was discretized into 22 classes. ○: individual records ($N = 2676$); ●: maximum records inside each class. Dotted line is the model H_t (or m_t) = αN^β fitted to maximum values, where H_t is shell height at time t , m_t is body mass at time t , N is density, and α and β are the parameters of the model. The model is interpreted as a boundary for size or mass at any given density

relationship, $R^2 = 0.72$; 95 % CI = $-0.52, -0.28$) and $\beta_s = -0.13$ (maximum height–density relationship, $R^2 = 0.62$; 95 % CI = $-0.18, -0.08$).

Beyond 200 clams m^{-2} the upper limit for size and mass became evident, showing a downward trend, and local biomass became asymptotic.

Temporal variation in individual size at a small scale

During 1982–1983, 1994 and 2003, density and clam size varied over time. Density was reduced by natural mortality, and clam size was increasing as a consequence of growth of the 1979 and 1980 cohorts and an absence of recruitment (Fig. 4a).

The area of substrate covered by clams was less than 35 % during the 3 time periods (Fig. 4b,c), even though clams can dig to different depths and use the substrate in 3 dimensions. Therefore, $L < 1$.

Cover as a function of density had a constant maximum but the 3 periods differed in the range of density. In contrast, cover as a function of biomass was similar across the time periods.

Growth rate over time

Back-calculated temporal trends of growth rate of clams at EM and LC in 1994 did not decrease monotonically as predicted by the growth model (Fig. 5). A cycle of contraction–expansion of the rings was temporally coincident between cohorts and sites. The narrowest rings corresponded to an age of 6 yr for the 1979 cohort, and an age of 5 yr for the 1980

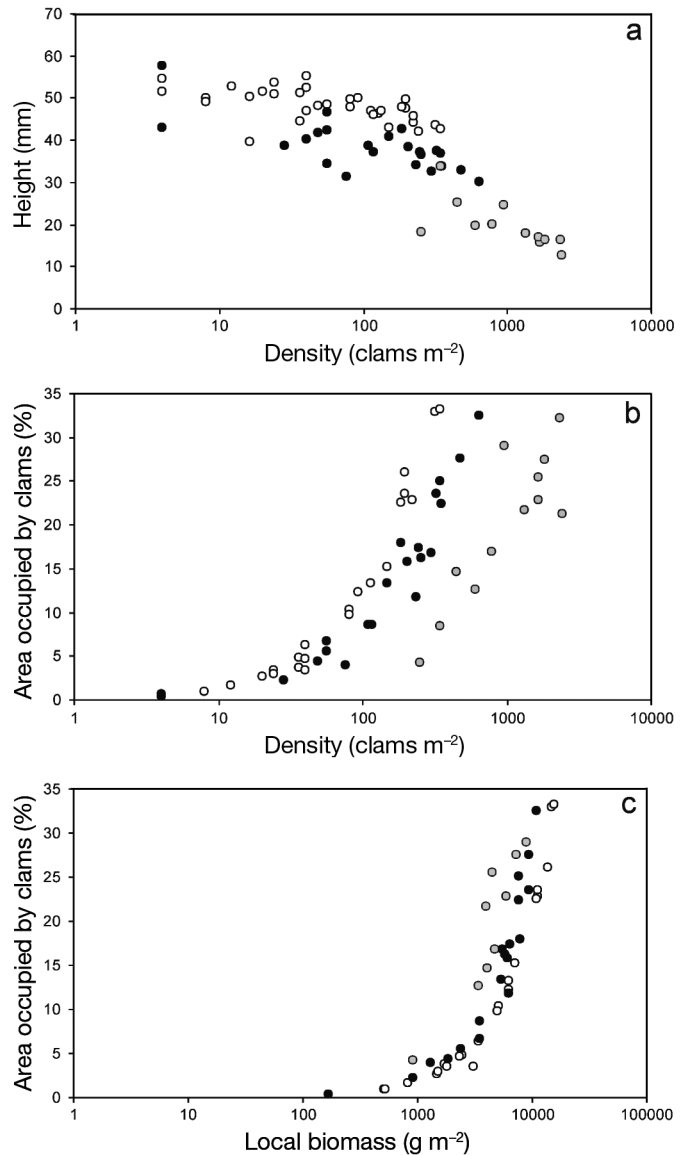


Fig. 4. *Amiantis purpurata*. (a) Variation of mean size at each sampling station of the La Conchilla (LC) and El Molino (EM) sites during 3 periods: 1982–1983 (○), 1994–1995 (●) and 2003 (○). (b,c) Area projection of clams per m^2 expressed in percentage in relation to density (b) and local biomass (c). Note that even when density is being reduced throughout the life history, both local biomass and maximum area occupied by clams remain stable for decades

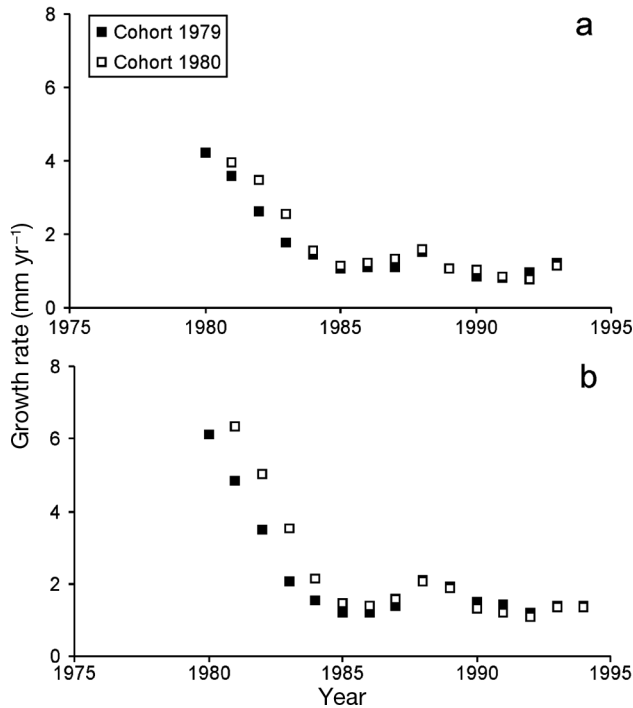


Fig. 5. *Amiantis purpurata*. Growth rate variation throughout the 1980–1995 period analyzed from growth ring width of the 1979 (■) and 1980 (□) cohorts, evidencing the contraction–expansion of growth rate. Data from (a) La Conchilla (LC), and (b) El Molino

cohort. Growth rate at EM was faster than at LC, but both patterns differed from the model estimates for a multi-cohort group (assumed as a density-independent condition) (Fig. 6). Growth rate was highest at IT, where mean density in 1995 was 4.9 clams m^{-2} .

Survivorship

Population density at EM and LC decreased over the 22 years (Fig. 7). Estimates of natural mortality were $M = 0.129 \text{ yr}^{-1}$ (95% CI = 0.102, 0.163) at EM and $M = 0.101 \text{ yr}^{-1}$ (95% CI = 0.061, 0.142) at LC; the estimates did not differ significantly between sites.

Temporal changes in biomass

In contrast to the declining trend of density, biomass was expected to increase until reaching a critical age at 8–10 yr, and decrease thereafter, forming a dome-shaped curve (Fig. 8). However, biomass remained high throughout time, even though it varied between quadrats at each site.

DISCUSSION

The purple clam population at the southern boundary of its geographic distribution was unusual because of its spatiotemporal mosaic of density and size (Morsan 2003) and its domination by just 2 year classes that settled in 1979 and 1980 (Morsan & Orensanz 2004). Growth differed more between sites than between cohorts, with a comparatively lower growth rate than other populations, suggesting compensatory density-dependent processes (e.g. competition for food and inhibition of larval settlement by resident adults).

Spatial pattern of size and mass

Once ages were determined, the most intuitive interpretation of the mosaic of density and sizes

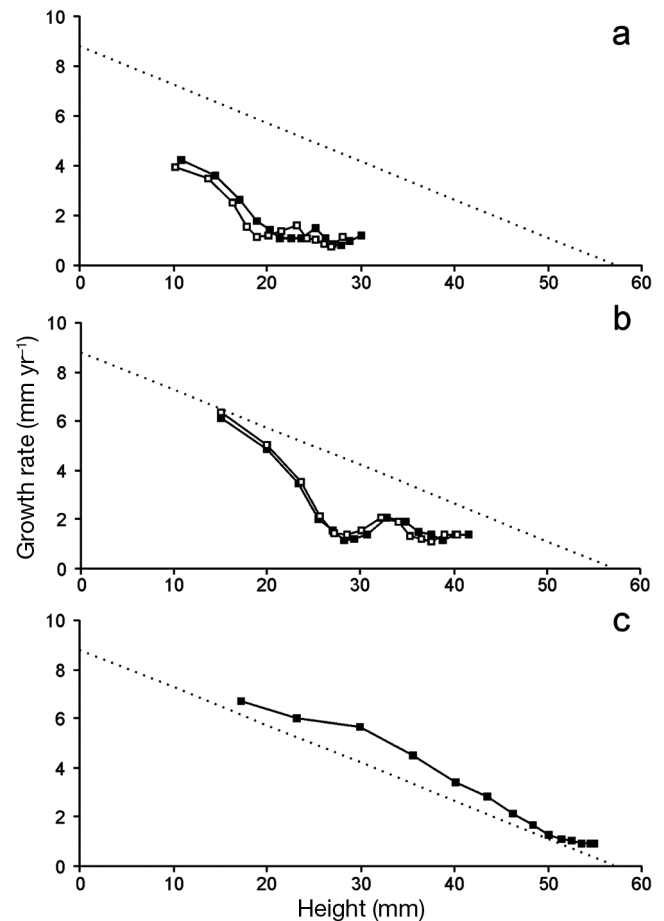


Fig. 6. *Amiantis purpurata*. Growth rate versus size of the 1979 (■) and 1980 (□) cohorts at (a) La Conchilla, (b) El Molino and (c) the intertidal zone (only 1979 cohort). Dotted lines represent the von Bertalanffy growth model estimated for a multicohort group settled in the 1965–1974 period (Morsan & Orensanz 2004)

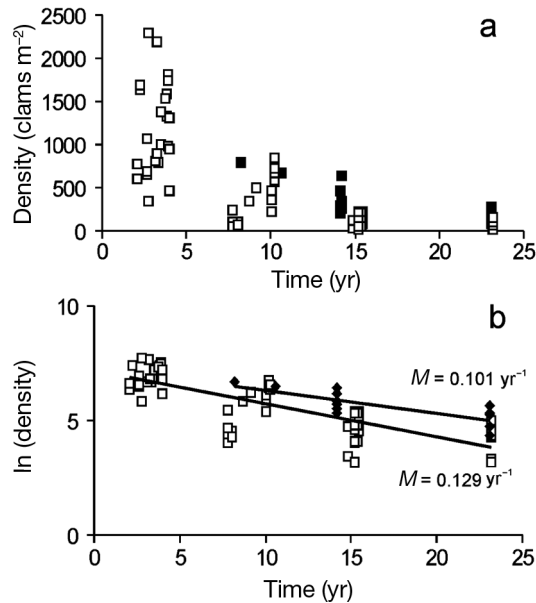


Fig. 7. *Amiantis purpurata*. (a) Density trend along the years elapsed since the last recruitment (1980). Each record represents a sample, at sites El Molino (EM, \square) and La Conchilla (LC, \blacksquare). (b) Log-transformation of density data and the estimation of natural mortality (M) by linear regression. EM (\square), LC (\blacksquare)

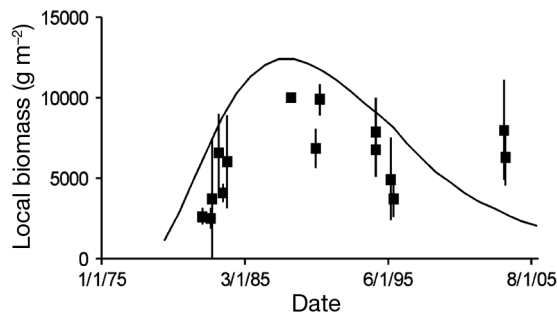


Fig. 8. *Amiantis purpurata*. Theoretical biomass trend (curve), estimated as a result of growth model, total mass–size relationship and survivorship, plotted against the average local biomass recorded within the sites. Dates are d/mo/yr. Vertical bars represent \pm SD

(and masses) observed in 1995 was a direct relationship between them. But individual size is a consequence of several factors, such as habitat conditions, and contingencies occurring during life history. Besides density, factors such as grain size, depth and water flow are sometimes interconnected. Morsan (2003) showed that there are complex interrelationships between several environmental parameters, which prevent determination of the influence of any single factor: the highest density occurred only at sites where the sediment

was dominated by fine sand, whereas sites with some percentage of gravel only had isolated clams. As a consequence, when individual size (or mass)–density relationships are represented as scattergrams, the distribution of data points fall into diffuse clouds beneath an upper limit. This limit is more evident when density increases, as there are no extreme sizes or masses at high density.

The discrepancy from linearity in the biomass–density relationship was in concordance with the maps of spatial distribution of both variables. Whereas density varied widely, maximum values of biomass were similar at several sites. These patterns were discordant with the spatial distribution of mean size and mass. Therefore, 2 sites with different densities could have the same biomass as a result of different average individual masses at age. Such a scenario could result from compensatory processes involving growth and mortality, occurring at the scale of individuals. As an individual grows in size and mass, the diameter of its siphons, the area of influence around it, and its food requirements all increase. For a given size of influence area, overlap occurs and the filtering activity of each individual will be affected by clams in its ‘neighborhood’ (Addicott et al. 1987, Orensanz et al. 1998).

Compensatory growth has been linked to food depletion as well as space limitation (Fréchette & Lefaiivre 1990). Fréchette et al. (1992) explored the hypothesis of interdependence of food and space limitation in mussels and concluded that they are not independent. Rather, they interacted to produce a response that is asymmetric with respect to size, as only small mussels were affected by crowding. We theorized an equivalent scenario in the purple clam population. However, when we analyzed size variation and densities at a small scale (i.e. within the EM and LC sites) across 20 yr, the negative size–density relationship became clearer for larger and older clams, and space was only partially occupied at less than 35% of the total area. In an experimental manipulation of 2 infaunal suspension feeders, Peterson (1982) observed reductions in growth rate and reproductive effort, even when the highest densities covered only 10% of the available space. In contrast to epifaunal species, which have the potential for strong density-dependent effects due to space limitation (Fréchette & Lefaiivre 1990, Guíñez & Castilla 1999), infaunal species can avoid space limitation because of 3-dimensional use of the habitat through burrowing (Wilson 1990).

Density-dependence of growth rate

Our results suggest that density dependence of growth rate could be linked to intraspecific competition for food resources, and its effects on size could be controlled by biomass rather than density; whereas density changed over time due to mortality, both percentage cover and biomass remained stable. This population has likely remained near its carrying capacity, compensating losses from natural mortality with an increased growth rate, thereby maintaining the local biomass. Growth rate decreased between 6 to 10 yr of age, as evidenced by the width contraction of external growth rings. This could be explained by 2 hypotheses. The first is dependence of growth rate on the biomass of the 2 consecutive cohorts. At a temporal scale, the life history of a cohort involves changes in the number of survivors, size and mass with a maximum biomass at a given time as a consequence. If there is no recruitment, both trophic and space requirements will follow the same pattern. The theoretical maximum biomass of 2 cohorts is expected to be almost coincident with the lowest growth-rate period. However, this hypothesis is not supported by the observation of stable biomass. The second hypothesis is related to environmental conditions. The synchrony of the growth-rate phase at all sites could be interpreted as a signature of climatic forcing, during which biological processes would be synchronized across sites. In the presence of adverse environmental conditions, the individual growth rate could decrease in all beds, and natural mortality rate could increase, relaxing the density dependence. For the clams at EM and LC, growth rate trajectories departed from model estimates by Morsan & Orensanz (2004) for a multicohort group settled during the 1965–1974 period (Fig. 6) and from the intertidal site.

The population of purple clams was opened to fishery exploitation in 1995, and after 2002 exploitation rates gradually increased until it became the main shellfish resource in terms of annual landings. But if fishing effort continues to increase (driven by favourable market conditions and low biomass of other resources) and recruitment continues to fail, the compensatory effect of growth rate for harvesting intensity will become ineffective and the persistence of the population could be jeopardized.

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Editorial responsibility: Romuald Lipcius,
Gloucester Point, Virginia, USA

Submitted: August 2, 2010; Accepted: September 29, 2011
Proofs received from author(s): December 6, 2011